

12

Predator–Prey Systems: Predator Dynamics and Effects on Prey

Are natural consumers able to regulate the populations of their prey? In Chapter 10, the consumer numbers (e.g., sheep or fishing boats) were regulated externally by us or by the government. Prey numbers were decreased by predator consumption, but predator numbers did not necessarily reciprocate. We have shown that a predator's prey consumption rate (its functional response) often increases with prey abundance. This alone provides some measure of regulation of prey, but realistic functional responses ultimately become asymptotic at high prey densities. Thus prey populations, if they are large enough, are able to escape numerically from the controls of predators, based simply on the predators' functional responses. However, the functional response of an individual predator is only part of predator dynamics; the other part is the **numerical** response of the predator population to changes in prey abundance (Solomon 1949). That is, the predator's birth rate may increase as it captures more prey and its death rate may decrease with more food to eat. In open populations (i.e., with immigration and emigration of prey and predator), consumers may move into areas rich in resources and leave areas when resources are depleted. Consequently, the numerical response of the predator population will complement the predators' functional response but may be temporally delayed. In this chapter we explore the dynamics of coupled predator–prey systems and the implications for the stability and regulation of predator and prey numbers.

An example of a numerical response is shown for a species of jaeger in Figure 12.1. Jaegers are related to seagulls but primarily feed on land. Here the number of breeding pairs increases as the density of their prey, lemmings, increases.

COUPLED GROWTH EQUATIONS FOR PREDATOR AND PREY

The general form for the interaction between a predator (or consumer, C , to be more general) and its prey (or resource, R) may be written as

$$\frac{dR}{dt} = f_1(R, C) \quad \text{and} \quad \frac{dC}{dt} = f_2(R, C). \quad (12.1)$$

In Chapters 10 and 11 we explored the prey, or resource, growth, f_1 , as it was affected by predator consumption. In this chapter we merge these considerations with those of the f_2 function. As predators consume prey, they give birth to new predators through the f_2 function, and these offspring, in turn, can consume more prey.

As usual we begin with a simple model. Imagine that the predators' numbers grow according to the following assumptions. Predator per capita birth and survival rates are functions only of resource abundance, not predator abundance. The more an individual consumer eats, the more offspring it can produce and the better its own chances of survival. You might think by this assumption that we are excluding predator–predator competition—yes and no. Predator exploitative competition for food is not excluded:

Figure 12.1
Numerical response of pomerine jaegers to lemming density. After Maher (1970).

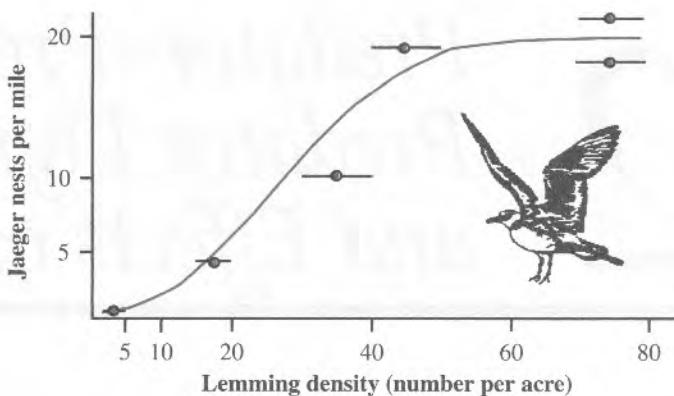
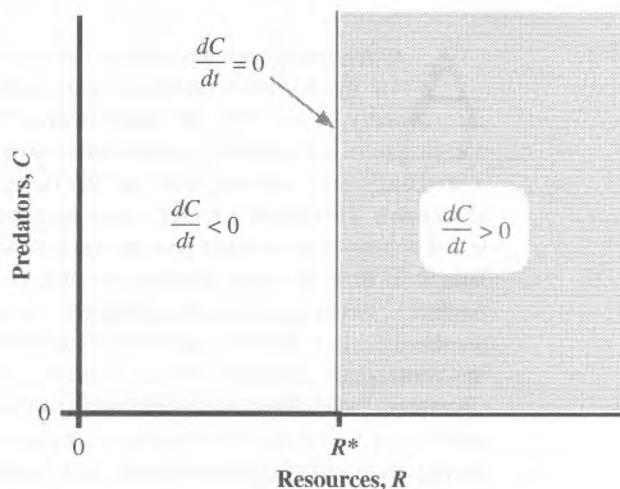


Figure 12.2
Regions of positive and negative growth for the predator population plotted in the phase space of predator and resource densities. The vertical line at $R = R^*$ shows all those values of C and R for which consumer population growth is exactly zero. At resource levels above R^* (the shaded region) the predator population increases in size. At resource levels below R^* , the predator population decreases.



The more predators that are consuming resources, the lower the resource growth rate is and the fewer resources are available for consumers. Thus the predator–predator competition is an indirect one, mediated through the depletion of the shared resources, R . The only type of competition excluded by this assumption is direct interactions among predators, over and above those having an impact on resources. Predator fighting and other forms of within-species interference are excluded.

With this one assumption, we can now write the predator growth equation, Eq. (12.1), as

$$\frac{dC}{dt} = f_2(R, C) = C[b(R) - d(R)]. \quad (12.2)$$

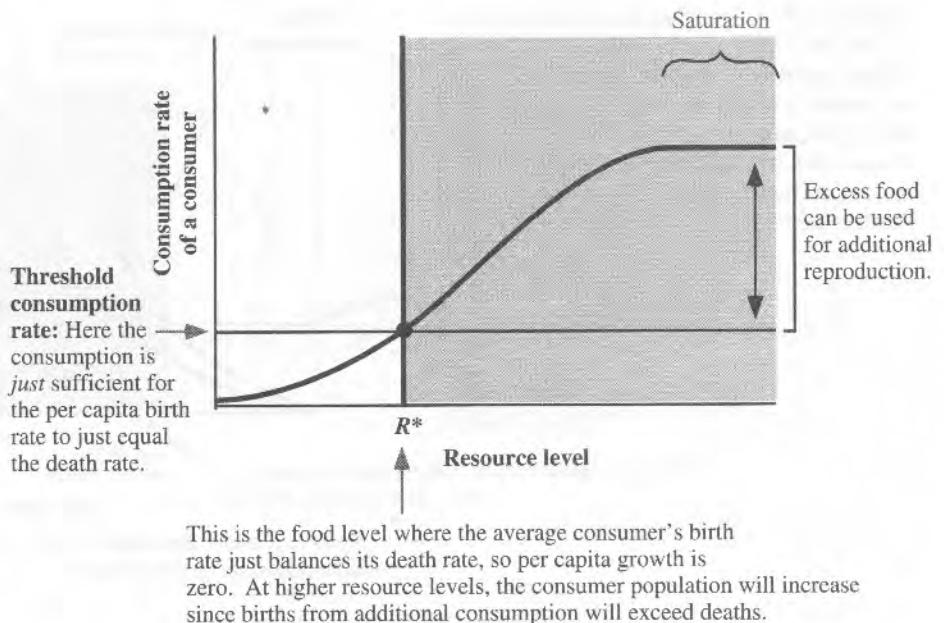
The instantaneous per capita birth function, $b(R)$, and the instantaneous per capita death function, $d(R)$, depend only on R , not on C . The $b(R)$ function is positive and increases with R , since we expect predator birth rates to increase with more resources available. As food levels R increase, the predator death rate $d(R)$ is expected to decrease, and thus dC/dt will increase. The total predator population, C , multiplies the per capita terms within the brackets to give the total populational change of numbers of predators in continuous time as dC/dt .

At equilibrium, $dC/dt = 0$. Consequently, Eq. (12.2) implies that at equilibrium either $C = 0$ or $b(R) = d(R)$. Regardless of the functional form of $b(R)$ and $d(R)$, both the birth and death terms involve only resource numbers, R , and not predator numbers. Thus, given the assumptions of the model, the equilibrium level of C is determined only by R . This set of circumstances is depicted graphically in Figure 12.2.

In Figure 12.2 the abundances (or densities) of predators are plotted on the y axis, and the abundances (or densities) of prey plotted on the x axis. For each point in this

Figure 12.3

The functional response of a single consumer superimposed on its replacement requirements (threshold consumption rate).



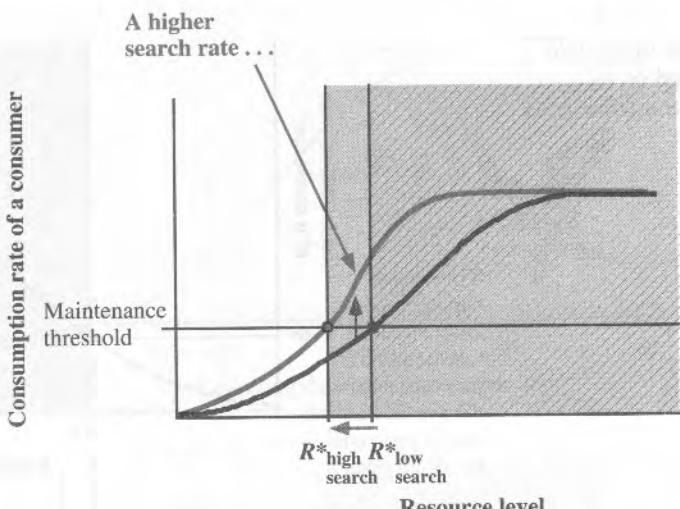
C-R state space, we can determine the predators' growth rate from Eq. (12.2). The shaded region of the ***C-R state space*** (also called the **phase space**) is the set of points where the predator population initially increases according to Eq. (12.2). At high levels of resources (i.e., values greater than R^*), the predators' birth rate exceeds their death rate and their numbers will increase; at low resource levels (below R^*), the predators' numbers must decline since their death rate exceeds their birth rate. Finally, there exists some level of resources, R^* , at which the predators reach equilibrium, $dC/dt = 0$. Since we're plotting this in *C-R* phase space and since per capita consumer growth is not affected by the number of consumers, C , according to our assumptions, a straight vertical line, indicating no dependence on C , separates the two regions: increasing predator numbers on the right and declining predator numbers on the left.

It may seem strange that in this figure, when resources are at R^* , the predator population will be at equilibrium no matter how many predators there are. How can that be, since predators are consuming the resources, and the more predators, the more resources will be consumed? The explanation is that we are imagining that we are fixing resource levels and then letting predator numbers dynamically adjust to the amount of resource present. Recall that in Chapter 10, we fixed predator numbers (sheep) and let resource levels (grass) adjust. Figure 12.2 describes the reverse thought experiment. Surely 100 sheep will consume grass 100 times faster than a single sheep. But that means we must "experimentally" replace the grass 100 times faster to keep the amount of grass fixed at R^* . This is why the equilibrium level of resource (grass) does not depend on the number of predators (sheep). We ultimately want to explore the dynamics when neither predator nor prey is kept fixed; we get to that analysis shortly.

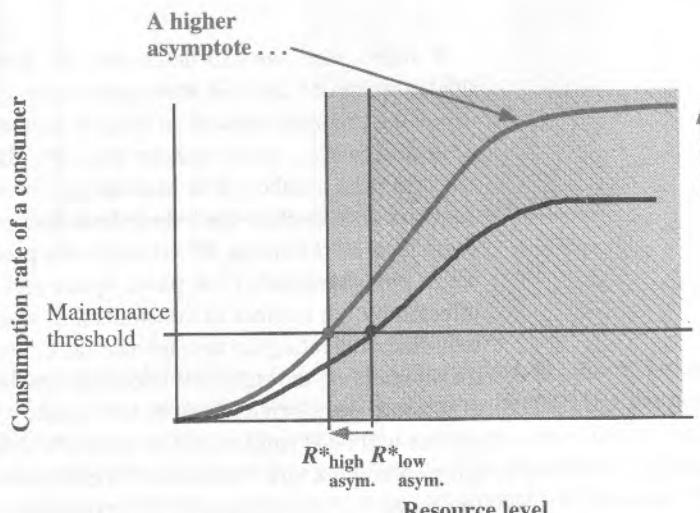
For now, let's explore the biological factors that influence the position of R^* , the threshold level of resource needed for positive consumer growth on the R axis. The dynamical Eq. (12.2) is posed in terms of effects of resource levels on predator per capita birth and death rates. As we discussed in the preceding paragraph, R^* is the same for any number of predators, so we can just consider a single predator's functional response—the amount of resource that an individual predator gathers per unit time. Some of the energy that it gathers from feeding must be devoted to maintenance costs simply so that it can survive and reproduce just enough to replace itself. Any additional harvested resources above those levels necessary for maintenance can be allocated to additional reproduction, as shown in Figure 12.3. If each individual predator produces more offspring than necessary just to replace themselves, then the population grows. But, if resource levels are below the maintenance threshold, R^* , then

Figure 12.4

A consumer (or predator) with a higher functional response curve can just break even on lower resource levels. The predator zero-isocline shifts to the left. Hatched or shaded regions show resource levels yielding positive per capita consumer growth.



(a)



(b)

reproduction cannot keep up with maintenance needs, the average predator will die before it replaces itself, and a population of such predators decreases in size.

The result of a higher search rate for a predator is a lower threshold resource level necessary for positive predator growth, as shown in Figure 12.4.

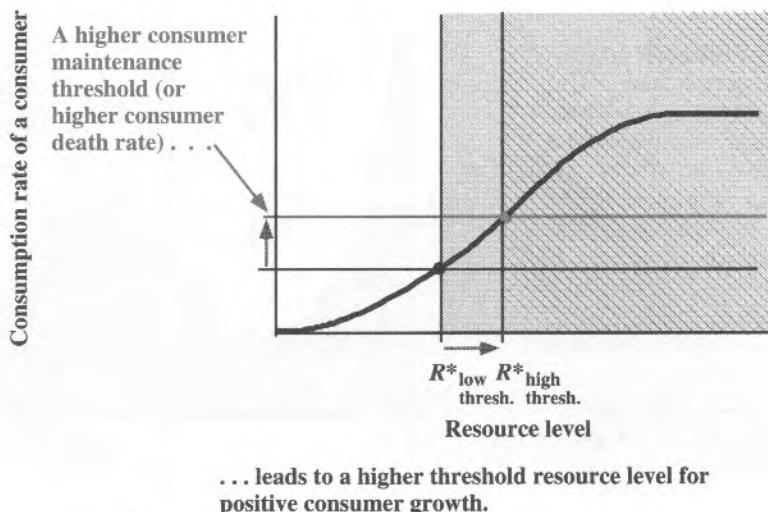
If the predator requires additional energy just to maintain survival, the result will be a higher threshold resource level for positive consumer growth as shown in Figure 12.5.

With this understanding of the factors determining the position of the predator zero-growth line ($dC/dt = 0$) on the R axis, we can finally couple consumer dynamics and resource dynamics so that both are free to vary. While the $dC/dt = 0$ relationship is simply a vertical line, what does the $dR/dt = 0$ relationship look like in $C-R$ space? This is exactly what we derived in Chapter 10 for the case of a type 3 functional response in the example of the grazing sheep and is plotted again in Figure 12.6 for convenience.

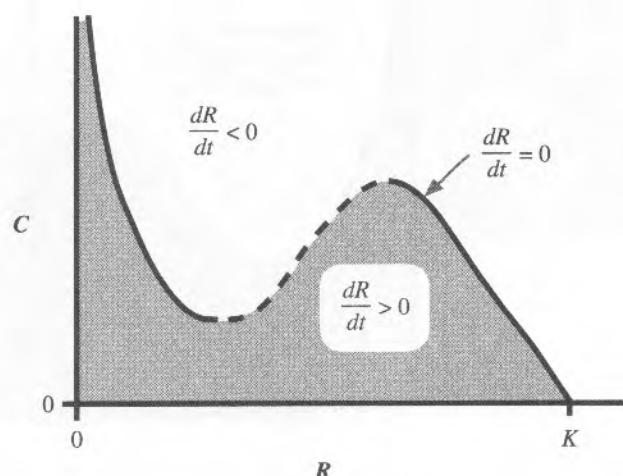
The joint equilibrium for both species occurs at those values of C and R that yield zero growth rates simultaneously for both species. The predator and prey dynamics are superimposed in Figure 12.7.

