

11

The Mechanics of Predation

As a prey population grows, predators respond locally in two ways. First, each predator potentially increases its rate of prey consumption (the predator's **functional response**). Second, with more to eat, predators have more energy and nutrients for reproduction, ultimately leading to higher predator numbers (the predator's **numerical response**, which we take up in Chapter 12). The functional response is more immediate while the numerical response requires some time to take effect; this time depends on the generation time of the predator. Here we develop a microscopic and economic look at predation by deriving the so-called **disk equation** and considering some choices that predators face in trying to maximize their prey intake.

THE DISK EQUATION

Our goal is to derive the shape of the functional response based on behavioral attributes of the predator. To begin, we describe an individual predator's foraging path as if the predator were a moving disk; the disk represents the two-dimensional sensory field of the predator as it searches for prey. The radius, r , of this sensory field will depend on the sensory acuity of the predator and also on the "visibility" of the prey. For example, large, brightly colored, smelly, and noisy prey species will be more obvious to the predator than small, cryptic, less smelly, and silent prey species. Consider the situations illustrated in Figures 11.1 and 11.2.

For a single foraging predator, what is the relationship between prey density, V (prey/area), and the consumption rate of those prey by the predator? We introduced three types of functional responses in Chapter 10 (illustrated in Figure 10.1). Now we derive the shape and formulas for these functional responses based on biological attributes of the predator.

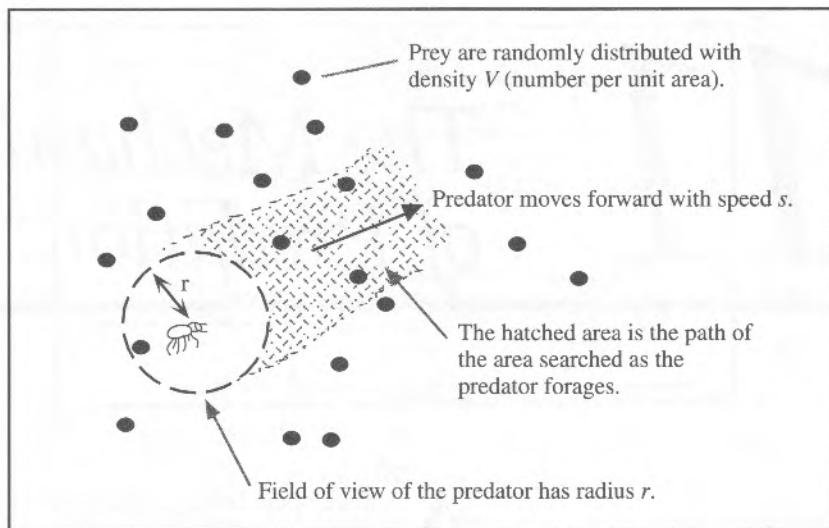
We take a geometric approach. As Figures 11.1 and 11.2 illustrate, the area searched by the predator = shaded area in the figures = (predator speed)(sensory diameter)(time spent searching) = $s2rT_s$. (Units are (distance/time)(distance)(time) = (distance)² = area.) Finally, not all prey within this area may be detected by the predator. Some prey could be hidden at the time the predator moves through. We therefore need to introduce another constant, the detectability fraction, k (ranging from 0 to 1) to express this limitation.

For notational simplicity we lump the constants $ks2r$ into a single constant a , **the prey encounter rate**, which expresses the number of prey encountered by a single predator per time period that it spends searching. Then we have

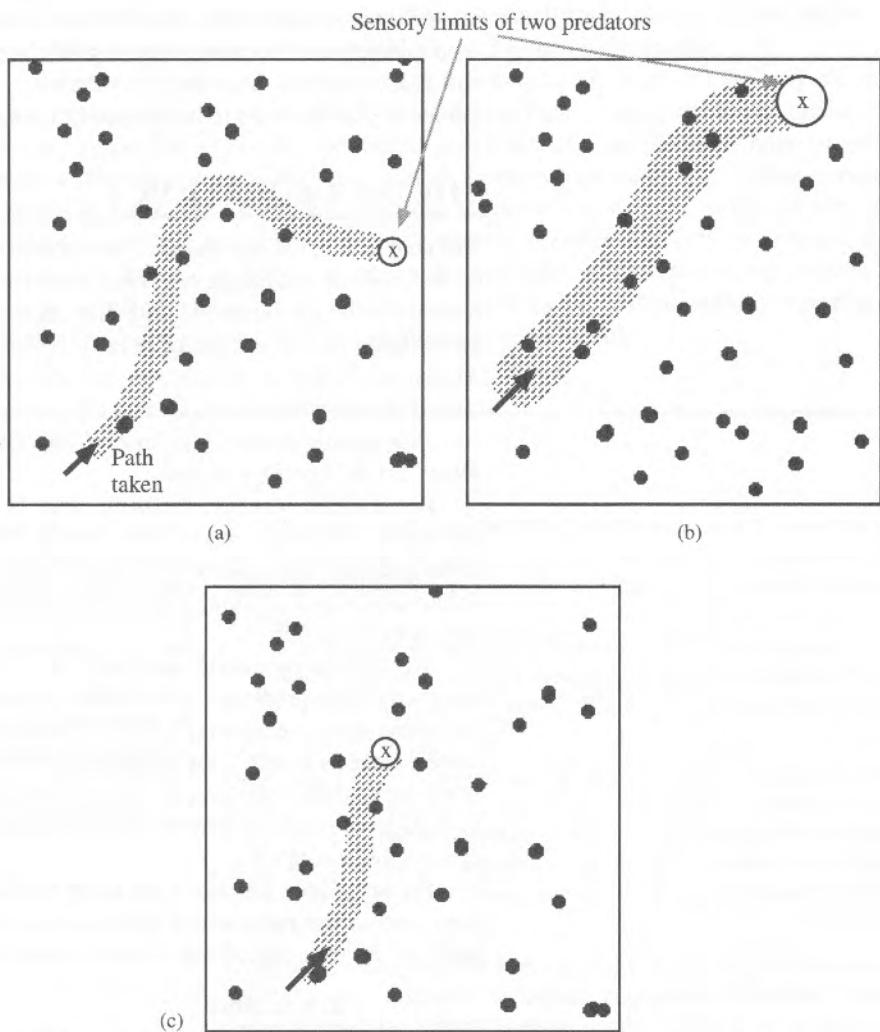
$$\left[\begin{array}{l} \text{The number} \\ \text{of prey} \\ \text{encountered} \end{array} \right] = [\text{detectability}] [\text{area searched}] \left[\begin{array}{l} \text{prey per} \\ \text{unit area} \end{array} \right].$$

Figure 11.1

A predatory beetle searching for randomly distributed prey. The area searched is determined by the predator's velocity and its sensory field.

**Figure 11.2**

(a) A predator with a narrow sensory radius. (b) A predator with a wide sensory radius, (c) a slower moving predator. Increasing the spatial sensory field leads to a larger swath of area searched per unit time. Similarly, all else being equal, faster search velocities lead to a larger area searched.



$$\text{Number of prey on path} = (\text{area searched})(\text{prey density}) = (\text{search velocity})(\text{sensory diameter})(\text{time spent searching})(\text{prey density})$$

Or, symbolically, using V for prey density and V_a for the number of prey encountered during a search of duration T_s , we get

$$V_a = aT_s V. \quad (11.1)$$

We'll assume that the predator attempts to pursue all the prey that it detects, so V_a is also the number of prey chased or attacked. The predator, however, may be successful in subduing only some fraction f of the prey that it attacks, so the number of prey successfully captured, V_c , is

$$V_c = fV_a = faT_s V. \quad (11.2)$$

When all prey that are encountered are subdued, perhaps, because they put up no resistance, then $f = 1$.