Figure 12.5

A consumer with greater survival costs will need higher resource levels just to break even. The predator zero-isocline shifts to the right.

**Figure 12.6**

The prey (resource) zero growth curve from Chapter 10 (Figures 10.10 and 10.11). Points inside the curve (shaded area) support positive resource growth rates, and points outside the curve yield negative resource growth rates.

**Figure 12.7**

Superimposing the predator, P , and resource, R , dynamics. The predator region of positive growth is shown in red. The two zero-isoclines intersect at (C^*, R^*) . This point is a feasible equilibrium since both C^* and R^* are greater than zero.

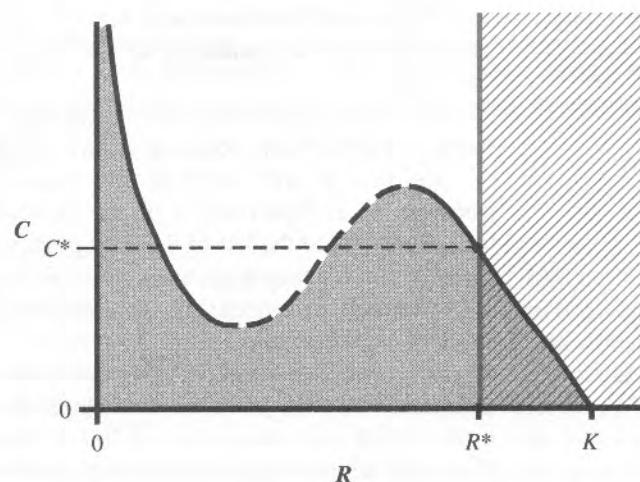
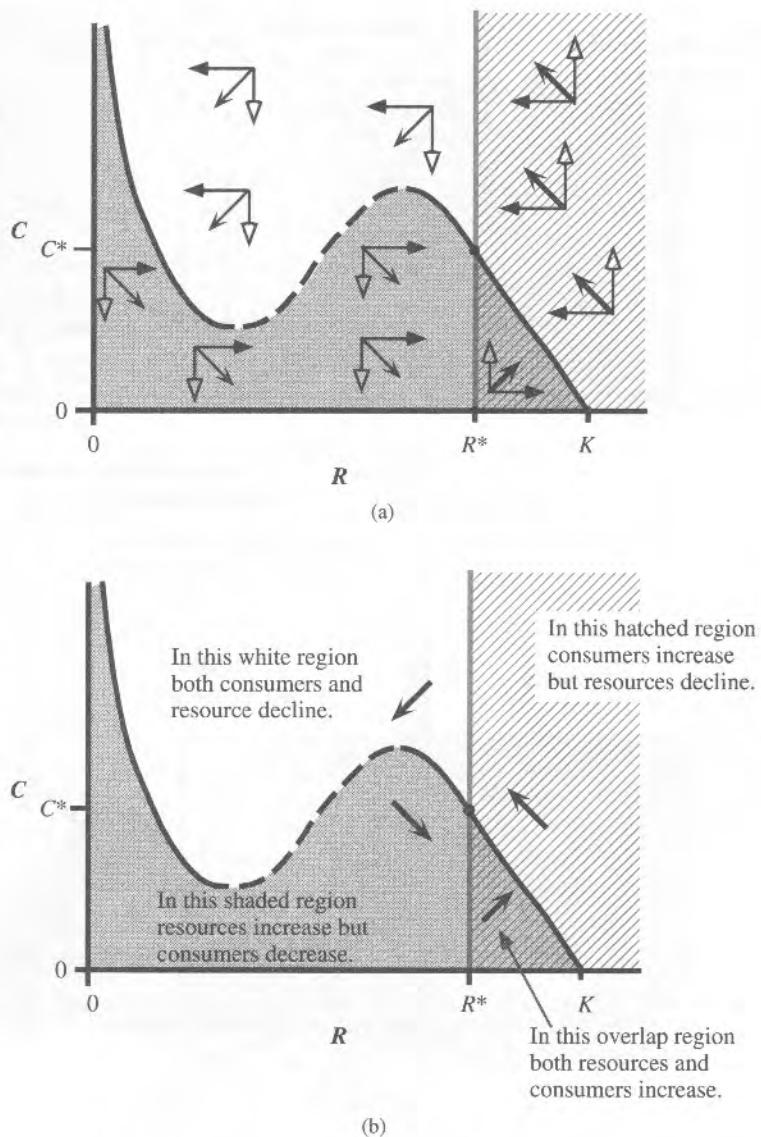


Figure 12.8

The regions of positive and negative growth for both prey, R , and predators, C , plotted in phase space. (a) The arrows show the qualitative trend of population growth for resources, R , and consumers, C . The black arrowheads are for resources, and the open arrowheads are for consumers. The overall qualitative direction of change in both R and C together is shown by the arrow in the middle of each arrow triplet. (b) State space may be divided into four regions based on whether the growth rate of each species is positive or negative.



We can categorize each point in phase space according to whether the predator and prey populations will initially increase or decline from that point as illustrated in Figure 12.8.

We may use these phase-space diagrams to evaluate qualitatively the position and stability of equilibrium points, as shown in Figures 12.8 and 12.9.

The zero growth curves for the two species populations are also called **zero-isoclines**. Recall from Chapter 10, that the dashed portion of the resource zero-isocline, the portion just to the left of the prey peak, yields unstable equilibrium points for the prey. The solid portions, on either side, correspond to stable equilibrium for prey. Figure 12.10 further explores the consequences of changing the point of intersection of the two zero-isoclines.

We expect trajectories to spiral inward to a stable predator-prey equilibrium point and spiral outward from an unstable equilibrium point. But in the latter case, if the equilibrium point is unstable, where will these trajectories ultimately end up? An example of the dynamics of a prey that grows logistically and its predator with a type 3 functional response is shown in Figure 12.11. In this case the parameters of the model are such that the zero-isoclines intersect to the left of the prey peak where the interior equilibrium point is unstable.

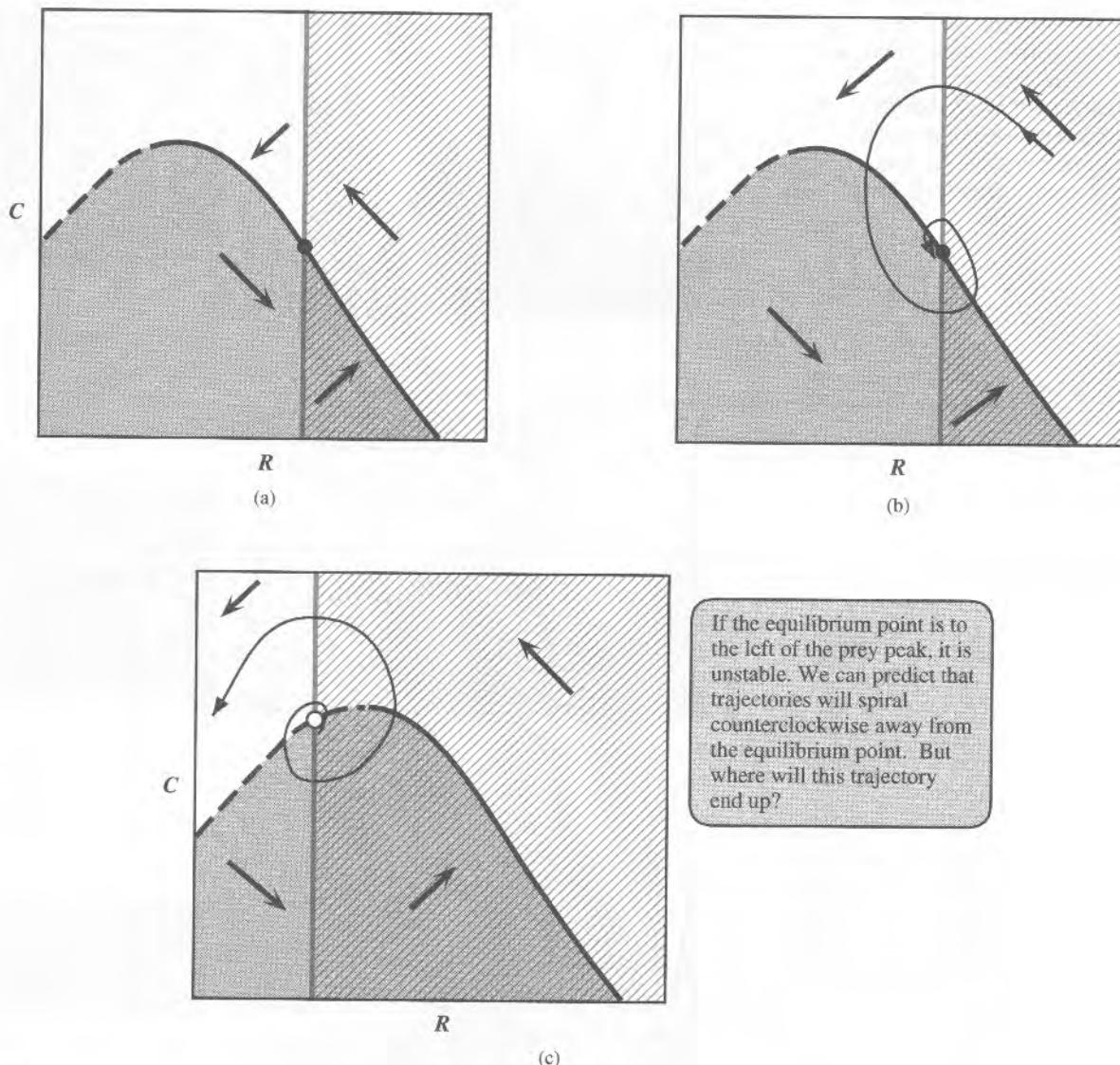


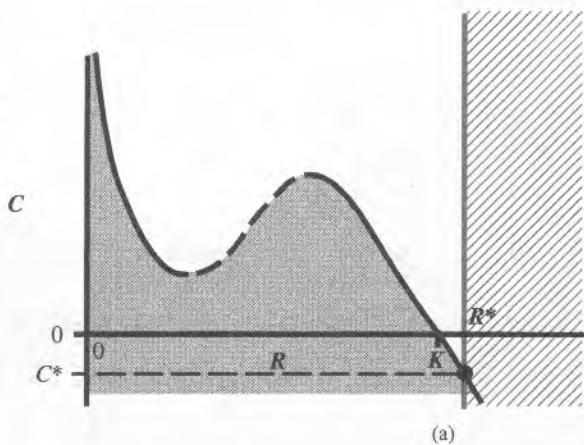
Figure 12.9

(a) and (b) A magnified part of Figure 12.8 in the vicinity of the feasible equilibrium point and a trajectory emanating from a point close to, but not exactly on, the equilibrium point. This equilibrium point falls to the right of the peak of the prey zero-isocline and thus yields a stable equilibrium point for R . Given the direction of the arrows, along with the knowledge that equilibria on the dashed line are unstable, we predict that trajectories will spiral counterclockwise, *inward* toward the equilibrium point. (c) The equilibrium point falls to the left of the prey peak, on the dashed portion of prey zero-isocline. The analysis in Chapter 10 showed that such an equilibrium point would be unstable for prey. Trajectories beginning near this equilibrium point will spiral counterclockwise *outward*.

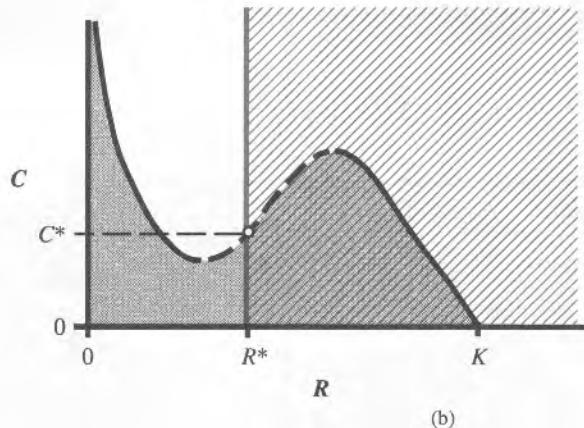
The trajectory spirals out to an egg-shaped **limit cycle**. Predator and prey numbers continually oscillate, and the amplitude and period of the oscillation are fixed. This limit cycle is stable in the sense that it “attracts” trajectories from inside and outside. If the system is initiated at a different point, say, one closer to the unstable equilibrium point, then the trajectory will ultimately cycle out to the fixed cycle shown in Figure 12.11. For predator–prey systems, the cycle is **counter-clockwise** (with predators plotted on the y axis), as shown by the direction of the arrows in Figure 12.8. As indicated in Figure 12.12, this means that the prey population begins to decline while the predator population is still increasing. Then, at the bottom of the cycle, the prey population starts to increase while the predator population is still declining.

Figure 12.10

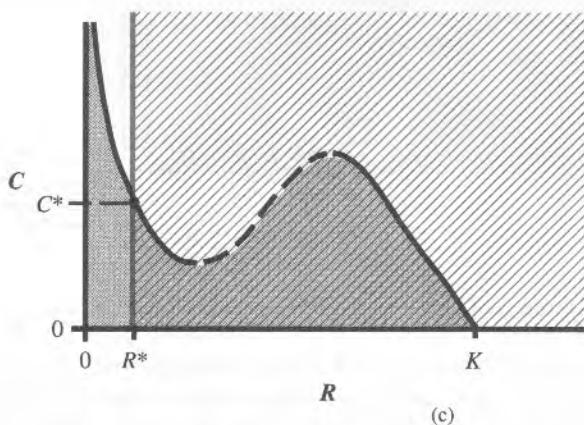
Different possible positions for the predator zero-isocline. Without knowing the exact relationship of the birth and death rates of the two species, we do not know exactly where the intersection of these two zero growth curves will lie. Parts (a)-(c) represent successively lower consumer death rates.



In this case the consumer cannot survive (it is has a negative equilibrium density). The interior equilibrium point is said to be **unfeasible**. The consumers will become extinct and the resources will grow to K , not to R^* .



In this case the consumer/resource interior equilibrium is feasible, but the equilibrium point lies on the **unstable** portion of the resource zero-isocline. Hence this equilibrium point will be unstable.



In this case the consumer/resource interior equilibrium is again feasible and stable.

Figure 12.11

Predator-prey limit cycle. These cycles arise when the interior equilibrium occurs to the left of the peak on the descending portion of the prey zero-isocline. The predator zero-isocline is red and the prey's is black. A sample trajectory (in black) beginning at the gray point is shown. You can look ahead to Box 12.1 to see the equations for this system, which are based on the development in Chapter 11. Other parameters are $a = 0.002$, $T_h = 4$, $k = 0.5$, $d = 0.1$, and $r = 0.5$.