The next step is to find an expression for the time spent searching, T_s , in terms of the total time available for feeding, T_t , in a day. The more prey that are encountered and attacked, the more time is devoted to chasing and then manipulating prey and the less time is available for the predator to search for new prey. We can express this trade-off in time allocation by allowing the time available for searching to be diminished by the time that is spent chasing and manipulating prey. If T_c is the average chase time per prey attacked (V_a) and T_m is the average manipulation time per prey captured (V_c), then search time is

$$\begin{array}{rcl} T_s & = & T_t - T_c V_a - T_m V_c \\ & = & T_t - T_c V_a - T_m f V_a. \\ \text{Time for} & \text{total} & \text{time spent} & \text{time spent} \\ \text{searching} & = & \text{time to} & - \text{chasing prey} & - \text{manipulating} \\ & & \text{feed} & \text{once they are} & \text{prey if they} \\ & & \text{encountered} & \text{subdued.} & \end{array} \quad (11.3)$$

Note that by this definition the total time feeding is simply partitioned into time spent searching and time spent pursuing and manipulating prey. We may also write Eq. (11.3) as

$$T_s = T_t - V_a(T_c + fT_m). \quad (11.4)$$

With the assumption that f is a constant, we may combine the chase and manipulating times to produce an overall prey handling time of $T_h = T_c + fT_m$. Then Eq. (11.4) becomes

$$T_s = T_t - V_a T_h. \quad (11.5)$$

Substituting T_s from Eq. (11.5) into Eq. (11.1), we arrive at a new equation for the number of prey attacked, V_a , per total time available per day (rather than just per search time):¹

$$V_a = aV(T_t - T_h V_a). \quad (11.6)$$

To complete the development Eq. (11.6) needs to be solved for V_a :

$$V_a = aVT_t - aVT_h V_a,$$

$$V_a + aVT_h V_a = aVT_t,$$

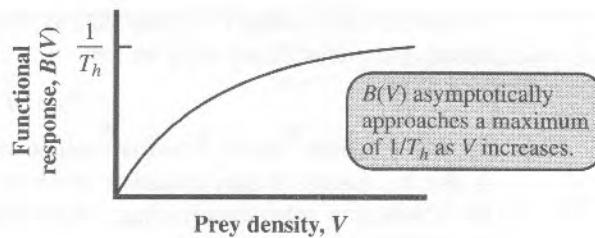
and

$$V_a = \frac{aVT_t}{1 + aT_h V}. \quad (11.7)$$

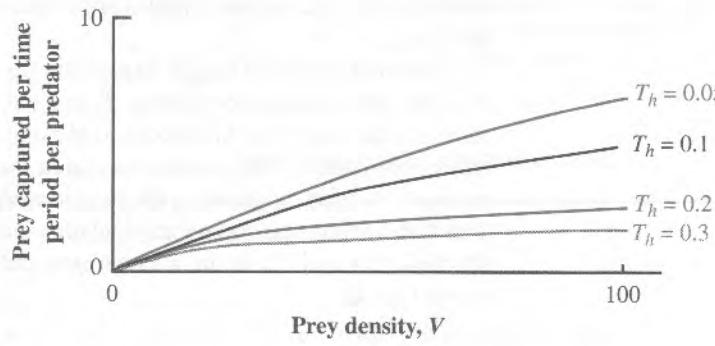
1. There is an additional complexity that we gloss over here. Every prey attacked and consumed leaves one less prey available; thus the density of prey changes over time. Moreover, looking at the paths of the predator in Figure 11.2, you can see that, over a stretch of time, the trail of a randomly foraging predator would circle back on itself. The area searched the second time around would contain less prey. In discrete time models, these factors require careful adjustment of the equations. However, here we assume infinitesimally small time units and differential equations, where the density, V , is effectively constant.

Figure 11.3

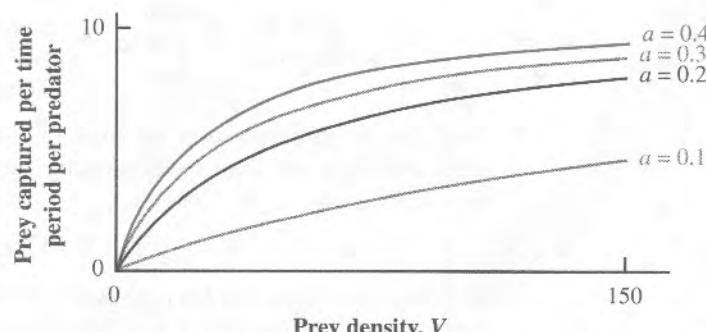
A type 2 functional response approaches an asymptote, which is the reciprocal of the handling time, T_h . The shorter the handling time, the higher is the maximum rate of food intake.

**Figure 11.4**

The effect of encounter rate, a , and handling time, T_h , on the shape of a type 2 functional response. (a) The encounter rates are the same for all these curves. All the functional responses have the same initial slope, but they become asymptotic at different prey capture rates. (b) All the handling times are the same ($T_h = 0.1$), but the encounter rates differ. All the curves will eventually reach the same asymptote, but they do so at different rates.



(a)



(b)

Equation (11.7) is called the **Holling disk equation** (Holling 1959) because it is based on a “moving” disk representing the predator’s moving sensory field (Figure 11.1). The functional response of a predator is the number of prey captured per predator per unit time, so it is simply Eq. (11.7) divided by T_h , or

$$\text{Functional response } B(V) = \frac{V_a(V)}{T_h} = \frac{aV}{1 + aT_h V}. \quad (11.8)$$

Equation (11.8) describes a type 2 functional response derived from “microscopic” considerations of predator behavior and time accounting. The parentheses indicate that the functional response is a function of prey density, as graphed in Figure 11.3.

To show that the maximum consumption rate is $1/T_h$, we divide both numerator and denominator of Eq. (11.8) by aV (the numerator). This yields

$$B(V) = \frac{1}{1/aV + T_h}. \quad (11.9)$$

As prey density, V , climbs to infinity, the first term in the denominator goes to zero, so the entire expression approaches $1/T_h$. The effect of different encounter rates and handling times on the rate that prey are consumed is illustrated graphically in Figure 11.4.

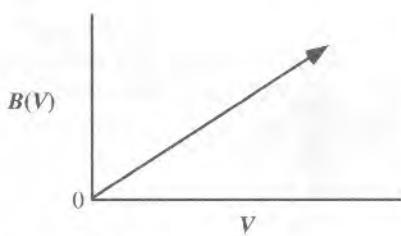


Figure 11.5
Linear (type 1) functional response. Ultimately, at high V , $B(V)$ may hit a maximum where it abruptly becomes flat.

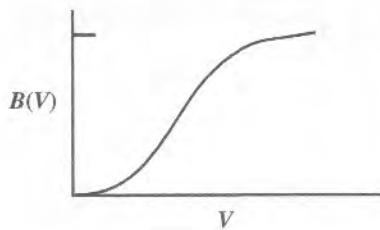


Figure 11.6
Type 3 functional response, as described by Eq. (11.11).

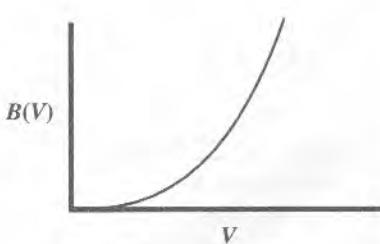


Figure 11.7
This functional response increases with the square of prey density.

Modifications to the Disk Equation

A type 1 functional response can be derived from the disk equation by assuming that the handling time is zero ($T_h = 0$). Then $B(V)$ will linearly increase with prey density, V . To see this, look at Eq. (11.9), but set T_h to zero to get

$$B(V) = \frac{1}{1/aV} = aV. \quad (11.10)$$

The functional response expressed in eq. (11.10) has a y intercept of 0 and increases linearly with slope a , as graphed in Figure 11.5. Even without any finite handling time, we might ultimately expect the consumption rate to hit some ceiling simply because the predator's gut will eventually become full.

For a type 3 functional response we assume that the encounter rate, a , is not constant across all prey densities but instead is an increasing function of V , so we write $a(V)$. This might be the case if predators gain experience with a particular prey when those prey are common, and this experience leads to increased prey detection rates. Predators might need the frequent reinforcement of high prey densities to recall their **search image** for the prey. With such a mental image, their sensory field effectively increases. The sigmoid curve of a type 3 functional response is achieved when $a(V)$ is a simple linear function, or $a(V) = aV$ in Eq. (11.8). Then

$$B(V) = \frac{V_a(V)}{T_t} = \frac{aVV}{1 + aVT_hV} = \frac{aV^2}{1 + aT_hV^2}. \quad (11.11)$$

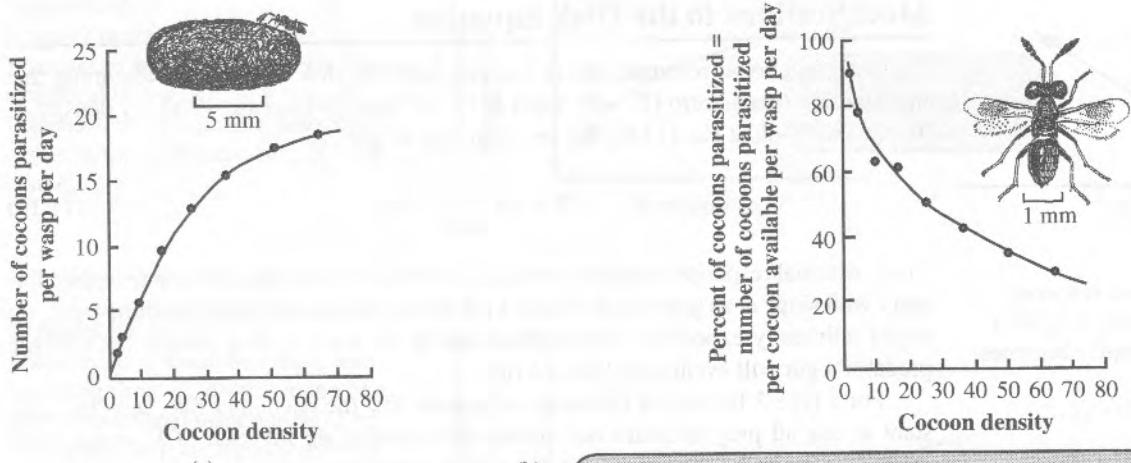
Note the similarity of Eq. (11.11) to Eq. (11.8) for the type 2 functional response. Yet the V^2 terms result in a functional response that is sigmoidal as depicted in Figure 11.6. Another reason that the encounter rate itself may increase with prey density is due to changes in the prey's detectability, k , with prey density, V . If prey hiding spots are limited, then as prey density increases a larger proportion of prey may be more exposed to the predator's sensory field. Again the result might be something like the curve shown in Figure 11.6.

Problem: For a type 3 functional response, derive the asymptotic value of $B(V)$ from Eq. (11.11).

The next functional response that we consider doesn't have a name in the ecological literature. It is probably biologically implausible since it never becomes asymptotic. It is worth considering, however, because it represents the case where $a(V) = aV$ (as for type 3) but the handling time $T_h = 0$ (as for the type 1). This functional response provides a very stabilizing situation for predator-prey dynamics because, as prey numbers climb, the predator's kill rate climbs even faster, as graphed in Figure 11.7. Thus prey outbreaks can be reduced by such a predator's functional response, even without any numerical response by the predator population.

So far, we've been looking at prey eaten from the predator's point of view. From the prey's point of view, we can define the probability that a *particular* prey is captured by a predator per unit time. This risk per prey can be calculated by dividing the functional response (which is in units of all prey eaten) by the prey density, V . An example of parasitism by a wasp on sawfly cocoons is shown in Figure 11.8.

Figure 11.9 summarizes the prey risk relationship for each functional response. For type 2 and 3 functional responses, the rate of prey capture increases with prey density but an *individual* prey has a lower probability of being captured at very high prey densities since the predator's functional response becomes maxed-out. Each predator's consumption cannot keep up with the increases in prey density and many prey go uneaten. The type 3 response shows the most complex behavior, since the S-shape approach to a maximum consumption rate leads to increases in risk at low prey density followed by declines in risk as prey density increases still more.



Conclusion: When cocoon density is relatively high, an individual cocoon is less likely to be parasitized because the wasps' time is tied up parasitizing other cocoons (i.e., the functional response approaches a maximum).

Figure 11.8

(a) The functional response of the chalcid wasp *Dahlbominus fuscipennis* parasitizing cocoons of the sawfly *Neodiprion setifer* by laying eggs on them in laboratory cages (Burnett 1956); sawflies are also a type of wasp. (b) The functional response from the vantage point of the cocoon: What is the risk of an individual cocoon being parasitized per day?

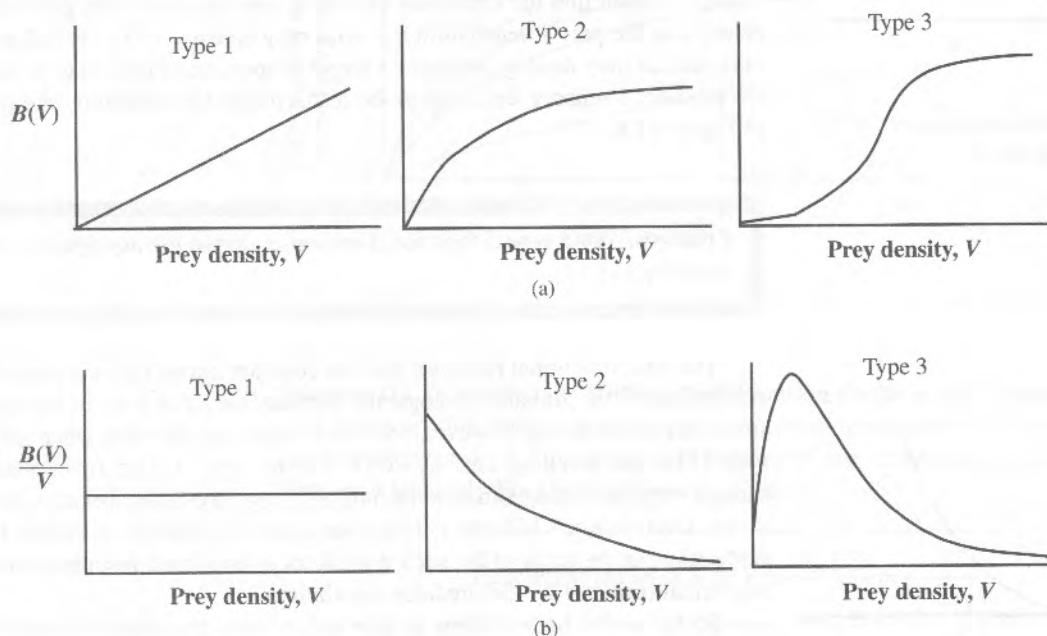


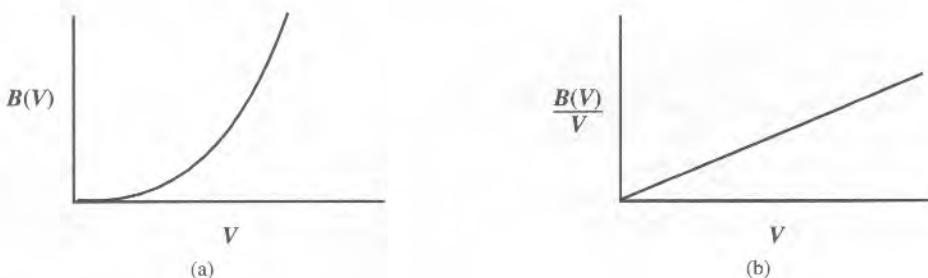
Figure 11.9

Summary of the relationship between prey consumption rates, $B(V)$, and prey consumption per prey available (individual prey risk): (a) Functional responses and (b) prey risk.

Problem: Show that a plot of prey risk for a type 1 functional response is equivalent to plotting the slope of the functional response at each prey density.

Figure 11.10

Another type of (a) functional response and (b) corresponding prey risk.



The comparable situation for the fourth type of functional response is shown in Figure 11.10. Unlike the other functional responses, as prey numbers increase, the prey's individual probability of being eaten continually increases.

MULTIPLE PREY ITEMS

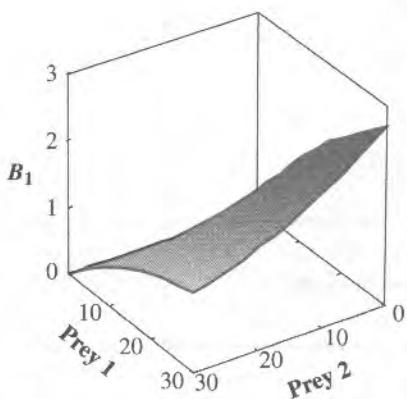
What happens when a predator has multiple types of prey, each with a distinct density V_1, V_2, V_3, \dots ? Now each time the predator stops to eat any one prey item, the time lost in handling that prey detracts from its search time for *all* types of prey. Therefore the functional response for V_1 , which we denote B_1 , will be a function of the abundances of each prey item, not just prey 1. We define a vector \mathbf{V} containing all the prey abundances as $\mathbf{V} = (V_1, V_2, V_3, \dots, V_n)$. Then

$$B_i(\mathbf{V}) = \frac{a_i(V_i)V_i}{1 + \sum a_j(V_j)V_j T_{hj}} \quad \text{for prey items } i = 1 \text{ to } n. \quad (11.12)$$

The notation of Eq. (11.12) allows a_i to be a constant or an unspecified increasing function of V_i , as would be the case for the type 3 functional response $a(V) = aV$.