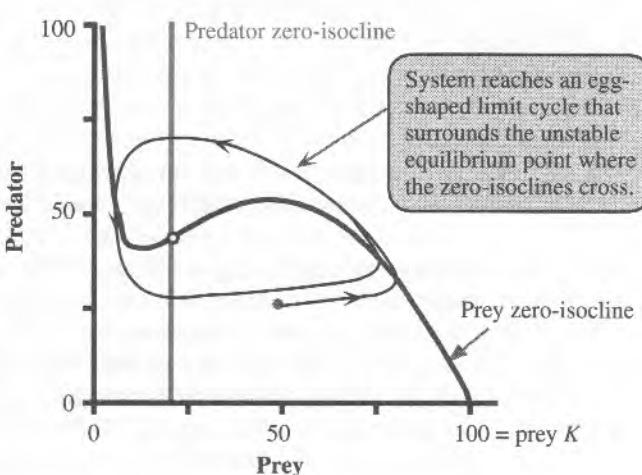
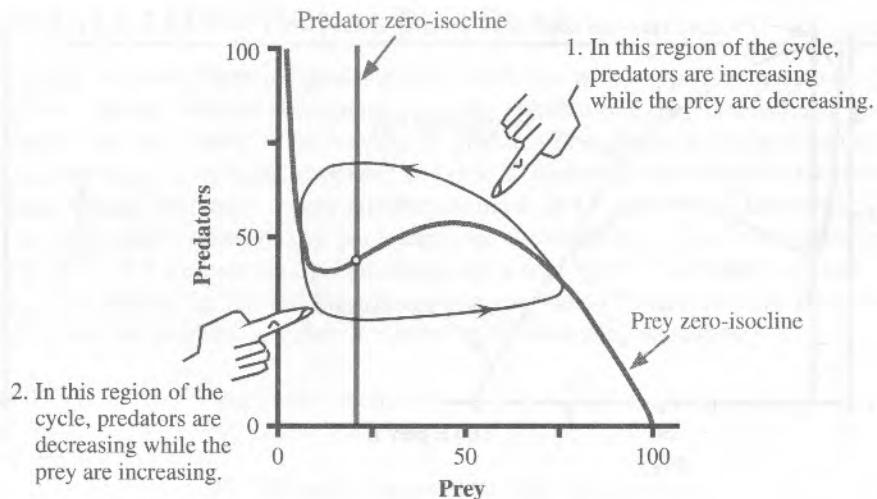
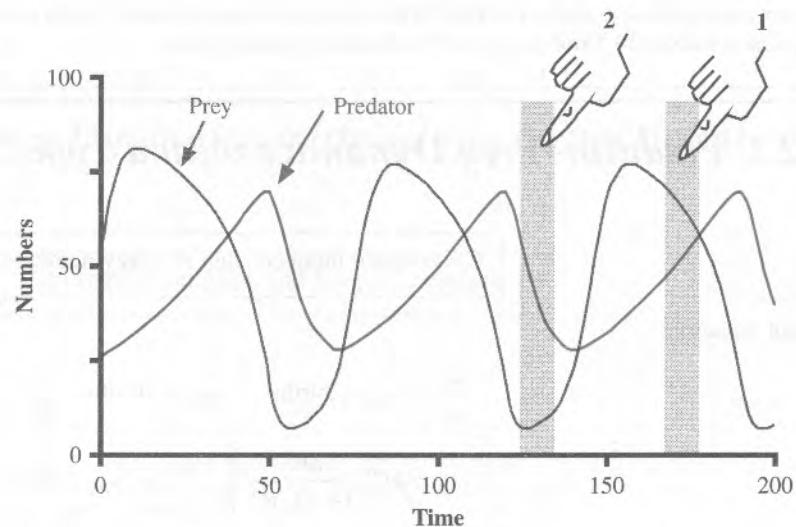


Figure 12.12

The limit cycle from Figure 12.11, indicating joint numerical trends around the cycle.

**Figure 12.13**

Predator and prey numbers over time for the trajectory depicted in Figure 12.12. The fingers point to the approximate positions of the cycle referred to in Figure 12.12.



This situation is more easily seen in Figure 12.13, which shows the time series for the trajectory plotted in Figure 12.11.

In contrast, if the parameters create a predator zero-isocline that lies even farther to the left (e.g., like that in Figure 12.10c), then the interior equilibrium point lies on the ascending portion of the prey zero-isocline and the interior equilibrium point is stable as shown in Figure 12.14.

The equations describing this interaction—which were used to produce the simulations illustrated in the preceding figures—are shown in Box 12.1. The equation for a type 3 functional response was developed in Chapter 11.

In the next sections we add some complications that vary some of these assumptions and allow for additional biological realism. Before proceeding, be sure that you understand where the two zero-isoclines get their particular shapes, why the predatory-prey cycle is counterclockwise, and why equilibrium points to the left of the prey hump's peak produce unstable equilibrium points. You may want to review Chapter 10 to reinforce these points.

Exercise: There are two other (boundary) equilibrium points in Figure 12.11. Where are they? Are they stable?

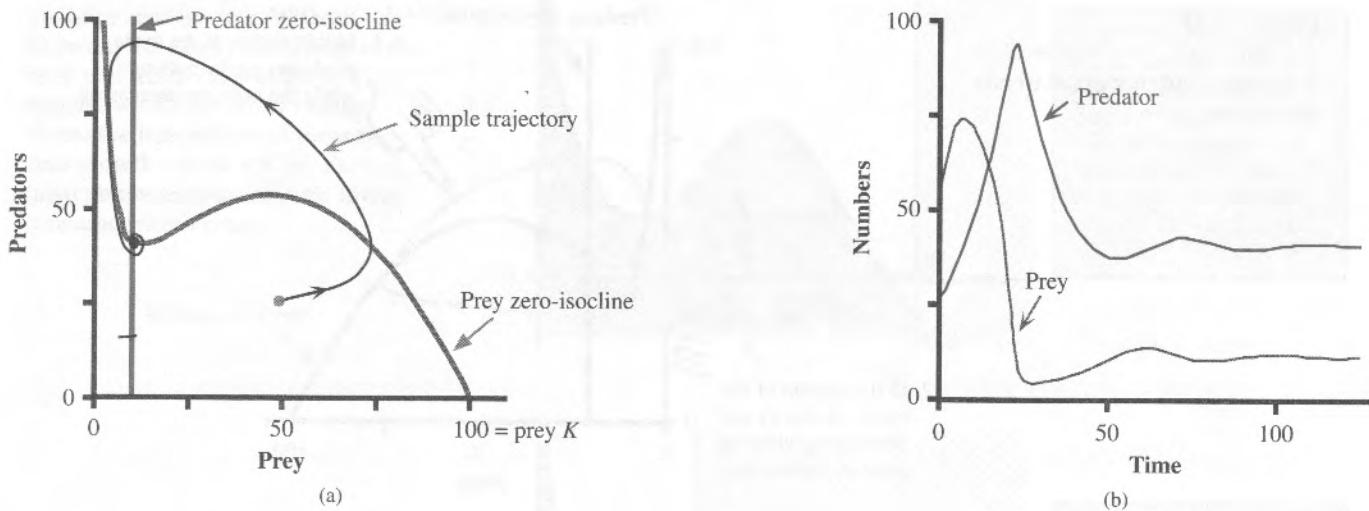


Figure 12.14

(a) The predator zero-isocline is shifted to the left (by decreasing the predator death rate to $d = 0.06$); now the interior equilibrium point is stable. (b) Time course for the trajectory shown in (a).

Box 12.1 Predator-Prey Dynamics with a Type 3 Functional Response

C = predator numbers, and R = prey numbers.

The predator equation:

$$\frac{dC}{dt} = \underbrace{kC \left(\frac{aR^2}{1 + aT_h R^2} \right)}_{\text{Consumption follows a type 3 functional response with encounter rate } a \text{ and handling time } T_h. \text{ For total consumption by the entire population, multiply this by the number of predators, } C.} - \underbrace{dC}_{\text{Consumers have constant per capita death rate } d \text{ independent of } C \text{ or } R.} \quad (\text{a})$$

The prey equation

$$\frac{dR}{dt} = \underbrace{rR \left(1 - \frac{R}{K} \right)}_{\text{Logistic birth rate function}} - \underbrace{C \left(\frac{aR^2}{1 + aT_h R^2} \right)}_{\text{Death due to consumption by predators equals the functional response multiplied by the number of predators, } C.} \quad (\text{b})$$

A TYPE 2 FUNCTIONAL RESPONSE

So far we have illustrated predator-prey dynamics with a type 3 functional response. This S-shaped functional response led to the creation of a prey zero-isocline with one valley and two peaks. What happens in predator-prey dynamics if the predator has a simpler type 2 functional response? The type 2 functional response has a positive slope that steadily decreases as prey numbers increase. In Chapter 11, we found that it could be expressed in terms of two parameters, an encounter rate, a , and the handling time, T_h . Box 12.2 presents the dynamical equations for a type 2 functional response.

By setting Eq. (c) and Eq. (d) to zero, you should be able to show that the zero-isoclines for predator and prey are given by the following equations.

$$\text{Prey zero-isocline: } C = \frac{r}{a} \left(1 - \frac{R}{K} \right) (1 + aT_h R). \quad (12.3)$$

$$\text{Predator zero-isocline: } R = \frac{1}{a \left(\frac{k}{d} - T_h \right)}. \quad (12.4)$$

Box 12.2 Predator-Prey Dynamics with a Type 2 Functional Response

C = predator numbers, and R = prey numbers.

The predator equation:

$$\frac{dC}{dt} = \text{births} - \text{deaths}$$

$$= kC \left(\underbrace{\frac{aR}{1+aT_h R}}_{\text{Consumption by predators follows a type 2 functional response with encounter rate } a \text{ and handling time } T_h. \text{ For total consumption by the entire population, multiply this by the number of predators, } C.} \right) - dC. \quad (c)$$

Consumption of resources is converted to reproduction of C according to the conversion rate, k

Consumption by predators follows a type 2 functional response with encounter rate a and handling time T_h . For total consumption by the entire population, multiply this by the number of predators, C .

Consumers have constant per capita death rate d independent of C or R .

The prey equation

$$\frac{dR}{dt} = \text{recruitment} - \text{deaths to predators}$$

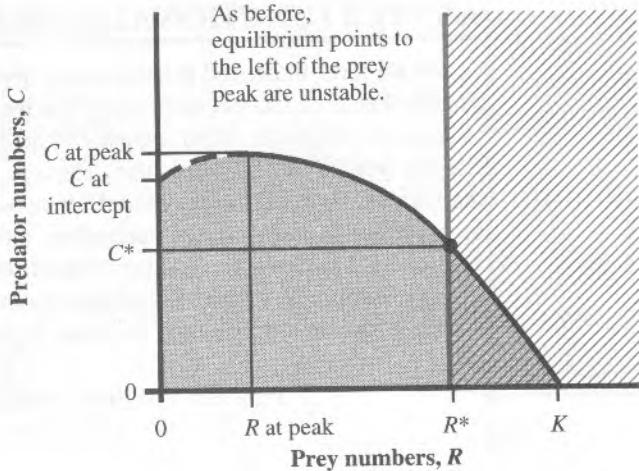
$$= rR \left(1 - \frac{R}{K} \right) - \underbrace{C \left(\frac{aR}{1+aT_h R} \right)}_{\text{Death due to consumption by predators equals the functional response multiplied by the number of predators, } C.}. \quad (d)$$

Logistic birth rate function

Death due to consumption by predators equals the functional response multiplied by the number of predators, C .

Figure 12.15

Predator-prey zero-isoclines when the predator has a type 2 functional response and the prey grows logistically. Phase-space regions of positive growth for each species are shaded. The predator's region of positive growth is pink and the prey's is gray.



Note that the predator zero-isocline does not involve predator numbers and thus is a vertical line in the C - R phase plane. The prey zero-isocline is the equation of a truncated parabola. Figure 12.15 illustrates the zero-isoclines for both predator and prey.

Exercise: For this model, use Eqs. (c) and (d) of Box 12.2 to verify the following three algebraic expressions:

$$R^* = \frac{1}{a\left(\frac{k}{d} - T_h\right)}, \quad (12.5)$$

$$C \text{ at intercept} = \frac{r}{a},$$

and

$$R \text{ at peak} = \frac{K}{2} - \frac{1}{2aT_h}.$$

Sensitivity Analysis

From Eq. (12.5), for the equilibrium resource level, R^* , you can see that unless $k/d > T_h$, the equilibrium level of prey, R^* , is negative. In reality if this were the case, the predator would decline to extinction and the prey population would then climb to its carrying capacity, K . The larger the death rate of the predator or the larger the prey handling time, T_h , the greater will be the equilibrium prey level, R^* . Increasing the handling time causes the prey zero-isocline curve to stretch upward and shifts its peak to the right, as depicted in Figure 12.16.

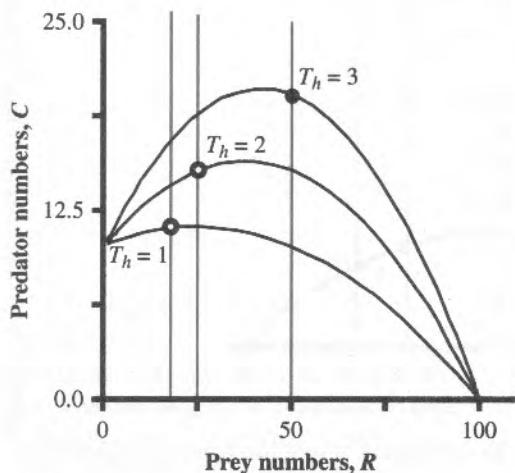
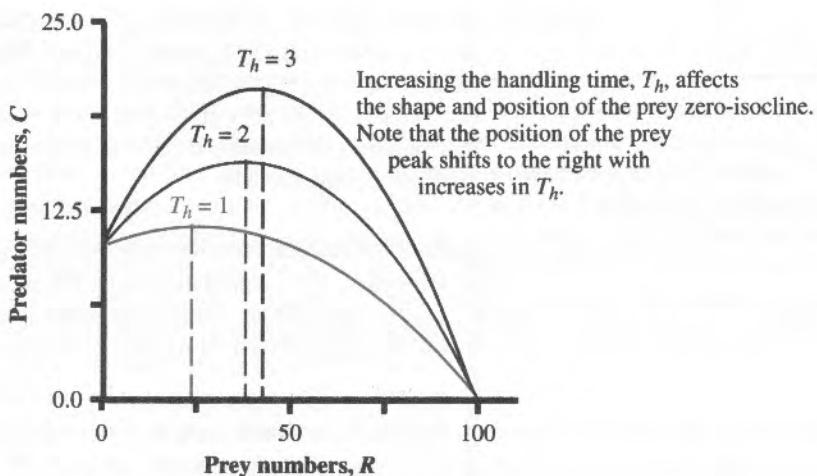
The position of the predator zero-isocline also shifts to the right with increases in T_h as you can see by examining Eq. (12.4) or (12.5). Figure 12.17 makes the visual comparison.

Increasing prey carrying capacity, K , affects only the prey zero-isocline since K is not a parameter in Eq. (12.4) for the predator zero-isocline. Figures 12.18 and 12.19 illustrate this condition.

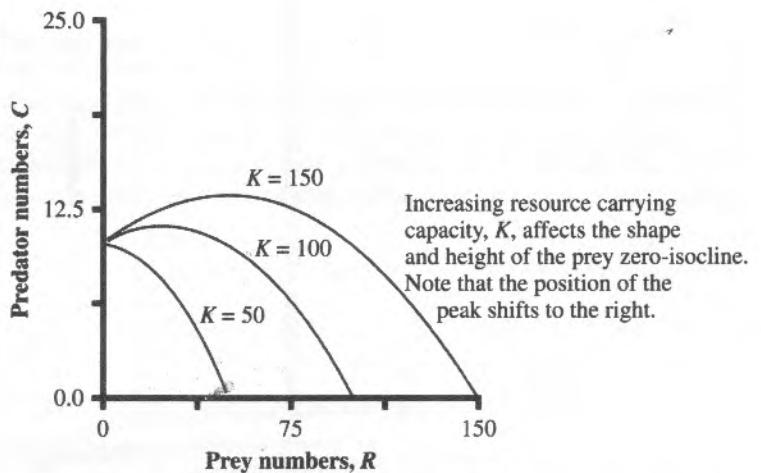
Increasing prey carrying capacity, K , increases predator numbers at equilibrium and can shift the interior equilibrium point to the left side of the peak of the prey hump. This, in turn, results in an unstable interior equilibria. As for a type 3 functional response (see Figure 12.10), limit cycles result. Moreover, the farther the unstable equilibrium is to the

Figure 12.16

The effect of different handling times on the prey zero-isocline. Other parameters from equations in Box 12.2 are $a = 0.02$, $k = 1$, $r = 0.2$, and $K = 100$.