Figure 11.11 shows an example of a functional response surface for prey 1 as a function of the densities of both prey 1 and prey 2 when a_i is a constant for both prey. Figure 11.11 is based on constant encounter rates; hence it yields a type 2 functional response surface. Note that the consumption rate of prey 1 increases with its own density but decreases with the abundance of prey 2. The more prey 2 available, the more prey 2 will be attacked, and therefore less time will be spent attacking prey 1.

Across the range of all possible densities of prey 1 and prey 2 we can also plot the *relative* consumption rates of the two prey species by the predator as a function of the preys' relative abundances rather than their absolute abundances. Figure 11.12 shows such a plot, using the parameters from the preceding example. Since prey species 2 is encountered more frequently than prey species 1 ($a_1 = 0.2$ and $a_2 = 0.4$), it is overrepresented in the diet of the predator.

**Figure 11.11**

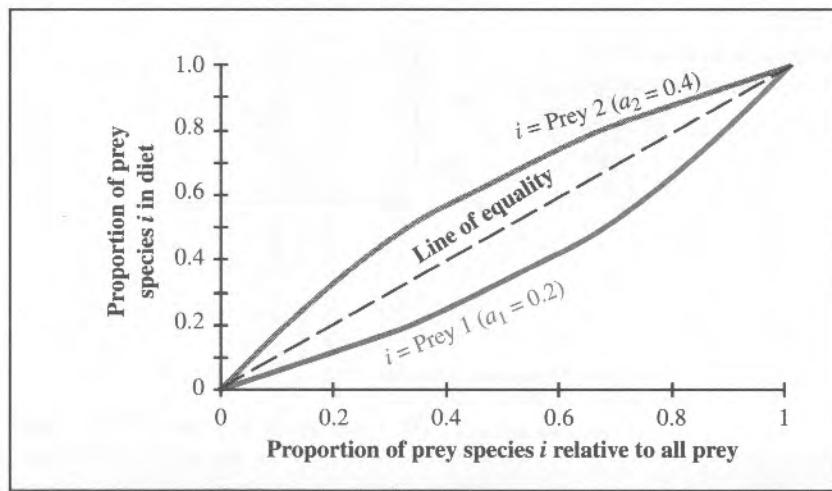
A functional response for prey 1 as a function of the abundance of prey 1 and prey 2 ($a_1 = 0.2$ and $a_2 = 0.4$; the handling times are $T_{h,1} = T_{h,2} = 0.2$).

Problem: Use Eq. (11.12) to show that the curves in Figure 11.12 do not depend on the absolute abundance of prey but only on their relative abundances. Also show that the curves are unaffected by the handling time values.

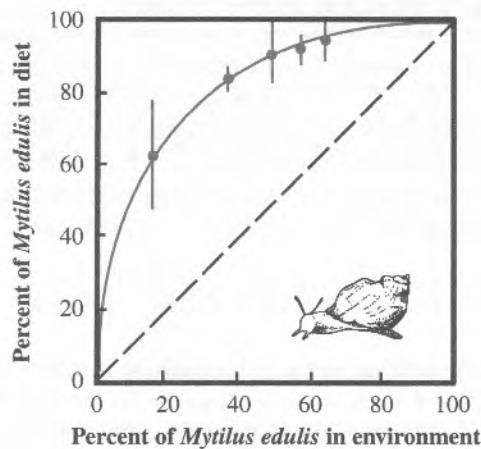
Up to now we have assumed that encounter rates, a_i , are simply influenced by predator velocity, sensory field, and the conspicuousness of the prey. However, the preference for one mussel over another shown by *Thais* snails is not easily explained by such factors. There is also an element of choice shown by the predator, as illustrated in Figure 11.13. The predator may prefer some prey species over others because more nutritious, has fewer defenses, or requires less handling time. Over evolutionary time, encounter rates and handling times may coevolve.

Figure 11.12

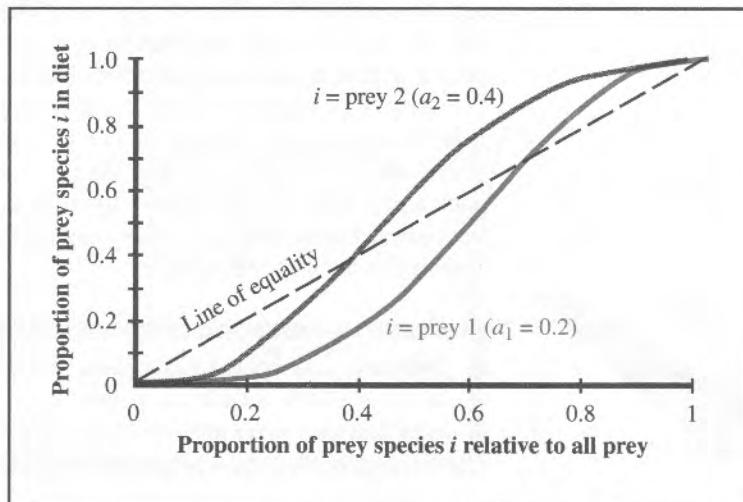
A predator consuming two prey with a type 2 functional response for both. The predator has a higher encounter rate for Prey 2 compared to Prey 1 ($a_2 > a_1$) and thus is more common in the diet for all values of prey ratios present in the field.

**Figure 11.13**

Predatory sea snails offered a diet of two mussels, *Mytilus edulis* and *M. californianus*. The average percent consumed (and standard errors) for each prey are shown. The snails prefer *M. edulis* regardless of its relative frequency in the environment (from Murdoch and Oaten 1975).

**Figure 11.14**

A predator with a type 3 functional response for two prey. Prey 2 is preferred over prey 1 ($a_2 > a_1$) and thus is more common in the diet for all values of prey ratios present in the field. For both prey, their consumption rate increases disproportionately as they become relatively more frequent up to the point that they are the most common prey in the diet.



If the functional responses are of the type 3 variety, then with the same parameters as in Figure 11.13, the plot would look like the plot shown in Figure 11.14. If the two prey species had the same encounter rates ($a_1 = a_2$) but different handling times, this would not lead to any difference in the functional response for the two prey. The numerator of Eq. (11.12) would be identical for both species; since it contains no term for handling time and the denominator is the same for both species. The additional handling

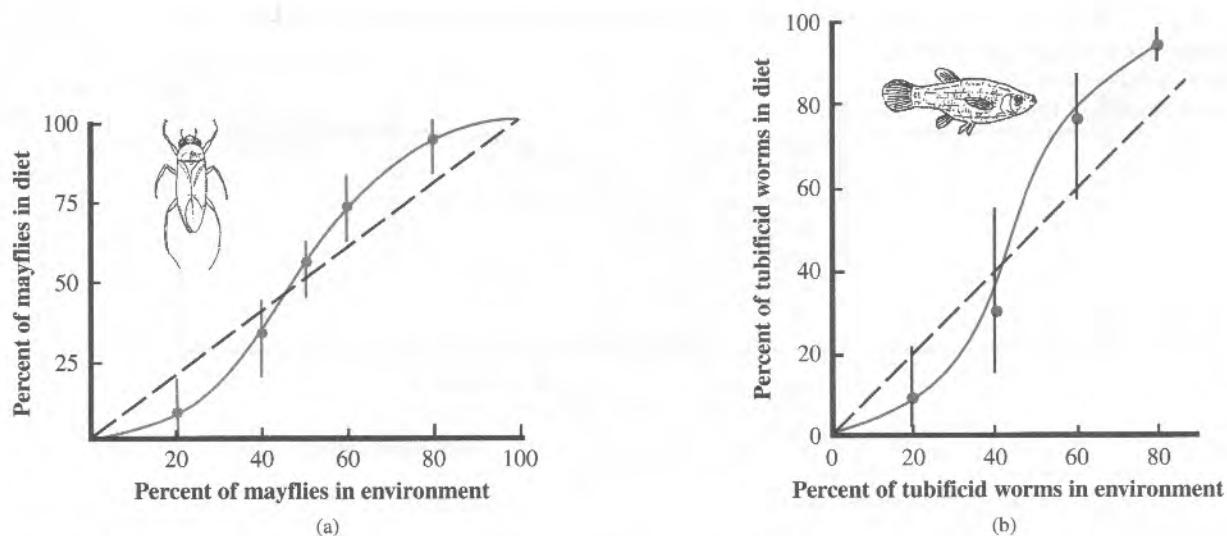


Figure 11.15

Switching predators. (a) Water bugs were presented with two types of prey—an isopod and larvae of the mayfly (Lawton et al. 1974). (b) Guppies feeding on a combination of fruitflies and tubificid worms (Murdoch and Oaten 1975).

time associated with one prey species subtracts equally from the search time available for hunting both prey species—hence identical plots.