**Figure 12.17**

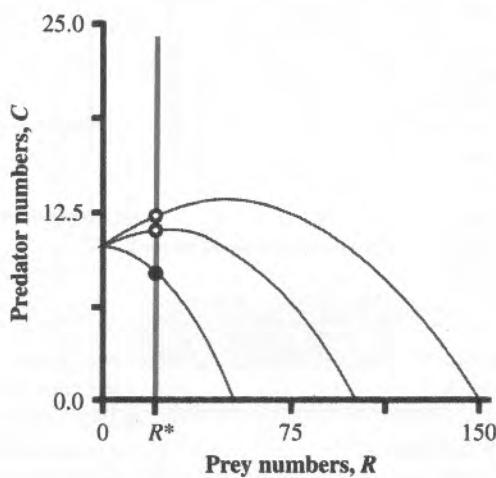
The handling time parameter influences both the predator and prey zero-isoclines. Other parameters as in Figure 12.16 and $d = 0.25$.

**Figure 12.18**

The effect of different prey carrying capacities, K , on the prey zero-isocline. Other parameters as in Figure 12.16.

Figure 12.19

Conclusion: Increasing prey carrying capacity can destabilize a stable predator/prey system. These three prey zero-isoclines differ only in K . A predator zero-isocline is superimposed on them. Higher K results in higher numbers of predators at the interior equilibrium point but does not change the equilibrium prey numbers. Higher K also shifts the relative position of the equilibrium point to the left of the prey zero-isocline's peak. Other parameters as in Figure 12.16 and $T_h = 1$, $d = 0.25$.



left of the prey hump, the larger the limit cycles become in amplitude, as shown in Figure 12.20. As these limit cycles become larger in amplitude, they come progressively closer to converging on one of the axes, with the subsequent extinction of a species.

Increasing the prey growth rate, r , as shown in Figure 12.21, results in higher predator numbers at equilibrium but does not destabilize the equilibrium point, at least in continuous time models.

Exercise: How would increasing the encounter rate, a , change equilibrium numbers of prey and predators? Is a predator-prey system of this type likely to be stabilized, destabilized, or unaffected by successive increases in the encounter rate?

Exercise: Three predator species eat the same prey. The predator species differ only in their death rates, d . Their zero-isoclines are as shown in the following diagram. Other parameters are $K = 200$, $T_h = 0.9$, conversion rate $k = 1$, and encounter rate $a = 0.02$. Only one predator will prevail. Which one and why?

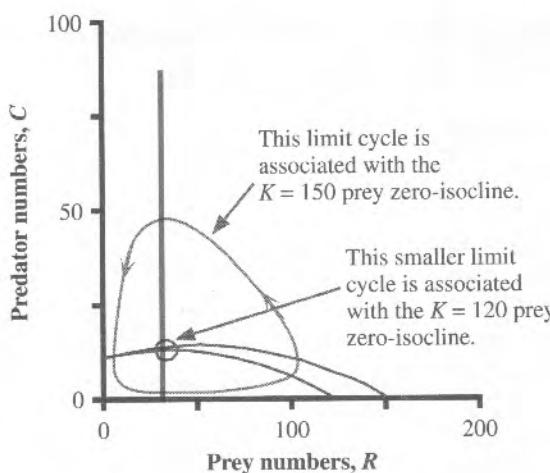
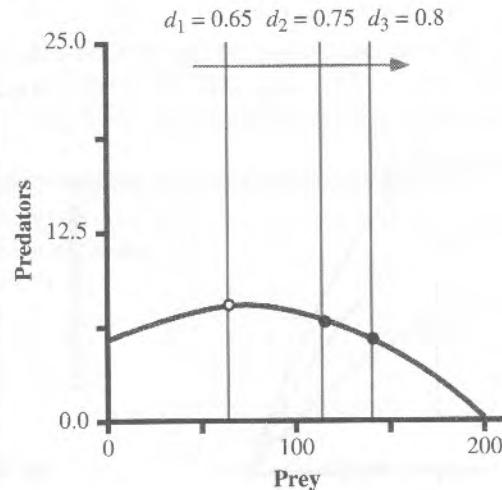


Figure 12.20

Two alternative prey with the same predator. One prey has $K = 150$, and the other has $K = 120$. All other parameters are the same for both predator and prey. Both equilibria fall to the left of the prey hump and so are unstable. However, the $K = 150$ equilibrium is relatively farther to the left. Other parameters are $a = 0.02$, $k = 1$, $d = 0.4$, $r = 0.2$, and $T_h = 1$.

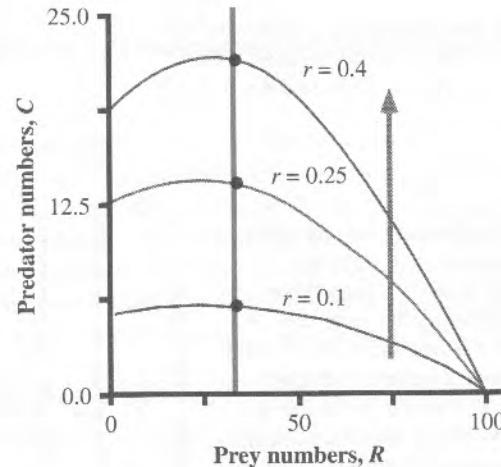


Figure 12.21

Increases in the prey intrinsic growth rate, r , affect only the prey zero-isocline; it increases the equilibrium abundance of predators but not of prey. Also, changes in r do not move the equilibrium point to the left of the prey zero-isocline peak.

PREY REFUGES CAN MIMIC A TYPE 3 FUNCTIONAL RESPONSE

Another mechanism can lead to a prey zero-isocline somewhat like that for a type 3 functional response. Imagine a type 2 functional response but also refuges for the prey to hide where they are safe from predators (Rosenzweig and MacArthur 1963). Let's suppose that a maximum of H prey can hide in these refuges. On the one hand, if prey numbers are below H , then no matter how many predators are present, all the prey will be secure. On the other hand, when prey levels exceed the number of safe sites, some prey will be exposed to predation. Figure 12.22 illustrates this process for a refuge size of $H = 10$. Clearly, refuges can be stabilizing in the sense that they prevent the predator from completely overexploiting the prey.

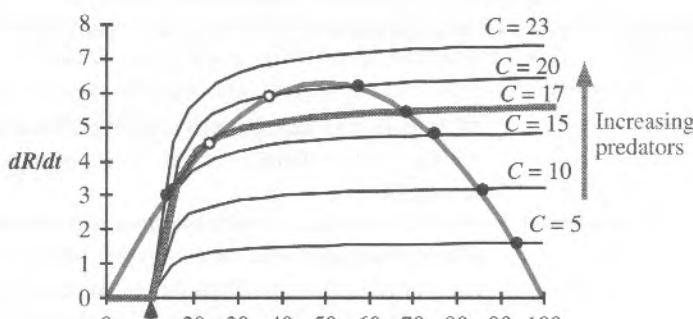
Exercise: Modify the equations for prey and predator growth rates, Eqs. (c) and (d) Box 12.2 to incorporate a refuge of size H . What is the new equation for the predator zero-isocline?

Laboratory Examples

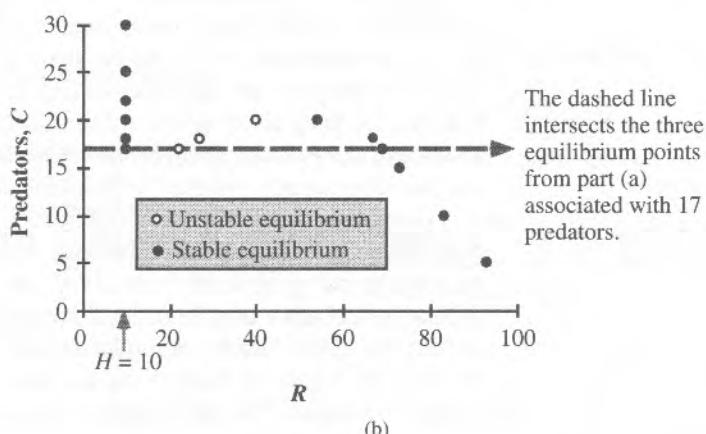
Maly (1969) used a microcosm composed of the protozoan *Paramecium* as prey and the rotifer *Asplanchna* as a predator. He studied species interactions in very small 1 ml depressions in microscope slides. Maly placed different numbers of predators and prey in many different depressions and observed their initial growth rates over short periods

Figure 12.22

The effect of a prey refuge on the prey zero-isocline. (a) Type 2 functional response with a prey refuge of size $H = 10$. (b) Other parameters are $r = 0.25$, $K = 100$, $a = 0.1$, and $T_h = 3$.



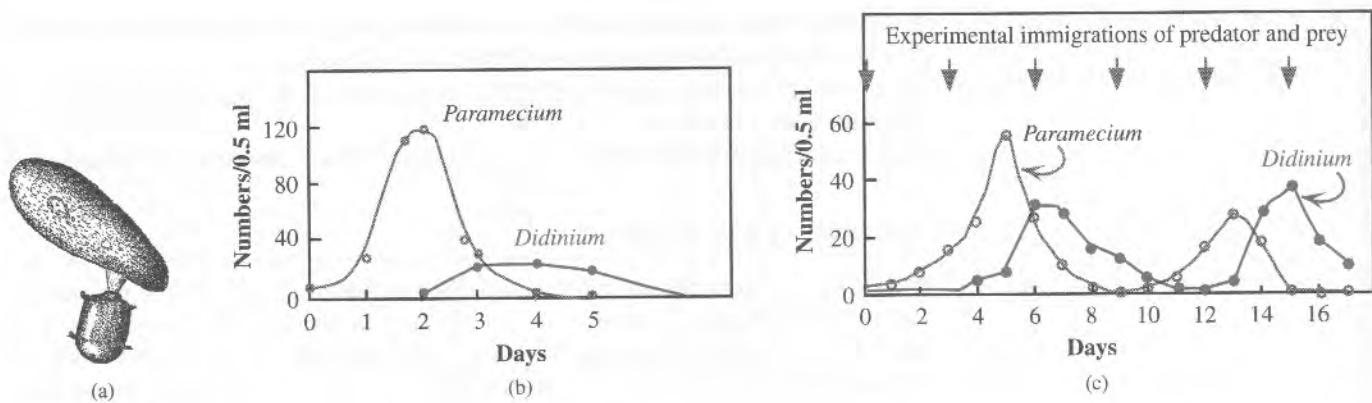
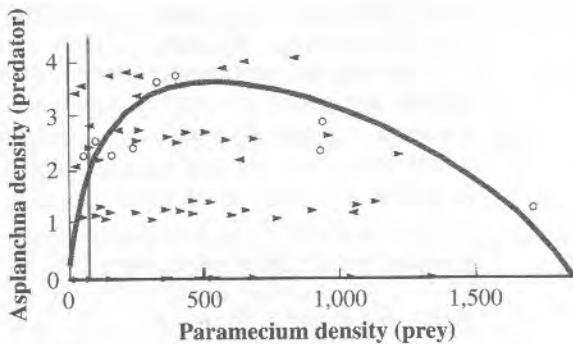
(a)



(b)

Figure 12.23

The arrows show the initial direction of growth for *Paramecium* at different numbers and with varying numbers of a rotifer predator. Open circles indicate populations that changed less than 5% in 24 hours. After Ricklefs (1979) from Maly (1969).

**Figure 12.24**

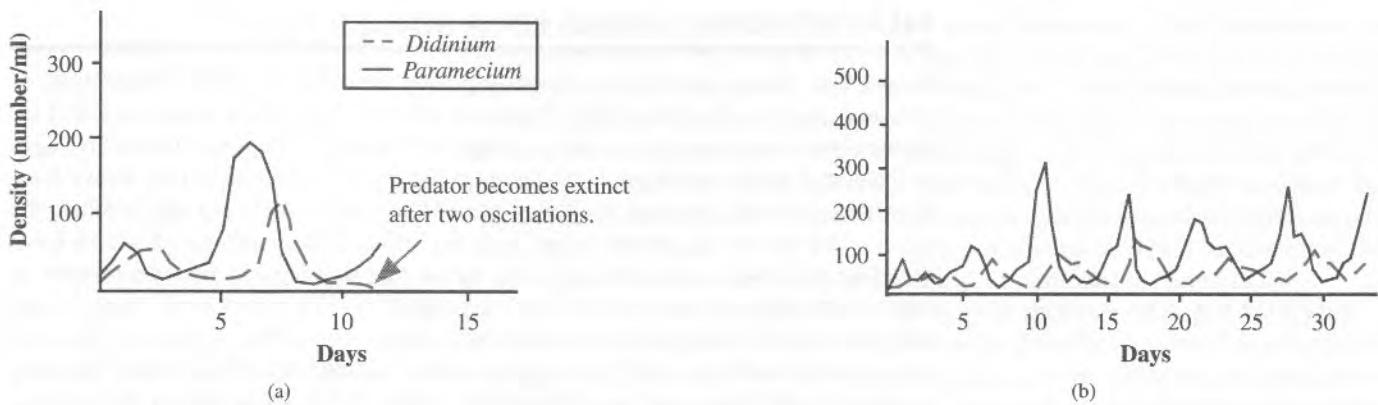
(a) *Didinium nasutum* devouring a *Paramecium caudatum*. (b) The prey *Paramecium* begins growing in a test tube at day 0. The predator *Didinium* is introduced at day 2. The predators rapidly multiply and eliminate all the *Paramecium* and then gradually die out themselves. (c) Same as (b), but Gause added one *Didinium* and one *Paramecium* to the test tube every third day. With this modification, the two species coexisted for 15 days, followed by the extinction of the *Paramecium*. After Gause 1934.

of time. In this way, he was able to construct the arrows in diagrams like those in Figure 12.8. From them he could infer the shape of the zero-isoclines, as depicted in Figure 12.23.

This predator-prey system seems to be unstable. Moreover, since the apparent equilibrium point lies far to the left of the prey hump and close to prey = 0, the limit cycle around this equilibrium is expected to be large and closely converging on the axes. Predator and/or prey are predicted to become extinct quickly—the result that Maly found in longer term experiments.

Another microcosm that has received substantial attention is that of *Paramecium* as prey and another protozoan, *Didinium*, as the predator. One of the pioneering studies by Gause (1934) explored the dynamics of this system. He found that *Didinium* was such an efficient predator that it overexploited the prey and that both species collapsed to extinction unless he took elaborate steps to keep this from happening. *Didinium* is smaller in size than the *Paramecium* that they consume, as shown in Figure 12.24(a), and they can keep dividing, becoming smaller and smaller for several days, even in the absence of any *Paramecium*. If *Paramecium* are now added, the *Didinium* are so numerous that they quickly overexploit their prey, as indicated in Figure 12.24(b).

Gause speculated that these two species coexist in nature in spite of local extinctions driven by overexploitation because these small *Paramecium* can quickly colonize new ephemeral water ponds where *Didinium* might be absent. (We explore this idea of regional coexistence in spite of local noncoexistence in Chapter 16.) Gause attempted a crude test of this idea by reintroducing one individual of each species every third day, as shown in Figure 12.24(c) to his test tubes. This periodic immigration allowed prolonged coexistence, but still only for two cycles.

**Figure 12.25**

Protozoan predator-prey dynamics: (a) with methyl cellulose (b) With methyl cellulose and reduced food for *Paramecium*. After Luckinbill 1973.

Luckinbill (1973) took up the challenge. He reasoned (according to the theory that we have just reviewed) that it should be possible to get more prolonged coexistence in this system by reducing the encounter rate of the predator with their prey. To accomplish this he made the water medium more viscous by adding methyl cellulose. Methyl cellulose slowed the swimming speeds of both predator and prey to about 3% of their previous levels. One of his typical results is shown in Figure 12.25(a). He was able to get coexistence for two cycles without periodic immigration of the two species.

Luckinbill next lowered prey K by reducing the food (i.e., bacteria) levels for the *Paramecium*. This lower K , in combination with the methyl cellulose, gave prolonged cycles, as indicated in Figure 12.25(b). In terms of the zero-isocline depiction, both measures theoretically result in shifting the intersection of the zero-isoclines more to the right (see Figure 12.23). Empirically, both populations still oscillate, indicating that the interior equilibrium point for this system is still to the left of the peak of the hump of the prey zero-isocline, but not so far to the left that oscillations are extreme and trajectories “hit” an axis.

PROBLEMS

1. Modify the predator growth equation (Eq. c) of Box 12.2 to include migrants that come into the system from outside at a constant rate m . This yields

$$\frac{dC}{dt} = m + k \left(\frac{aRC}{1 + aT_h R} \right) - dC.$$

Sketch the predator zero-isocline for this modified model. Does this confer or detract from stability?

2. Sometimes the migration rate of predators into an area is in response to available food levels in that patch. Modify the predator growth equation (Eq. c) of Box 12.2 to include migrants that come into the system from outside at a rate proportional to the abundance of resources. This yields

$$\frac{dC}{dt} = m'R + k \left(\frac{aRC}{1 + aT_h R} \right) - dC.$$

Sketch the predator zero-isocline for this modified model. Does this confer or detract from stability?

3. Consider the model in Box 12.1 with a type 3 functional response. Show that the equilibrium level of resource, R^* , is modified from that in Eq. (12.3), namely,

The equilibrium resource level from Box 12.1 is

$$R^* = \frac{1}{\sqrt{a \left(\frac{k}{d} - T_h \right)}}.$$

4. Suppose that an unstable equilibrium point exists for this case of a type 3 functional response. Could increasing the prey carrying capacity, K , ever stabilize the system?

MULTIPLE PREDATORS ON A SINGLE PREY

In another classic laboratory experiment that provides a useful illustration of predator-prey theory, Utida (1957) examined a system comprising a bean weevil (*Callosobruchus chinensis*) as prey and a wasp (*Heterospilus prosopidis*), which lays eggs in the weevil larvae, as the predator. The eggs hatch into larvae that kill the weevil host. Parasites with this behavior are called **parasitoids**. After the wasp egg hatches, the wasp larvae devour the beetle larvae from the inside. The abundance of weevil hosts therefore influences the number of wasp larvae that develop and thus the number of adult wasps that emerge in the following generation. The prey weevils feed on and oviposit in beans, which Utida placed in petri dishes. Population densities of the weevil and wasp oscillated, with the parasitoid cycles lagging behind the cycles of the prey as expected by theory and as illustrated in Figure 12.26. Even though the physical experimental system is very simple and relatively homogeneous, the two species coexisted for nearly 30 generations (or four complete cycles)—at which time Utida discontinued the experiment.

Next Utida added a second wasp parasitoid (*Neocatolaccus mamezophagus*). Both wasps were forced to compete for the single host species. Populations fluctuated dramatically, but all three species coexisted in these simple petri dishes for more than 70 generations, as shown in Figure 12.27.

This result is exceptional because it is usually very difficult to achieve coexistence in the confined and homogeneous arrangements of most laboratory experiments. The result is interpretable, however, with a simple extension of predator-prey theory. The two wasps apparently had different functional responses so that one wasp did relatively better, as judged by the number of emerging wasps per generation, at prey densities below a density of about 200 weevils, while the other wasp did relatively better at high weevil densities, above 200, as plotted in Figure 12.28.

Figure 12.26

Predator-prey oscillations of the bean weevil (*Callosobruchus chinensis*) and a parasitoid wasp (*Heterospilus prosopidis*) in petri dishes. After Utida (1957).

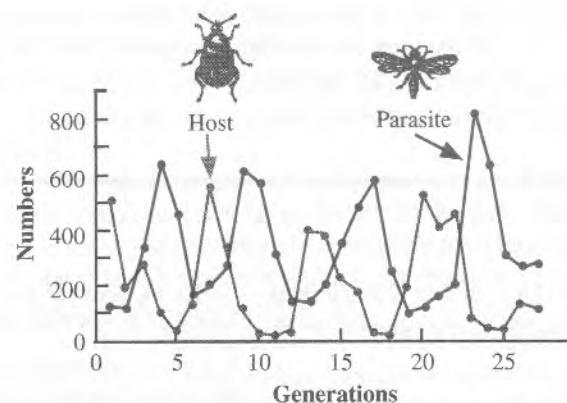
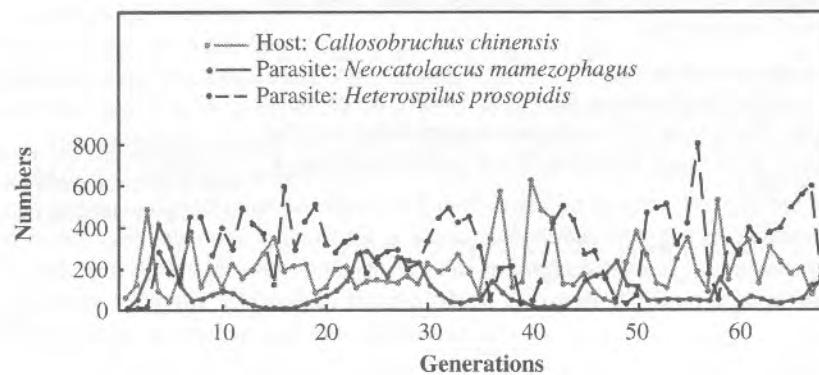


Figure 12.27

Two parasitoid wasps coexisting on a single host species of bean weevil. The total duration of this experiment was about 4 years. After Utida (1957).



If the wasps are otherwise identical, this result implies that, if host densities can be kept experimentally at relatively high levels, then the second wasp should outcompete the first. Yet if host densities are kept at low prey levels, the first wasp should prevail. Finally, if weevil numbers fluctuate, sometimes being greater than the crossover density of 200 and sometimes being less, then it might be possible for the two wasps to coexist. But what might drive such a fluctuation? One reason that beetle numbers fluctuate is because the wasp/beetle interaction itself produces a limit cycle. We saw such oscillations with the one wasp system (see Figure 12.26). We next explore this situation within the context of the predator-prey theory that we have just developed, as illustrated in Figure 12.29.

The two predators compete for the same prey species, which grows logistically ($K = 200$, $r = 0.1$). Figure 12.30 shows the zero-isoclines for each predator when alone with the same prey under two different predator death rates. With the decreased death rates for the two predators (Figure 12.30b), the predators' zero-isoclines move to the left (review Figure 12.5) and become more similar in position. The different shape of the predators' functional responses (as determined by parameters a and T_h) causes the reversal in the relative position of their zero-isoclines. From equation 12.4, the position of the predator zero-isocline is at

$$R^* = \frac{1}{a\left(\frac{k}{d} - T_h\right)}.$$

Thus the position of the predator zero-isocline depends on its death rate, d , its handling time, T_h , and the encounter rate, a . Applying this formula to the situation shown in Figure 12.30(a), for predator 1, $R^* = 1/[0.04((1/0.75) - 1.2)] = 187.5$ and for predator 2, $R^* = 1/[0.02((1/0.75) - 0.9)] = 115.3$. In Figure 12.30(b) for predator 1, $R^* = 1/[0.04((1/0.65) - 1.2)] = 73.90$ and for predator 2, $R^* = 1/[0.02((1/0.65) - 0.9)] = 78.30$.

The time series for all three hypothetical species shows that for the case of lower death rates, limit cycles emerge and both predators can coexist on this single prey, as shown in Figure 12.31. Is the coexistence of Utida's beetles completely explained by

Figure 12.28

Total number of parasitic wasps of two species emerging from larvae of the host weevil plotted as a function of host weevil density. After Utida (1957) and Pianka (1994).

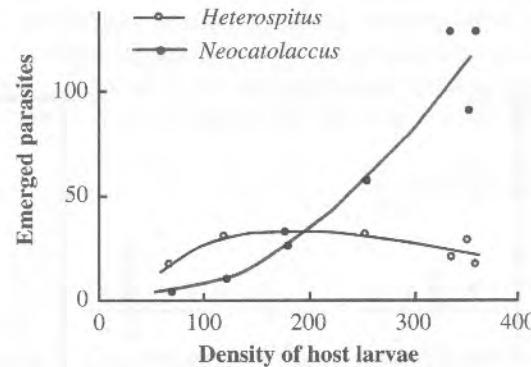
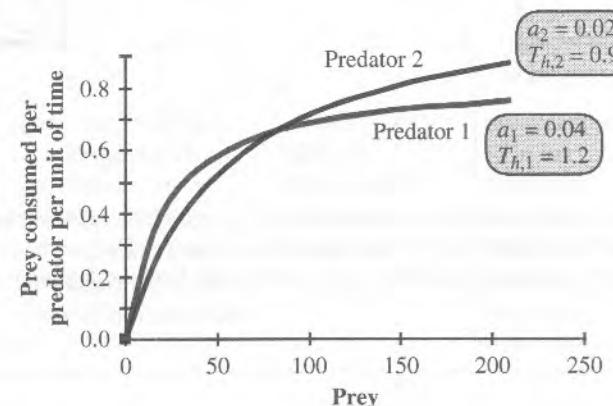
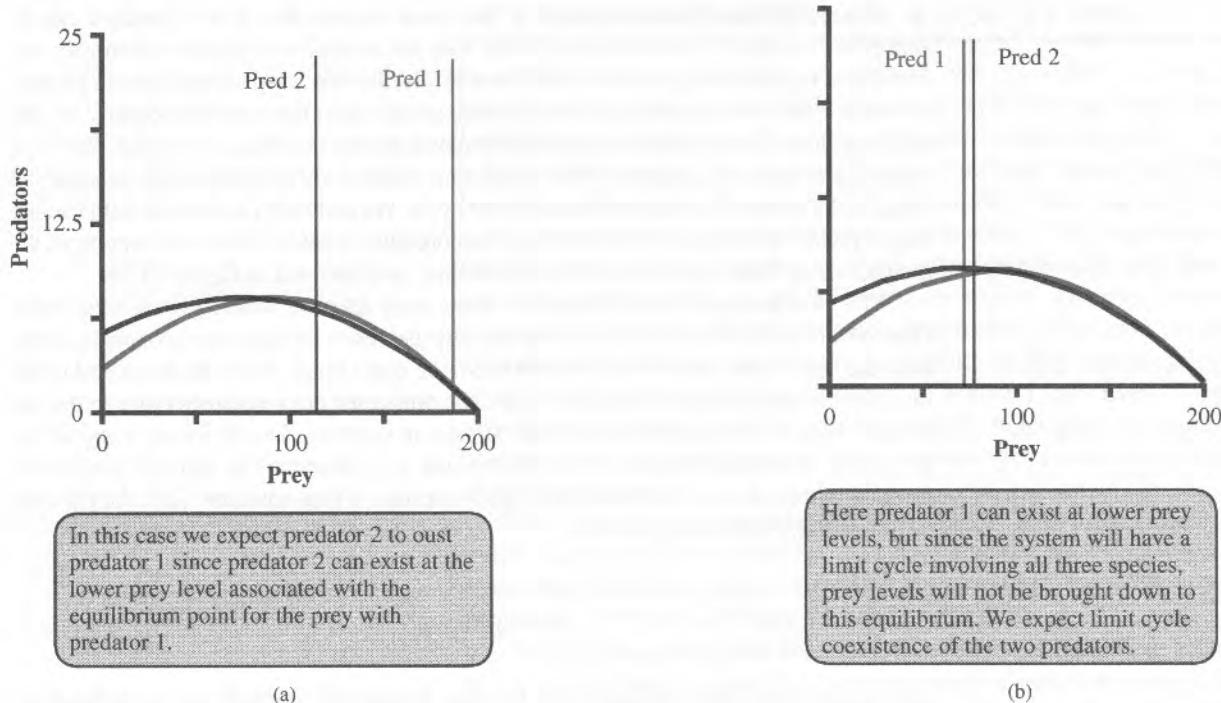


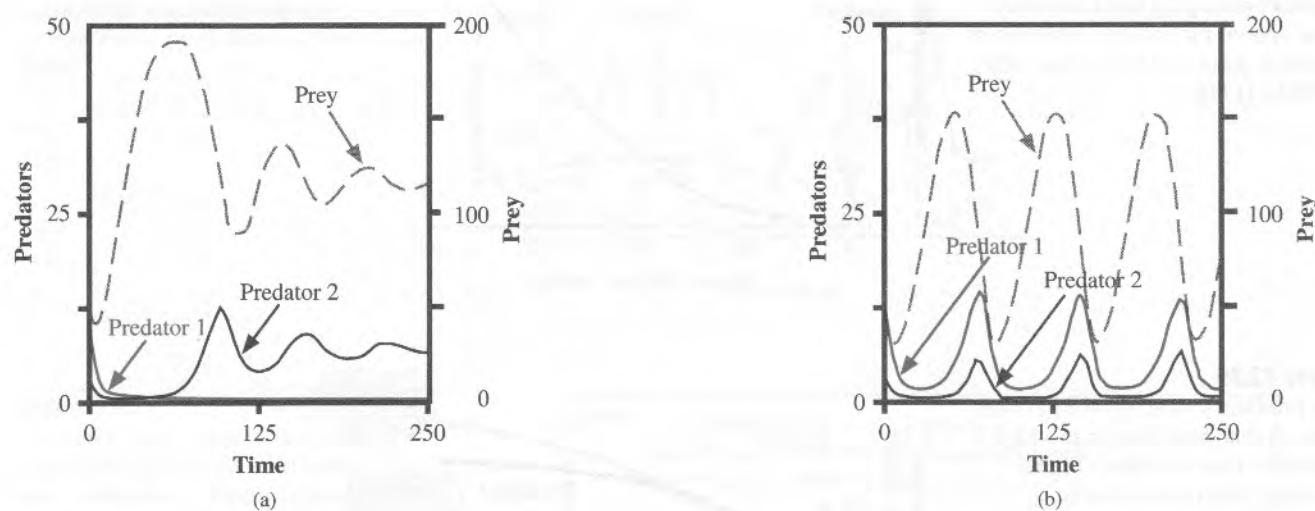
Figure 12.29

Two predators' functional responses differ so that predator 1 has a higher encounter rate and also a higher handling time (thus a lower asymptote) than predator 2.



**Figure 12.30**

Both parts of the figure show a zero-isocline for two alternative predators feeding on the same prey. The prey species is the same for both predators, but because the zero-isocline of the prey depends on the predator's encounter rate and handling time parameters, there are two prey zero-isoclines in each case. (a) The predators' death rates are relatively high at 0.75, and each predator, when alone with the prey, has a stable interior equilibrium point. (b) The two predators and prey are the same as in (a), but the predators' death rates have been lowered to 0.65. Consequently, the predators can now increase at lower prey levels (the predator zero-isoclines shift to the left). The prey and predator zero-isoclines intersect at an unstable equilibrium point, producing limit cycle dynamics. Other parameters are $k = 1$, $r = 0.1$, and $K = 200$.