An example of the S-shaped relative consumption curves from an experiment by Lawton et al. (1974) is shown in Figure 11.15. The investigators presented predacious water bugs with two types of prey, an isopod and larvae of the mayfly. Another example is provided by guppies feeding on a combination of fruitflies and tubificid worms (Murdoch and Oaten 1975).

An important ecological feature of type 3 functional responses for alternative prey items is that the predator takes a disproportionately larger proportion of whatever prey item tends to be the numerically most common in the environment (again refer to Figure 11.14 and compare the curves to the line of equality). This is called **predator switching**. Recall that we invoked the presence of search images to explain why encounter rates might increase with prey abundance. We now see that when this is the case, predator switching results. The community-level consequences are important. With switching, whenever one prey becomes rare relative to another—perhaps because it is an inferior competitor under present environmental conditions—the rare prey will experience relatively less predation than the more common prey. In this way, a relative competitive inferiority is compensated for by a relatively lower predation rate. This tendency for predator switching to give an advantage to the rarer of several competitors is very stabilizing in ecological systems since it may prevent one prey species from out-competing the others (Roughgarden and Feldman 1976).

FOOD DEPLETION (ADVANCED)

How long will it take an animal with a type 2 functional response to completely deplete the food in a patch? The situation is graphed in Figure 11.16.

The equation of a type 2 functional response is

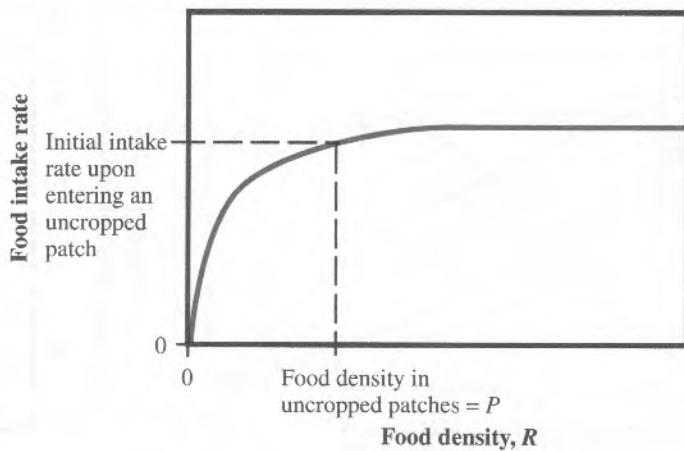
$$\text{Intake rate, } B(R) = \frac{aR}{1 + aT_h R}.$$

As food is consumed, its density, R , declines according to the rate of consumption:

$$\frac{dR}{dt} = -B(R). \quad (11.13)$$

Figure 11.16

Food intake rate is a type 2 functional response to food density in initially uncropped patches of food.



To find the time, T , it takes to reduce the patch from $R = P$ to $R = 0$, we need to solve this differential equation. We begin by rearranging Eq. (11.13) to separate the terms:

$$\frac{dR}{-B(R)} = dt.$$

Now we integrate each side; the patch begins at $R = P$ and is consumed to 0 as time t passes from 0 to T :

$$\int_P^0 \frac{dR}{-B(R)} = \int_0^T dt$$

or

$$\int_P^0 -\frac{1 + aT_h R}{aR} dR = T.$$

The left-hand side of this equation may be split into the sum of two integrals:

$$-\frac{1}{a} \int_P^0 \frac{1}{R} dR - \int_P^0 T_h dR = T.$$

After performing the integration we arrive at

$$T = \frac{\ln P - \ln 0}{a} + T_h (P - 0). \quad (11.14)$$

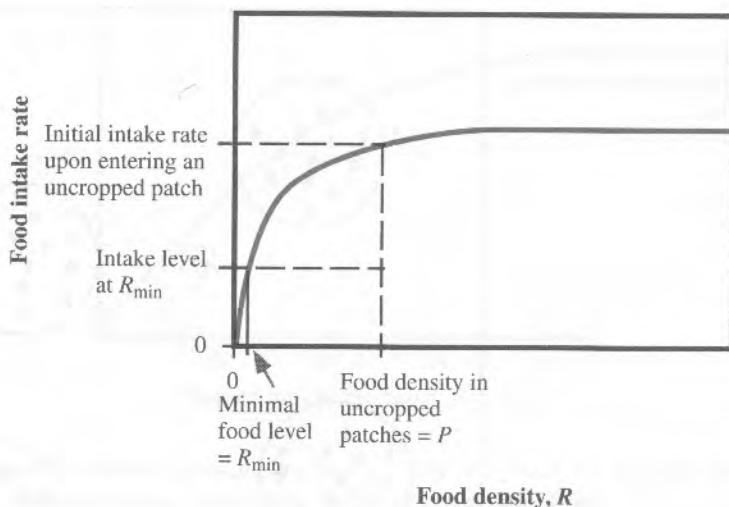
Since $\ln 0 = -\infty$, the time, T , needed to reduce the resources in the patch from P to 0 is infinite.

This result initially seems paradoxical, since the patch contains a finite amount of food and animals consume food at some finite rate. The problem is that the functional response $B(R)$ lets the consumption rate go to zero as food levels approach zero. As food density becomes smaller, the amount of food consumed per time unit becomes smaller, approaching zero, and food levels can thus only go to zero asymptotically in infinite time. This strange result is probably unrealistic. If an animal consumes the food to some minimal level, R_{\min} , greater than zero, then even if this level is very small—just a few specks of food—the equation will now have a finite solution for T , the time to reduce the food patch to this minimum level, as illustrated in Figure 11.17.

After all, we don't entirely "clean our plates" during a meal; we leave a tiny bit of residual food or grease on the plate, even if it is of microscopic proportions. Why should an animal spend increasingly longer times trying to reduce the food level in a single patch to zero if it could increase its food intake rate by moving to another patch where food had not yet been exploited?

Figure 11.17

Food intake rate as a function of food density. Beginning with uncropped patches of food having P food units, food can be harvested to a minimal level, R_{\min} .



If an animal gives up searching for food in a patch when food levels in that patch fall to some minimum level, R_{\min} , then the give-up time, T (the time it takes to reduce the food level in the patch from P to R_{\min}), from Eq. (11.14), is

$$T = \frac{\ln P - \ln R_{\min}}{a} + T_h (P - R_{\min}). \quad (11.15)$$

Continuing with this line of logic we might imagine that animals behave in an optimal way with respect to the parameter R_{\min} . An animal that is maximizing energy intake per unit time would want to leave a patch when its expectation of further food intake by leaving and finding a new patch with more food exceeds the expected food intake rate from staying in the same patch and depleting it still further. An optimal level of R_{\min} could be determined if we knew the time it takes, on average, to find a new patch, the food density in each patch, and the shape of the functional response. In the next section we show how this optimal “give-up” time can be calculated.

OPTIMAL GIVE-UP TIMES (ADVANCED)

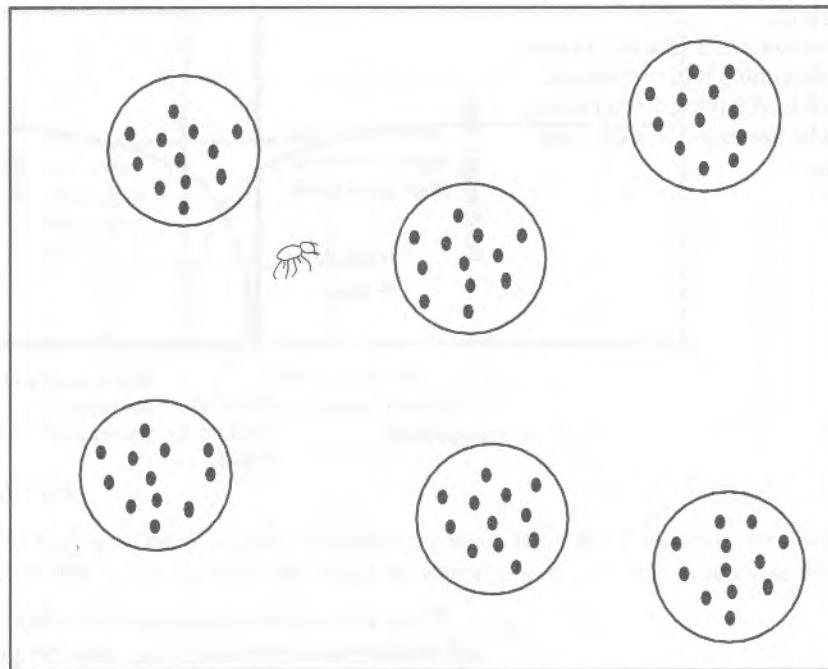
When should an animal stop foraging in a patch and move on to look for another? Consider the beetle foraging on discrete patches of food in Figure 11.18. Let's assume that the animal, through its previous experience in the habitat, knows the average rate of capture to expect in the entire habitat and that it mentally compares this to its current rate of food intake within the patch where it is now foraging. If it has these cognitive powers, then it should leave its present patch when its rate of food intake falls below the anticipated average rate of food intake over the entire habitat. This is called the **marginal value theorem** for optimal foraging (Charnov 1976). As an animal stays in a patch, its rate of food intake can only decline. But, if the animal moves, there will be a period when food intake is zero as it searches for a new patch. Once that patch is found, food intake rates can potentially increase.