**Figure 12.31**

One prey with two predators, based on the situation depicted in Figure 12.30. (a) The predator death rates are high ($d_1 = d_2 = 0.75$), so prey levels are kept high; only one predator survives. (b) The predator death rates are lower ($d_1 = d_2 = 0.65$), and the equilibrium prey density (although unstable) is at a low level. Now both predators coexist with limit cycle oscillations.

this model? The results diverge from theoretical expectations in two ways. The erratic behavior of the three insects does not seem to show the regular limit cycles suggested by the model, although this may simply be due to some additional environmental noise superimposed on the system. More important, in Utida's experiment the fluctuations of the two wasps seemed to be largely out of phase with one another (see Figure 12.27), yet the theory predicts that the cycles of the two predators should be in phase (see Figure 12.31b). Although one wasp is relatively more successful than the other at low weevil densities while the reverse is true at high beetle densities, both wasps do *absolutely* better at high beetle densities (see Figure 12.28); hence theory predicts that the two wasps will positively covary. Perhaps the discrepancy between theory and these empirical results is because the two wasps respond differently to uncontrolled environmental features of this experiment, or, alternatively, they may directly interfere with each other. It is also important to keep in mind that this host/parasitoid system may not be perfectly analogous to predator-prey equations with a type 2 functional response.

PREDATOR INTERFERENCE, ALLEE EFFECTS, AND OTHER MODIFICATIONS TO PREDATOR- PREY INTERACTIONS

In summary, to help you understand the dynamics of interacting species, we introduced a method of plotting zero-isoclines in state space along with the regions of positive and negative growth for each species. Without actually solving the coupled differential equations of population growth, we have been able to make reasonable inferences about trajectory direction and the local stability of equilibria. This is valuable because the coupled differential equations that we have been exploring do not even have closed form analytical solutions. Yet it is important to remember that our instability determination for equilibrium points to the left of the prey zero-isocline peak has been based on an assumption of a **linear numerical response** for the predators. We have assumed, for example, that the consumption of five sheep is five times as great as the consumption of a single sheep and the per predator growth equation is multiplied by 5 to get the total growth rate for this five-predator population. If this linearity assumption is violated, then the stability of equilibria along the prey curve may change. In Box 12.3 we explore a possible departure from this assumption, involving intraspecific predator interference.

If we write the per capita form of the consumer growth equation, Eq. (e), we note that it involves a term in fC , the interference term, or

$$\frac{dC}{C dt} = kB(R) - d - fC. \quad (12.6)$$

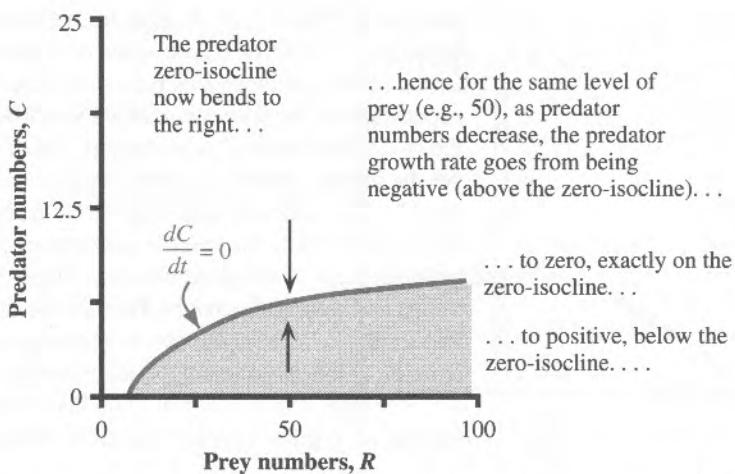
Box 12.3 Predators with Intraspecific Interference

$$\frac{dC}{dt} = k[B(R)C] - dC - fC^2. \quad (e)$$

The growth rate of the consumer population	$=$ consumer birth rate. It is proportional to prey intake per consumer, $B(R)$, (Type 2 functional response) times the number of consumers	minus density independent consumer death rate	minus a new term for consumer interference. The death rate is density dependent.
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Figure 12.32

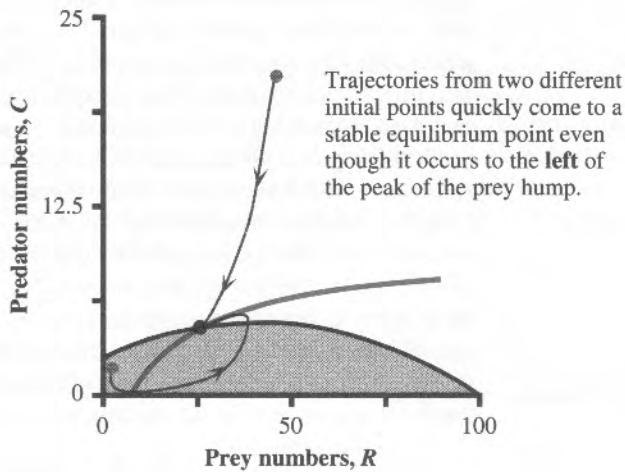
With predator self-interference the predator zero-isocline is no longer vertical.



Conclusion: The fewer predators, the less time they spend squabbling with each other, and thus the more time they spend foraging. Greater food intake, in turn, leads to higher predator birth rates.

Figure 12.33

Predator (red) and prey (black) zero-isoclines.



By setting Eq. (12.6) equal to zero, we may solve for the consumer zero-isocline,

$$C = \frac{kB(R) - d}{f}.$$

Now we plug in a type 2 functional response for $B(R)$ to get

$$C = \frac{1}{f} \left(\frac{kaR}{1 + aT_h R} - d \right). \quad (12.7)$$

The consumer zero-isocline bends to the right, as shown in Figure 12.32.

The effect of the incorporation of predator self-interference on the overall dynamics is stabilizing since now predators have a self-limitation in addition to the limitation set by resources (Figure 12.33).

This is not to say that predator interference necessarily leads to stable points and eliminates limit cycles but only that, if it is sufficiently strong, it has this potential to do so, as Figure 12.34 illustrates.

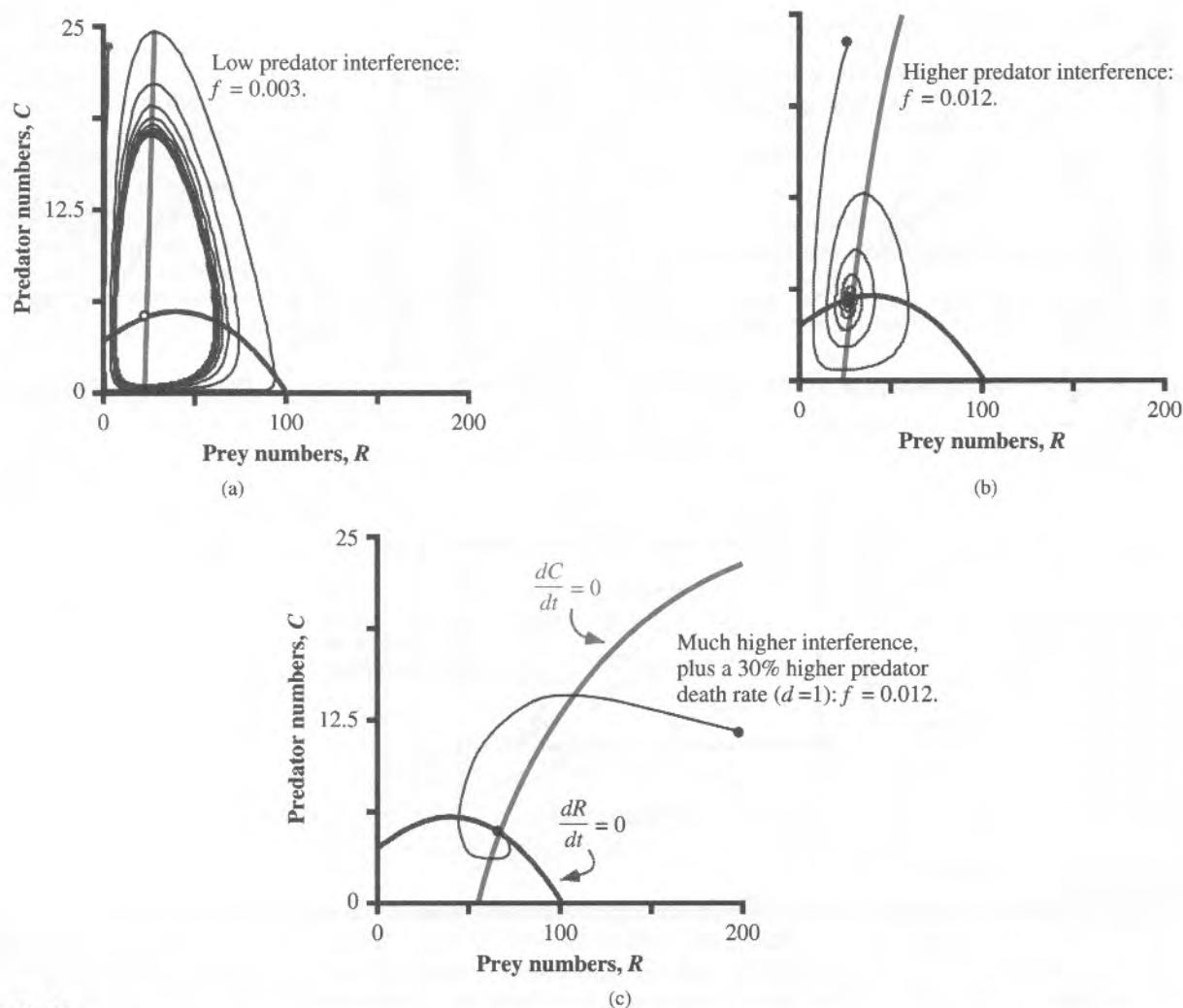


Figure 12.34

(a) Even with a low predator interference rate, f , the system has a stable limit cycle. (b) Predator interference is increased, which leads to a stable feasible equilibrium point even though this point falls to the left of the peak of the prey zero-isocline. (c) The predator death rate is increased by 30% so that the equilibrium point now falls to the right of the prey peak. The trajectory quickly reaches the feasible equilibrium point. All trajectories begin at the grey dots. Other parameters are $a = 0.06$, $k = 1$, $d = 0.7$, $r = 0.2$, $K = 100$, and $T_h = 0.7$. The predator zero-isocline is given by Eq. (12.7).

Exercise: We have been using a graphical argument based on the superimposition of a logistic prey recruitment curve and combined predator consumption curves (e.g. Figure 10.14), producing a picture of resource dynamics, which we then used to account for the instability of the two-species equilibrium point when it lies to the left of the peak of the prey zero-isocline. While this is valid when the predator zero-isocline is vertical, we have now seen that it falls apart when predator self-interactions are present, for example, if the sheep of Chapter 10 interfered with one another in grazing disputes. How does predator interference qualitatively allow for the stability of equilibrium points even if they lie to the left of the peak of the prey zero-isocline?

In Chapter 5, we explored the consequences of an Allee effect on the population dynamics of a single species. We now add an Allee effect to prey growth in the context of predator–prey interactions. To do this we adjust the prey’s logistic growth so that per capita prey growth at low prey densities is negative, as illustrated in Figure 12.35.

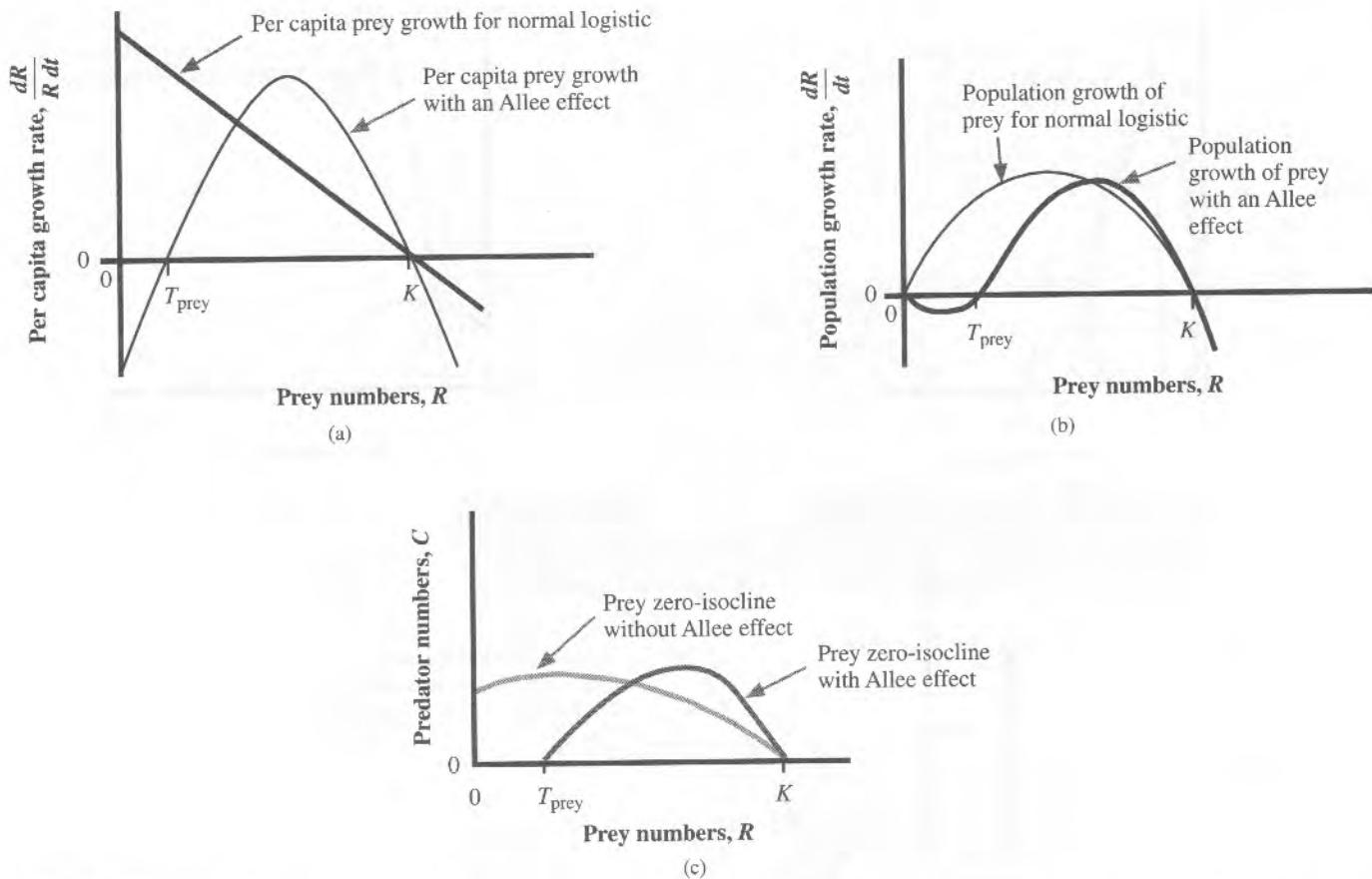


Figure 12.35

An Allee effect for the prey changes its zero-isocline. (a) The prey's per capita growth rate may be reduced at low prey numbers because it is harder to find mates, to forage solitarily, or to defend against predators. This is called an **Allee effect**. Prey numbers must exceed the threshold level, T_{prey} , for positive growth. At high densities, crowding leads to declines in per capita growth as before. (b) Population growth curves for the logistic compared to an Allee effect. The curve in (a) is multiplied by R . (c) When the Allee effect in (b) is combined with consumption by a predator with a type 2 functional response, the result is to shift the prey zero-isocline to the right. Prey growth is negative when prey numbers are below T_{prey} .