To solve for the optimal give-up time, we first need to assess the rate of food intake in a patch as a function of the time spent foraging in that patch. Let's assume that the depletion rates from current foraging far outstrip the rate of new recruitment of food to the patch so that every bite of food consumed leaves that much less food available. Let us rewrite Eq. (11.15) in terms of how much food remains in a patch, $R(T)$, after a specified amount of time, T , foraging in the patch:

$$T = \frac{\ln P - \ln R(T)}{a} + T_h (P - R(T)). \quad (11.16)$$

Figure 11.18

A predator forages in a habitat composed of distinct patches, each with P food units.



The cumulative amount of food consumed by the animal after T time units foraging in a patch is equal to the amount of food initially present, P , minus the amount remaining. We call this $G(T)$ (for gain) as a function of elapsed time T , or

$$\text{Cumulative food consumed after time } T = G(T) = P - R(T). \quad (11.17)$$

We now try to solve for $G(T)$ as a function of time, T , in the patch. Unfortunately, we soon find that it is impossible to rearrange Eq. (11.16) to get $R(T)$ alone on the left-hand side of the equation. In other words, there is no analytical solution for the cumulative gain from this type 2 functional response. After rearranging Eq. (11.16) and collecting terms in $R(T)$, we can write

$$R(T)T_h + \frac{\ln R(T)}{a} = -T + \frac{\ln P}{a} + T_h P, \quad (11.18)$$

which can be solved numerically for $R(T)$, given the parameters a , T_h , and P . We can also guess the general shape of $G(T)$. At $T=0$, the cumulative gain will be 0 since the animal has not yet consumed any food. As time T progresses, the accumulated gain, $G(T)$, will increase but it must become asymptotic at P , since the animal cannot consume any more food than there is to begin with, even given an infinite amount of time as shown in Figure 11.19.

Generally, we would also get about the same shape for this gain curve for either a type 1 or type 3 functional response. The slope of this curve at any particular time gives the rate of gain. As time goes on, the rate of gain becomes zero, regardless of the exact shape of the functional response.

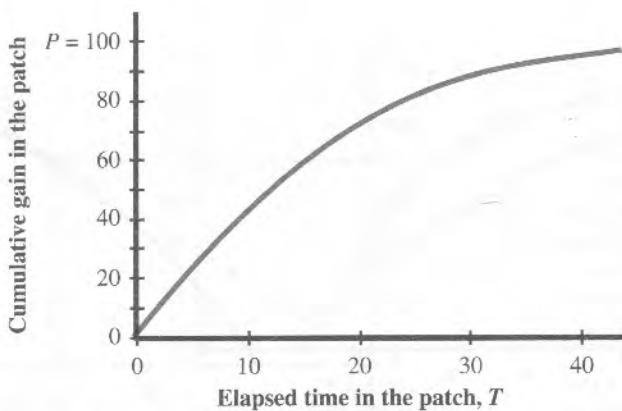
Exercise: Show that if a type 1 functional response is substituted for a type 2 in the development beginning with Eq. (11.13), that the closed-form solution for the cumulative gain $G(T)$ by the predator as a function of its time T spent foraging in the patch is:

$$G(T) = P - e^{\ln P - aT}$$

Now, if an animal stops foraging after a while and moves to another patch, its gain will be zero during the time it is in transit but then its gain will increase again when it enters a new patch. We seek the average rate of gain for this process, including time in

Figure 11.19

Cumulative gain curve, $G(T)$, for an animal foraging in a patch with an initial food density of $P = 100$. The gain curve is solved numerically by using a handling time of 0.1 and an encounter rate of $a = 0.1$.



transit and time foraging in a patch. While in a patch, the average rate of gain is $G(T)/T$, which of course varies with T . The average rate of gain, including the typical transit time, T_t , to a new patch, will depend on the spatial distribution of patches. The average rate of gain including both transit and foraging time combined is

$$A(T) = \frac{G(T)}{T + T_t}$$

The optimal give-up time can be solved by taking the maximum of this expression. When elapsed time T is zero, $A(T)$ must also be zero since no food has been consumed. At the other extreme, when T is very large, the denominator becomes very large and $A(T)$ must therefore become small. Thus $A(T)$ has some intermediate maximum. From calculus, we can find this maximum, by taking the derivative of $A(T)$ with respect to T and setting it to 0:

$$\frac{dA(T)}{dT} = 0 \quad \text{or} \quad \frac{d\left(\frac{G(T)}{T + T_t}\right)}{dT} = 0.$$

We wish to find the optimal value of T —call it T^* . Applying the chain rule for derivatives gives

$$\frac{G'(T^*)}{T^* + T_t} - G(T^*)(T^* + T_t)^{-2} = 0,$$

and thus T^* satisfies the formula

$$G'(T^*) = \frac{G(T^*)}{T^* + T_t}, \quad (11.19)$$

where G' is the derivative of $G(T)$ with respect to T . Equation (11.19) has a particularly simple graphical solution, as shown in Figure 11.20, with the $G(T)$ curve displaced by T_t units.

Suppose, however, that patches contained not $P = 100$ units of food, but $P = 400$ units. Is the optimal give-up time affected? Figure 11.21 shows that, with a fourfold increase in patch food density, the optimal give-up time increases only by about twice.

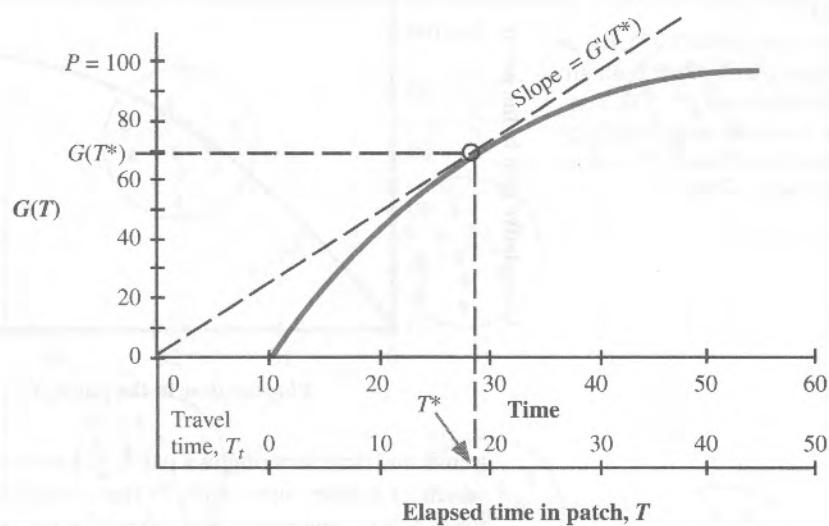
The optimal give-up time increases if the travel time increases, as illustrated in Figure 11.22. It pays to keep foraging in the same patch if it's a long trip (without food) to the next patch.

Finally, the optimal give-up time decreases if the foraging rate within a patch increases, as shown in Figure 11.23.