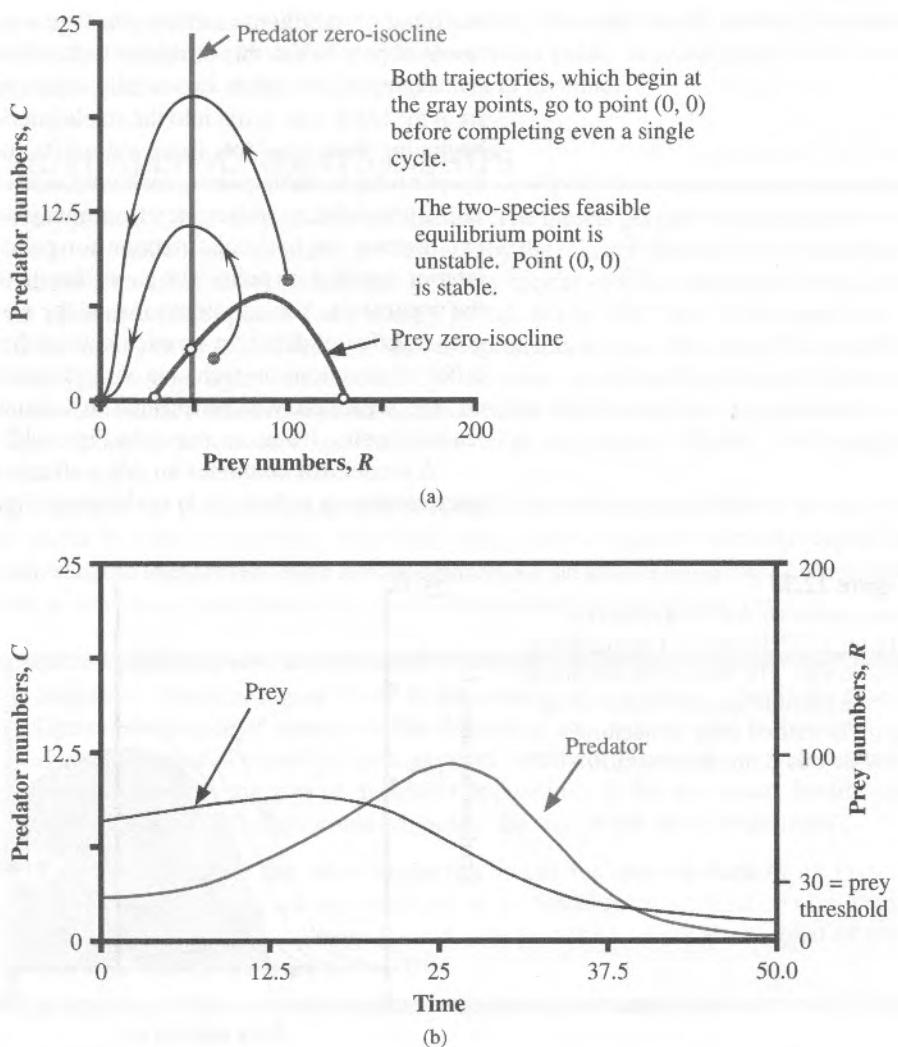
Figure 12.36 combines the prey zero-isocline in Figure 12.35 with a predator zero-isocline and shows some sample trajectories (again assuming a type 2 functional response). The result is a typical vertical predator zero-isocline with an unstable interior equilibrium point if it intersects on the left of the prey peak. Now, however, unlike the situation in Figure 12.20 without an Allee effect, here there is no stable limit cycle. All the trajectories lead to the extinction of both predator and prey. Point $(0, 0)$ is globally stable.

But, as before, if the predator zero-isocline lies to the right of the prey peak, the interior equilibrium point is locally stable, as shown in Figure 12.37. But point $(0, 0)$ is also locally stable. In short, the incorporation of an Allee effect eliminates the possibility of limit cycles in this model. Moreover, if the intersection of the predator and prey zero-isoclines occurs to the right of the prey hump, stable coexistence is possible, but if the intersection occurs to the left of the prey hump, the prey and predator crash to extinction. Once the predators bring the prey down to very low numbers, even if the predators subsequently become extinct, the prey still decline from the Allee effect; their numbers are now below the level necessary for positive growth.

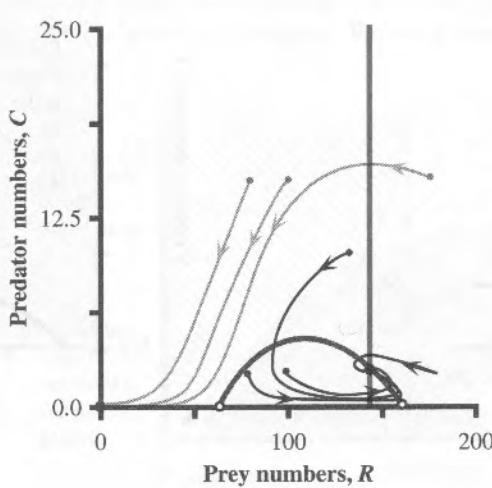
Note that point $(0, 0)$ is also stable in Figure 12.37. The prey's social facilitation (Allee effect) means that prey are more prone to extinction if their numbers become low. Even if this prey were reintroduced to an area where predators are absent, it would not be successful unless the number of introduced individuals was above the left-most

Figure 12.36

Prey have an Allee effect and the predators have a type 2 functional response. (a) In the phase-space diagram the interior equilibrium point occurs to the left of the prey peak. (b) Time course of the lowermost trajectory on the phase-space diagram in (a). Other parameters are $k = 0.8$, $a = 0.02$, $r = 0.2$, $K = 130$, $T_h = 1$, $d = 0.4$, and $T = 30$.

**Figure 12.37**

The prey has an Allee effect, and the predator has a type 2 functional response. The predator has a lower encounter rate or a higher death rate than in Figure 12.36; hence its zero-isocline has shifted to the right. In this case, there is a stable feasible interior equilibrium. The point $(0, 0)$ is still locally stable. Starting points are shown as dots. Trajectories are black or grey curves. Starting points that lead to point $(0, 0)$ are shown in gray. Now, however, the interior equilibrium point represents an alternative domain of attraction. Starting points that lead to the stable interior equilibrium point, where the zero-isoclines cross, are shown in black. Other parameters are $k = 0.9$, $a = 0.02$, $r = 0.12$, $K = 160$, $T_h = 1$, $d = 0.66$, and $T = 60$.



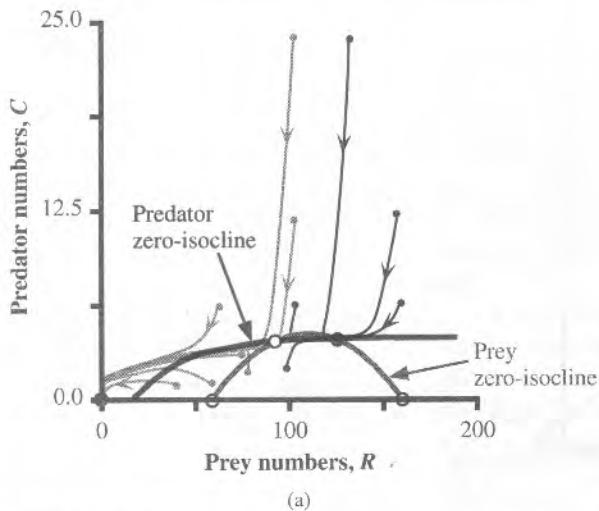
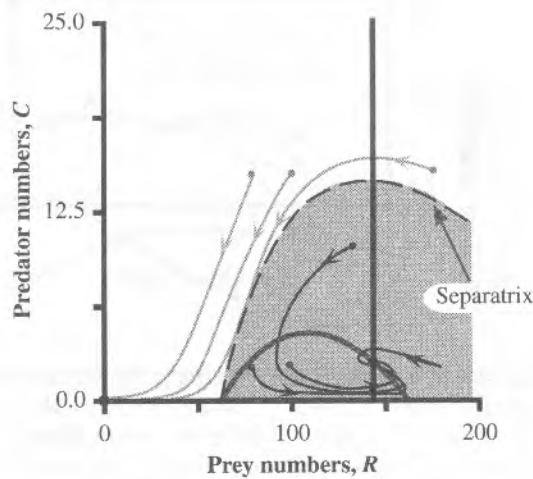
threshold of their zero-isocline (see Figure 12.37). Since point $(0, 0)$ is locally stable, levels of prey below this threshold will only decline further to 0.

Figure 12.37 shows two locally stable equilibrium points. Trajectories that begin from the black dots spiral into the stable interior equilibrium point, while starting points beginning from grey dots move toward $(0, 0)$. We have already discussed the possibility of multiple stable points, each with some domain of attraction (see Chapters 5 and 10). By simulating trajectories from many points, the state space can be divided into two regions: the basin of attraction for point $(0, 0)$ and the basin of attraction for the interior equilibrium point. The curve that divides these two basins of attraction is called the **separatrix**. You can think of it as the watershed line of a mountain range. Runoff goes a different direction on each side of the watershed line, just as trajectories go in different directions on each side of the separatrix. For most ecologically plausible models, the separatrix will be difficult to calculate analytically, but it can be determined readily by simulation, as shown in Figure 12.38.

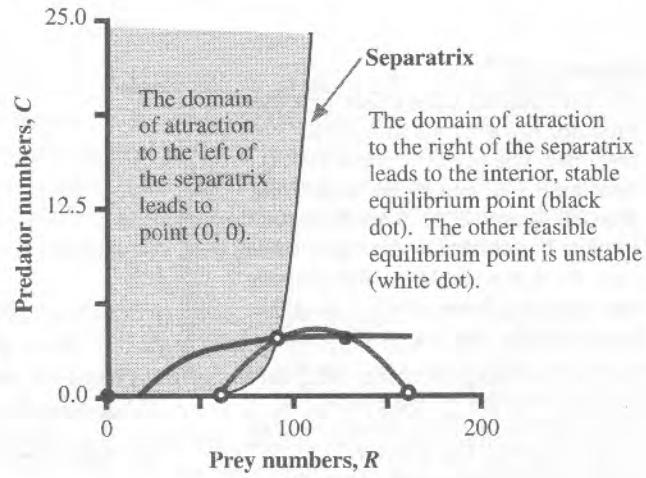
A model that combines an Allee effect in the prey with very strong predator self-interference (as in Box 12.3) is shown in Figure 12.39. This model has one stable and

Figure 12.38

The separatrix for the system in Figure 12.37, based on tracing many trajectories. The domain of attraction for the feasible interior equilibrium point is shaded grey. Trajectories outside this domain go to $(0, 0)$.



(a)



(b)

Figure 12.39

Predators have a type 2 functional response, and they also interfere strongly with one another; prey have an Allee effect. (a) Of the several trajectories shown, some (gray) end up at $(0, 0)$ and others (black) end up at the stable interior equilibrium point (black circle). There is also an unstable interior equilibrium point (open circle). (b) As is generally the case, the separatrix between the two domains of attraction intersects the unstable equilibrium points. Other parameters are $k = 1$, $a = 0.08$, $r = 0.2$, $K = 160$, $T_h = 0.7$, $d = 0.5$, $T = 60$, and $f = 0.2$.

one unstable interior equilibrium point. Point (0, 0) is also locally stable. The separatrix runs through the unstable interior equilibrium point. Its exact shape is influenced by the values specified for several parameters in the model.

MUTUALISTIC RELATIONSHIPS

Many plants depend on insects for pollination. The insects get resources from nectar and sometimes pollen, and the plants are fertilized by the transfer of pollen from other plants. Each species in a plant-pollinator pair probably requires a minimum density of the other for existence. Each species can probably be satiated by the other; plants need only so many insects to enable successful sexual reproduction—and they may be limited by other factors (e.g., light, nutrients, and space). Insects may also be limited by resources other than nectar (or pollen supplies), such as larval food, warm days for growth, or suitable habitat space for breeding. The zero-isocline depiction in Figure 12.40 integrates these features.

Despite the positive interspecific feedback inherent in any mutualistic relationship, a stable feasible equilibrium point may exist due to negative (density dependent) intraspecific interactions. Note too the direction of the arrows in Figure 12.40, suggesting an absence of oscillatory trajectories in these mutualistic interactions.

Exercise: Consider Figure 12.40. In the absence of any plants, what is the equilibrium abundance of insects? In the absence of any insects, what is the equilibrium abundance of plants? If the maximum density of plants were doubled, what would happen to the size of the insect population? If the maximum density of plants were halved, what would happen to the size of the insect population?

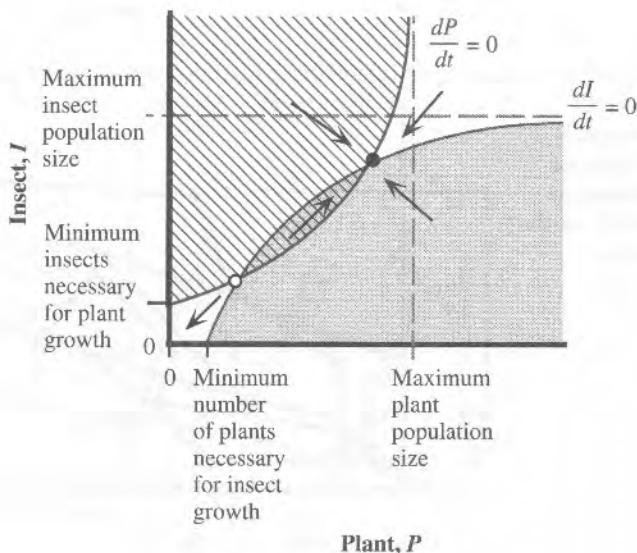
Exercise: Compare the relative selective forces for specialization of an insect species to one flower species compared to the forces for specialization of a plant species to one insect pollinator species. Are these two forces about equal or are they lopsided in one direction?

An Example of a Predator-Prey Cycle in Nature

Snowshoe hares and their lynx predators are found primarily in the boreal zone of the northern United States. Charles Elton (1942) accumulated data on the trapping results of the Hudson Bay Company. We have already shown the 10-year lynx cycles in

Figure 12.40

A zero-isocline depiction for a plant-pollinator interaction. As usual the hatched regions yield positive growth rates. Each species has internal self-damping as well as a positive interspecific effect.



Chapter 6. In Figure 12.41, these data for lynx are superimposed on the population fluctuations of the snowshoe hare. Note the two different scales for the y axis. We cannot scale these numbers to absolute population densities because we do not know what area these pelt returns encompass and exactly how trap success for each species is related to population density. However, if we assume that hares and lynx have equal trapping rates, then relatively speaking, hare numbers are about twenty-fold higher than lynx numbers.

Are these hare–lynx cycles consistent with the limit cycles that we explored earlier in this chapter? For such limit cycles, it is the interaction of predator and prey that drives the cycle, rather than the predator simply riding out a cycle that the prey would make in their absence.

Some have argued that these cycles are not predator–prey limit cycles since the hare seem to cycle on a 10-year period in the absence of lynx on Anticosti Island, Quebec. However, observations indicate that the amplitude of the cycles there is not as great as on the mainland. Moreover, it could be that alternative predators on the island (e.g., fox) compensate for the absence of lynx and drive the hare cycle anyway. In fact, 10-year cycles are a common feature of vertebrate populations in the boreal zone and are evident in muskrats, foxes, coyotes, skunks, martens, mink, fishers, and wolverines (Finnerty 1980).