Of course, all this assumes that, when an animal gets to a new patch, that patch contains P food items, and the animal's foraging rate returns to the level associated with P . If many predators are simultaneously foraging in the same area (and again assuming that the recruitment rate of new food to a patch is low), an individual predator that moves may only find patches that are as depleted as the ones that it just left. Any truly optimal give-up time must also take into account the activities of other predators foraging in the

Figure 11.20

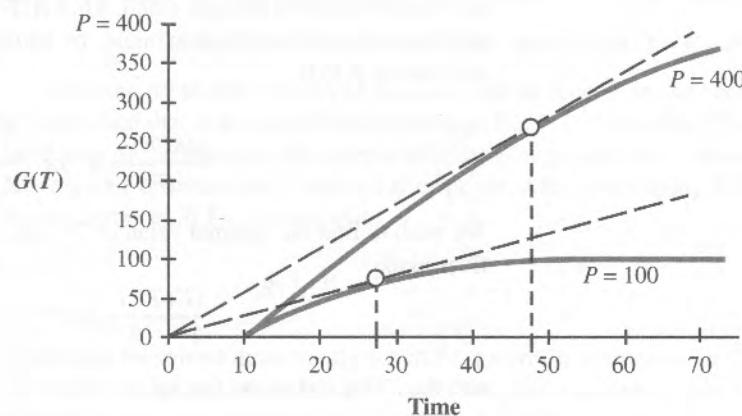
A graphical method to find the optimal give-up time, T^* , in a patch. The typical travel time between patches is 10 time units so the $G(T)$ curve (in red) begins on the left at Time = 10. The dashed line from $(0, 0)$ is tangent to a point on the $G(T)$ curve where the open dot identifies T^* on the x axis. The optimal give-up time here is about 18, corresponding to a cumulative gain rate of about 69.



$$\text{Note that } T^* \text{ satisfies the relationship } G'(T^*) = \frac{G(T^*)}{T^* + T_t}.$$

Figure 11.21

The effect of increasing the density in a food patch on the optimal give-up time. A fourfold increase in food per patch, compared to Figure 11.20, leads to about a doubling in the give-up time. The gain curve (in red) is solved numerically by using Eqs. (11.16) and (11.17). The optimal give-up time here is about 37.

**Figure 11.22**

Increasing travel time between patches, which might be due to slower speed or to patches that are farther apart, leads to an increase in the optimal give-up time. The optimal give-up time for $T_t = 10$ is $28 - 10 = 18$. The optimal give-up time for $T_t = 5$ is $17 - 5 = 12$.

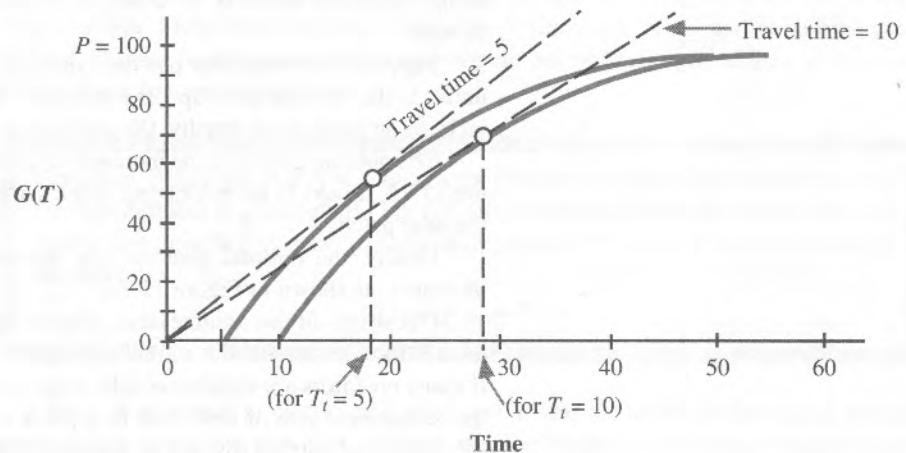
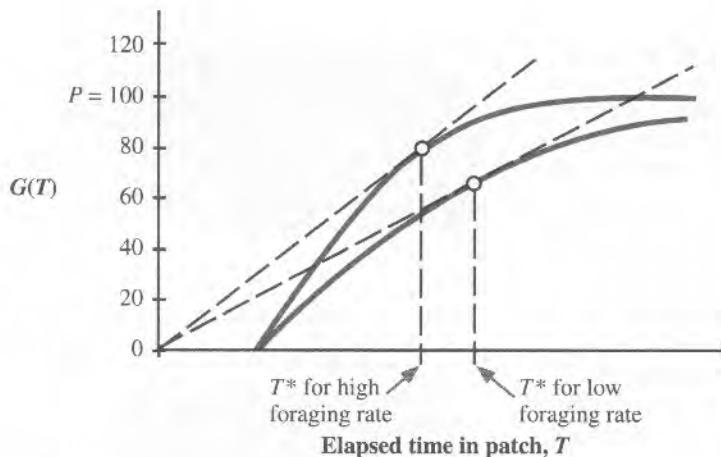


Figure 11.23

The optimal give-up times for two different foraging rates, $a = 0.1$ and $a = 0.3$. This figure is based on a type 2 functional response with $T_h = 0.1$.



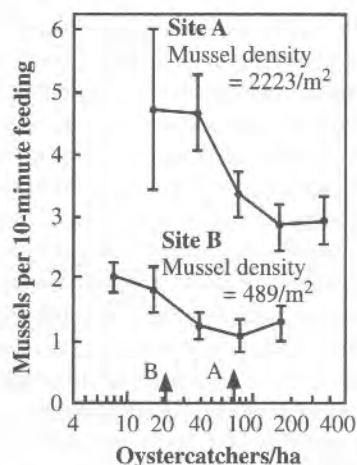
same habitat and the recruitment rate of resources to patches. Such cognitive abilities may be beyond the abilities of most animals and may be one reason why they are instead territorial, defending their foraging space against intruders. In this way, they can control their return times to patches to synchronize them with the resource recovery times to level P , without concern that someone else will get to the patch before they do.

THE IDEAL FREE DISTRIBUTION

Different habitats may have different potential profitabilities for consumers. Consider two habitat types that differ in resource productivity and that are large enough to hold several foraging consumers simultaneously. The consumers are free to move back and forth between these two habitats. If only a single consumer were present, it would make sense for it to choose the high productivity habitat since its consumption rate would be higher than it would be in the low productivity habitat. As consumer numbers grow in this habitat, however, resources become depleted and consumers interfere with one another by aggressive behavior or by scaring away mobile prey items. An example of this effect is shown in Figure 11.24 for oystercatchers feeding on intertidal mussel banks exposed at low tide. The oystercatcher intake rate decreases as the number of other oystercatchers nearby increases. In this case, most of the decline is not due to resource depletion but rather to direct interference between individuals (Zwarts and Drent 1981). The two sites differ in their mussel density.

The average consumer will just be able to numerically replace itself when its consumption rate balances its maintenance and only the reproductive effort necessary to replace itself. Any additional consumption can be turned into a net excess of consumer births or could support the immigration of more consumers into the habitat, as shown in Figure 11.25.

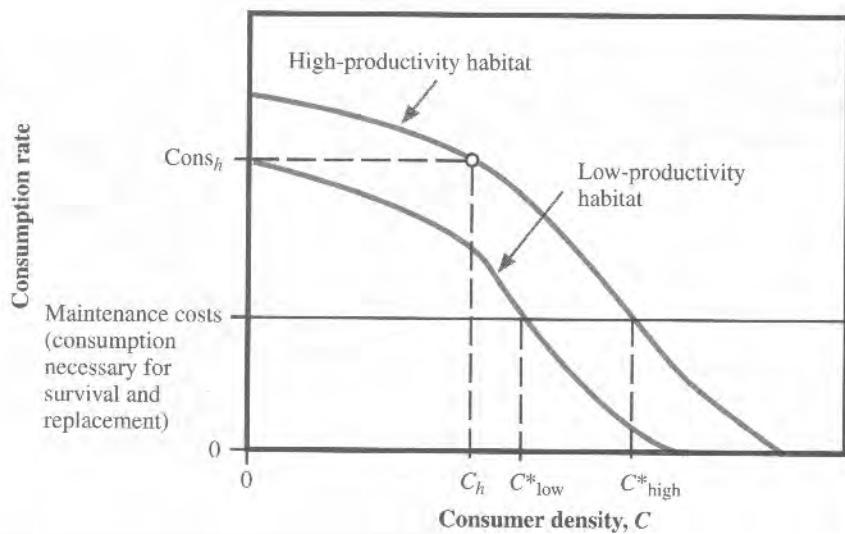
As long as habitats have dissimilar consumption rates, consumers should move to the more profitable habitat. At the point that consumer density in the high-productivity habitat equals C_h . However, the next additional consumer will find that its consumption rate is equivalent (at Consh) in both habitat types. Therefore, additional individuals will settle equally in both habitats. Assuming that maintenance costs to the consumers are the same in both patches, the consumers should move and settle in the two habitats until they come to numerical equilibrium such that consumption rates equal maintenance costs. This equilibrium consumption rate will be the same for both habitats. The equilibrium density of consumers in the high-productivity habitat (C_{high}^*) will be greater than that in the low-productivity habitat (C_{low}^*). Extending this argument to multiple habitat types at equilibrium, all habitats, regardless of their innate productivities will have identical profitabilities because of the adjustments of consumer densities. They will also have identical densities of resources at equilibrium if the functional response of the predators is identical in the different habitats.