Gilpin (1972) plotted the lynx–hare data from 1875 to 1906 in predator–prey phase space. The results are shown in Figure 12.42; the different colors separate different cycles.

Our theory holds that predator–prey cycles should run counterclockwise. Surprisingly, the cycles here seem to be in the shape of a figure 8, and the biggest lobe of the 8 is running clockwise. This seems to imply the nonsensible result that hares eat lynx! Perhaps, then, this is not a predator–prey driven cycle. Yet, even if lynx numbers were

Figure 12.41

Hare–lynx cycles from fur returns to the Hudson Bay company. After Elton (1942).

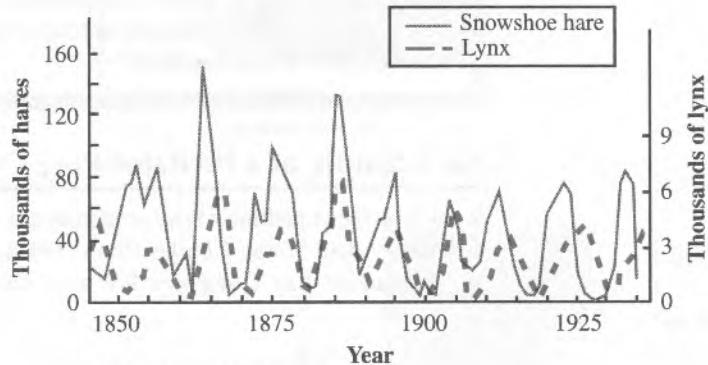
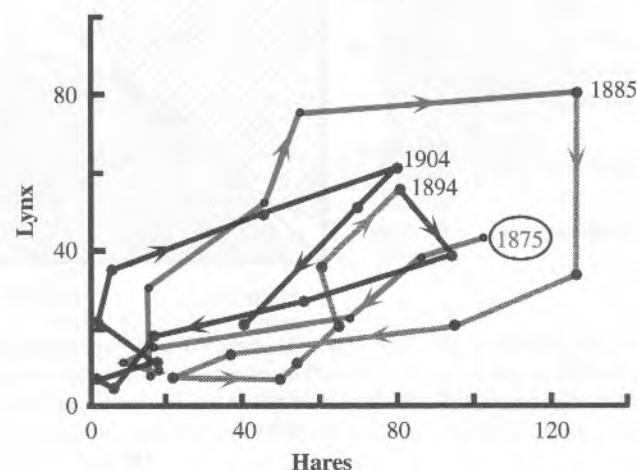


Figure 12.42

Snowshoe hare and lynx numbers from 1875 to 1906 plotted in phase space. After Gilpin (1972) based on data from Charles Elton (1942) on the fur returns to the Hudson Bay Company.



simply tracking the number of hares, the phase of the lynx cycles would still lag behind the phase of the hare cycles (not be ahead of them). Gilpin suggested that hare might be serving as vectors or reservoirs for diseases that were transmitted to lynx. Another possibility is that trappers wait for hare populations to increase before going out to trap either hares or lynx. This would bias the data, making it appear as if hares lag behind lynx. Some support for this explanation comes from more recent studies where hare and lynx counts through one cycle are determined by scientists not trappers (Boutin et al. 1995). The lynx clearly follow the hare cycle, and in phase space the cycle is counter-clockwise, as theory predicts and as shown in Figure 12.43.

Perhaps the most difficult feature of these cycles to reconcile with predator-prey theory is that so many different predators and prey have the same cycle period, 10 years, although they may be out of phase with each other by a few years. Even some forest moths show a similar 10-year cycle, as depicted in Figure 12.44. Myers (1988) suggests that these cycles may be caused by epidemics of disease. These different species with 10 year cycles have different generation times, death rates, birth rates and life histories, so it is not difficult to understand how the cycles may be out of phase.

However, in the predator-prey theory that we just developed, these same parameters also influence cycle period. Thus the paradox: Why are these very different predators all expressing approximately the same period? Perhaps some still unknown external force is synchronizing or entraining the cycles to bring these several different species into the same period. Sinclair et al. (1993) used evidence from tree rings and ice cores to show that 10-year solar-spot cycles may be a factor influencing weather and thus playing this role.

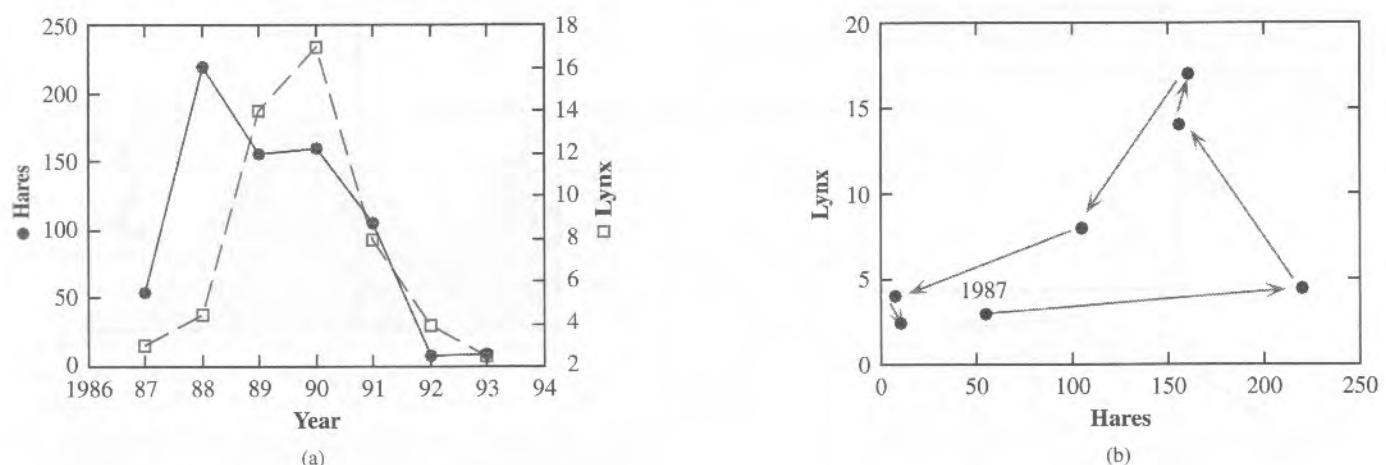
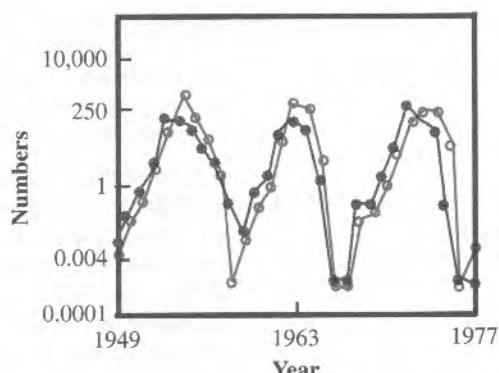


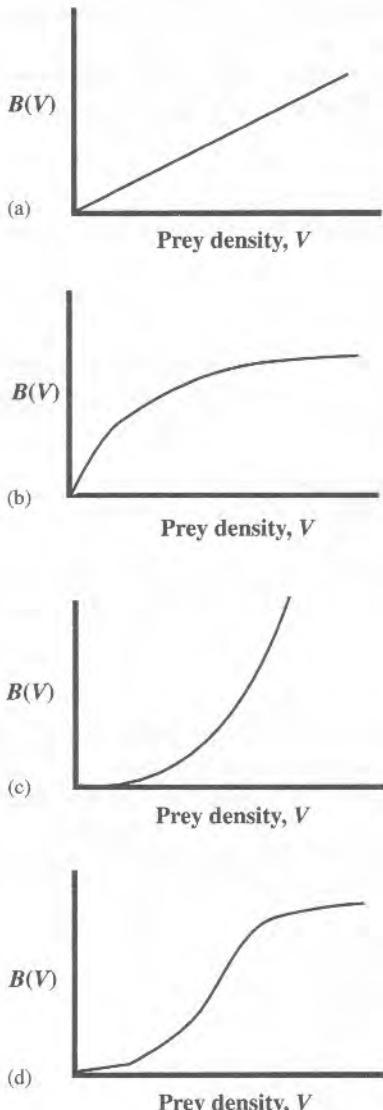
Figure 12.43
A hare-lynx cycle from 1986 to 1993 in the Yukon (from Boutin et al. 1995): (a) Time course and (b) trajectory in phase space. Densities are numbers per 100 km². Hare data are the average of three control grids, each 32.5 km² in area.

Figure 12.44
Population oscillations of the larch budmoth (*Zeiraphera diniana*) at two sites in the Engadine valley of Switzerland. After Myers (1988).



PROBLEMS

- Suppose that the prey equation, Eq. (d) in Box 12.2, included an additional term for a density independent death rate. How would this affect the interior equilibrium prey density, predator density, and their stability?
- Suppose that the prey equation, Eq. (d) in Box 12.2, had a θ term to the recruitment of prey, $1 - (R/K)^{\theta}$. Draw a qualitative sketch of the prey zero-isocline for θ greater than 1 and for θ less than 1.
- Draw the predator and prey zero-isoclines for a situation where the predators have a type 2 functional response and a numerical response dominated by an Allee effect at low predator densities and a self-interference effect at high densities. The prey recruitment is logistic. Evaluate the stability of the various equilibrium points.
- Consider these four alternative shapes for a predator's functional response (plotted as $B(V)$).



- Which of the four functional responses is most stabilizing for a predator-prey interaction? Circle one: A, B, C, D.

c. Which is a type 2 functional response? Circle one: A, B, C, D.

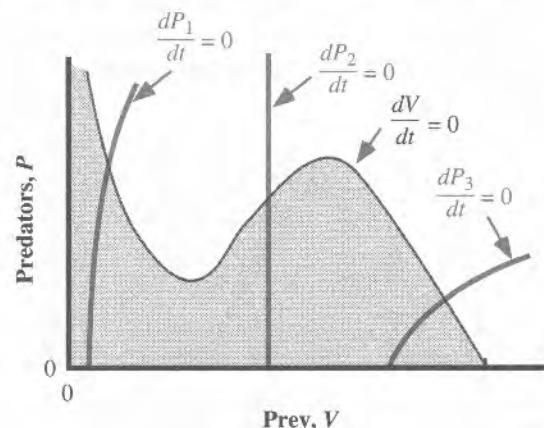
- For which functional responses does the risk of predation for an individual prey drop to zero as prey numbers climb toward infinity? Circle the correct letter(s): A, B, C, D.

- For which functional responses does the risk of predation for an individual prey increase as prey numbers climb toward infinity? Circle the correct letter(s): A, B, C, D.

- If there were alternative prey for the predator, which functional response curve would most likely result in prey switching? Circle one: A, B, C, D.

- For each of the four cases, draw the prey and predator zero-isoclines in state space. Assume that the prey population grows logistically in the absence of the predators and that the predator's per capita growth rate depends only on resource abundance (not predator abundance). Shade the regions of positive population growth and remember to label the zero-isoclines.

- The following diagram depicts the zero-isoclines of a predator-prey system with three alternative predators, P_i feeding on the same prey.



Rank the three alternative predators from highest to lowest in terms of:

- Predator density at the interior two-species equilibrium point.

- Predator self-interference rates.

- Stability of the two-species equilibrium point.

- Predator per capita death rate.

- Draw the time course for the prey population when predator 2 is introduced at very low numbers to the prey population at its carrying capacity. (All the other predators are completely absent.)

- Repeat the plot in (e), but now draw the time course for the prey population when predator 1 is introduced at very low numbers to the prey population at its carrying capacity. (All the other predators are completely absent.)

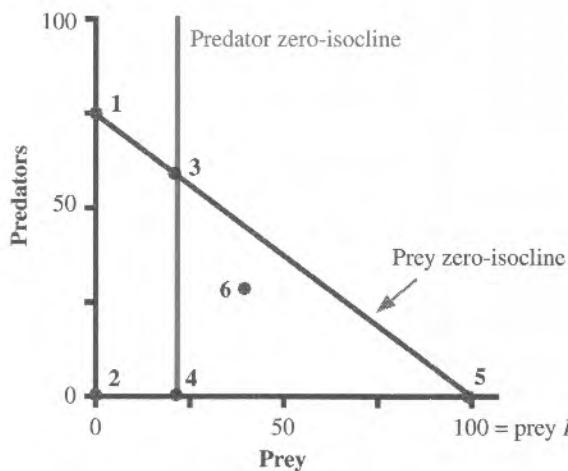
- Suppose that you have been doing some experiments in petri dishes containing kidney beans, a bean weevil that lays its eggs in the beans, and a wasp species, A, that parasitizes the weevils. You do all your experiments in a carefully controlled temperature and humidity chamber. You observe that regardless of how many weevils and wasps that you start with, you always end up with an equilibrium number of about 100 weevils and 25 wasps. Now you find a new wasp species, B,

Answer the following questions.

- What are the units of $B(V)$?

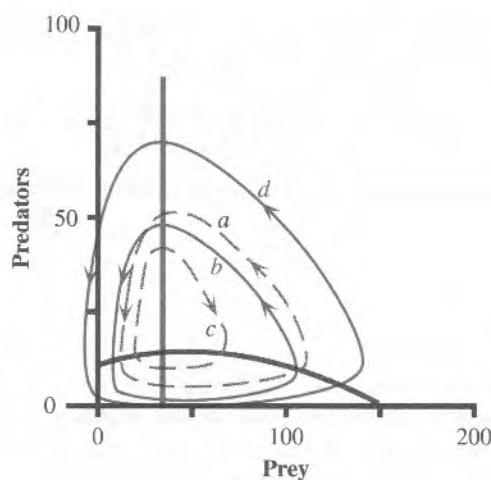
which can find and parasitize bean weevils at a faster rate. You repeat the experiments with this new wasp, B, (and not wasp species A), and observe that regardless of how many weevils and wasps you begin with, wasp species B's numbers and weevil numbers fluctuate with a fairly regular period and amplitude. Draw two zero-isocline diagrams, one for the weevil/wasp species A system and the other for the weevil/wasp species B system to explain these results.

7. Consider the following predator-prey zero-isoclines. Which of the six labeled points are equilibrium points? Which are locally stable? Which are globally stable? On the diagram, carefully draw the trajectory that begins at point 6.



8. Consider a deer population, D, and a tick population, T, that feeds exclusively on these deer. Deer numbers are food limited and deer grow logistically with a carrying capacity K . The ticks feed on the blood of deer but cause no deer mortality or changes in deer birth rates, regardless of tick numbers. Tick reproduction is proportional to the food supply (i.e., deer numbers). The tick population requires at least S deer before it can increase. In addition ticks have an upper limit to their population size, U , set by their own predators and parasites. Tick numbers cannot exceed U , even if deer numbers are extremely high. Draw zero-isoclines for deer and ticks consistent with this description; put deer numbers on the x axis and ticks on the y axis. Shade the regions of positive growth and place the points U , S , and K on the figure. Are deer tick-limited? Are ticks deer-limited? Are deer numbers stable in the absence of ticks? Is there a feasible interior equilibrium point? Is it stable?

9. Only one of the following four limit cycles (a , b , c , or d) represents a mathematically feasible cycle for a predator-prey system. Which is it and why?



10. Three predator species eat the same prey. The predators differ only in their death rates, d . Their zero-isoclines and that of the prey are as shown. Suppose that this system is initiated at equal numbers of all three predators ($P_i = 2$ for all i) and prey = 200. As time goes on, which predator species will prevail? What will happen to the prey population? Suppose that the predators represented three different genotypes at the same locus $P_1 = AA$, $P_2 = Aa$, and $P_3 = aa$. What happens to the gene frequency of A as time goes on? What happens to the total abundance of predators and prey?