**Figure 11.24**

Oystercatchers feeding on mussels at two sites in the Netherlands. For each site, the feeding rate declines with increasing oystercatcher density. The higher density of mussels at site A, translates into higher feeding rates overall per oystercatcher densities (from Zwarts and Drent 1981). The vertical lines indicate one standard error. The mean density of oystercatchers at the two sites is indicated by the arrows at the bottom.

Figure 11.25

The per capita consumption rate for consumers as a function of consumer density, C , in two habitats. In high-productivity habitats the consumption rate is higher than in low-productivity habitats for all levels of C . At a consumer density of C^* consumption rates equal maintenance costs; high-productivity habitats can support more consumers than low-productivity habitats ($C^*_{\text{high}} > C^*_{\text{low}}$). Imagine that the habitats start out void of consumers. The first consumer to enter will maximize its energy gain by settling in the high-productivity habitat. At the point that consumer density in the high-productivity habitat equals C_h , the next additional consumer will find that its consumption rate is equivalent (at Cons_h) in both habitat types, and thus may settle in the low-productivity habitat. Additional consumers will settle such that consumption rates are equal in both habitats. At the limit, the high-productivity habitat will support a density of C^*_{high} consumers, and the low-productivity habitat will support a density of C^*_{low} .



This process is called **ideal free distribution** (Fretwell and Lucas 1970). It is *ideal* because predators are assumed to have ideal knowledge of resource distributions and profitabilities across habitats. It is *free* because predators are assumed to be free to move in such a way that they can take advantage of any discrepancies.

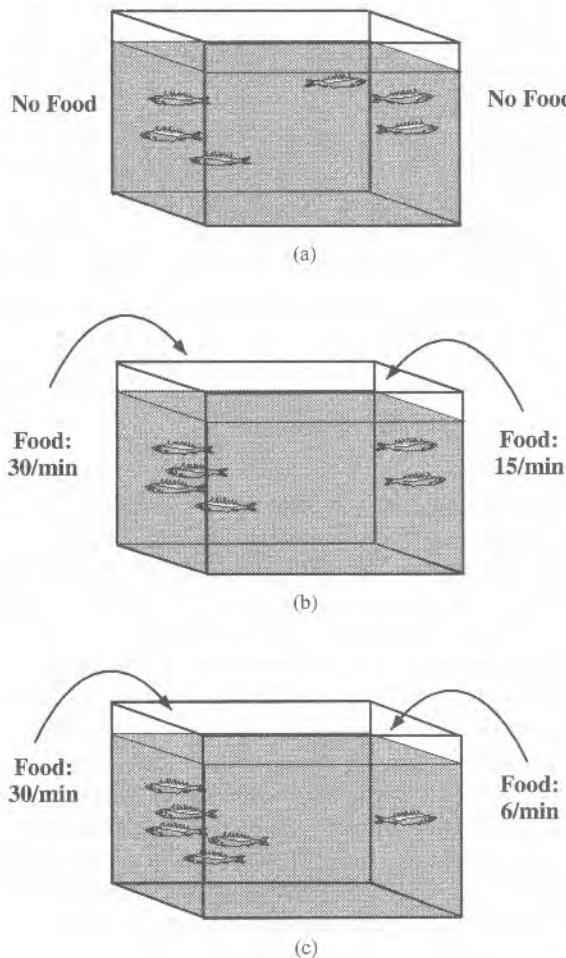
Imagine a long, narrow aquarium containing six small fish. If food is added to one end at five times the rate that food is added to the other end, we expect five fish to be at the high-food end and one fish to be at the low-food end, as long as the total amount of food added does not exceed the maximum consumption rates of the fish. The results from just such an experiment are shown in Figure 11.26.

An important assumption of ideal free distribution is that the potential success of a new individual settling or being born in a given habitat is equal to the average of all the individuals already residing there. Many animals will not reach an ideal free distribution across habitats because they do not have ideal knowledge of the profitabilities of various habitats, because they do not have equal physical access to all habitats, or because some resident individuals have different functional responses than others or keep resources to themselves through aggressive dominance over newcomers (Fagen 1987). Finally, consumption rates are only one component of overall fitness. In some cases animals may find it desirable to aggregate even if consumption rates are reduced because groups have additional protection from predators or easier access to mates. The desirability of habitats will not usually be based solely on consumption rates. Protection from predators, nest site availability, and access to water and nesting materials will all be factors. A more general model of habitat selection would be based on overall fitness in each habitat type, as affected by density rather than just by consumption rates.

Ideal free distribution also contradicts the notion that in a landscape context some subpopulations may be net sources while others will be net sinks of individuals through dispersal (see Chapter 2). We have already demonstrated that, if movements are random (diffusive), some subpopulations (sinks) depend on others (sources) for their continued persistence. It is an empirical question of when and how often, with more directed movements of individuals, a system of subpopulations will maintain a source–sink relationship or will reach an ideal free distribution. A final complication arises if we allow dispersal rate to be an evolving attribute in a source–sink model. If individuals outside the source population experience lower fitness, on average, then dispersal rates will evolve to be lower. And if dispersal rates evolve to lower levels, sink populations will become extinct (Holt 1997), leaving only populations that are self-supporting. For these populations, the average individual would have the same fitness regardless of the patch it was in, assuming that all patches equilibrate at a mean fitness of $\lambda = 1$. Because dispersal usually involves some search costs, dispersal should evolve to zero. However,

Figure 11.26

Six sticklebacks (a species of small fish) are kept in a long aquarium and fed at the two ends. (a) When no food is added, the fish congregate in about equal numbers on each side of the aquarium. (b) When food (in the form of water fleas) is added at twice the rate on one end as on the other end, by the ideal free distribution, fish should aggregate until they are twice as common at the high-food end; this is generally the result observed. (c) When food is added at five times the rate on one end as on the other end, fish are generally five times more frequent at the high-food end than at the other end. After Milinski 1979.



environmental fluctuations will create new opportunities and hazards that shift unpredictably across space. Thus it is likely that the assumption of fitness equilibration will not be met and that some level of dispersal is expected that would be proportional to the level of unpredictable environmental fluctuations.

PROBLEMS

- Consider a predator that feeds on two prey, P_1 and P_2 . The constants of prey consumption are $a_1 = 0.1$, $a_2 = 0.2$, $T_{h,1} = 1$, and $T_{h,2} = 1$. If the predator has a type 2 functional response, plot the functional response for the prey levels of 0, 5, 10, 15, and 20 for prey 1, assuming that it is the only prey item available. Repeat for prey 2. Now repeat for both prey, assuming the predator has a type 3 functional response.
- Using the parameters in Problem 1, imagine that both prey are simultaneously available to the predator at the following densities for prey 1 and prey 2: (0, 20), (5, 15), (10, 10), (15, 5), and (20, 0). Thus there are a total of 20 prey in each case. Use Eq. (11.12) to determine the prey consumption rate for each prey at each of the five density combinations, first assuming a type 2 functional response and then a type 3 functional response. For each of the two functional responses, next make a plot of percent prey 1 available on the x axis versus percent prey 1 consumed on the y axis. How do the shapes of these plots differ for type 2 and 3 functional responses? What would these plots look like if you plotted percent prey 2 consumed on the y axis?
- Again, consider a two-prey system. Now, however, the predator has a type 1 functional response to prey type 1 but a type 3 functional response to prey type 2. Can switching result?
- In the development of the model to predict optimal give-up times, we assumed that the recruitment rate of resources into a patch was zero so that for each prey eaten there was one less prey available for future consumption. If we alter this assumption so that each prey consumed is replaced at a rate of 0.5 per hour and if the average transit time to go from one patch to another is about 2 hours, what will the optimal give-up time be? (Assume that there is only a single individual predator.)
- In what way do the data in Figure 11.24, showing oystercatcher consumption rates at two sites, appear to violate the predictions of ideal free distribution? These two sites are on different islands that are separated by about 60 km.