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Encounter rates and functional responses

An item that is not encountered cannot be eaten. Hence, the dynamics of encounter hold a central position in foraging theory. They also play a central, if too often only implicit, role in population and community dynamics by determining which and how many individuals, populations, and species can interact strongly with each other or with abiotic variables at a specific location. Encounter rates of immigrants with unoccupied space can control recruitment and local population growth rates. Encounter rates (e.g., of organisms with suspended sediments) further dictate many of the effects that organisms can have on abiotic variables. Encounter, however, is only the first step of interaction. Rates at which organisms handle suspended particles and each other, for example, can be set by either encounter rates or any subsequent steps, such as capture, handling, or digestive processing. The issue of rate limitation by either encounter or by subsequent steps is so fundamental to so many biological and interdisciplinary issues that it deserves its own chapter.

Encounter rates

A readily generalized approach (Evans 1989) in the estimation of encounter rates [$N T^{-1}$] is to identify the boundary length [L] or area [L^2] over which encounter occurs, an effective density of items that can be encountered [$N L^{-2}$ or $N L^{-3}$], and a mean encounter speed [$L T^{-1}$], where that speed v_e is defined as the scalar component of the relative velocity vector of the body doing the encountering with respect to the body encountered. In all the subsequent encounter rate equations in this section, these three terms are set off by parentheses and kept in this same sequence. The equations, therefore, often are not in their most compact forms; my intent instead is to leave their meanings transparent.

Real geometries of encounter vary in dimensionality. For the simplest and most easily visualized two-dimensional case (Fig. 3.1A), consider a predatory individual crawling on or swimming over the seabed at a constant speed v_d . Here and throughout the book, the subscript d denotes the predator and y denotes the prey (because they are the first letters of the two nouns that are not held in common). Set the density of sedentary prey at N_y and detection distance of the prey by the predator at d_e . The moving predator cuts a swath $2d_e$ wide through the prey. Then encounter rate per predator, E , is given simply by:

$$E = (2 d_e)(N_y)(v_d) \quad . \quad (3.1)$$

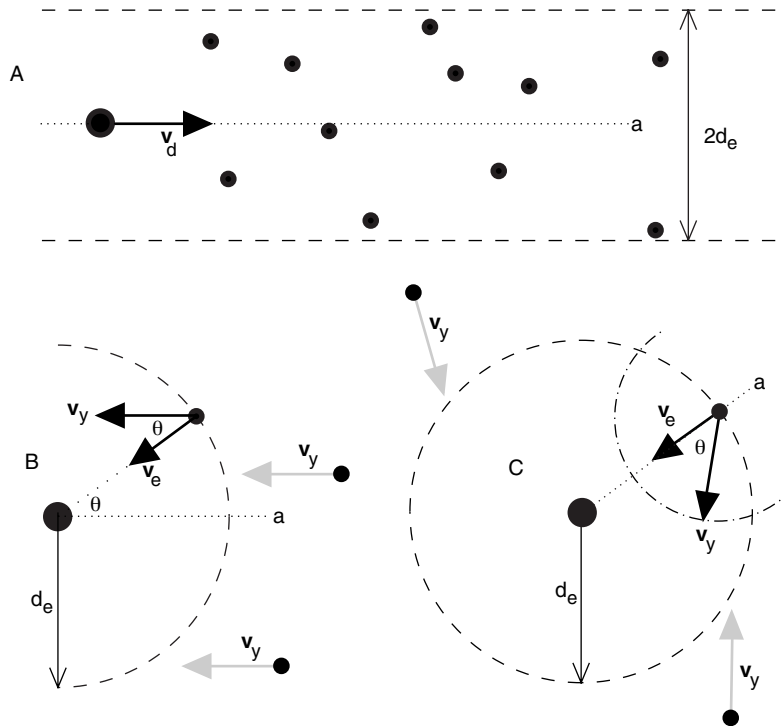


Fig. 3.1 Geometric representations of encounter, where prey are small (filled circles) and predators are large (filled circles). **A.** A predator moves over a surface with velocity v_d and detects prey a distance d_e to either side of its path. **B.** Prey have a unidirectional, uniform velocity v_y , and the predator is stationary (e.g. prey in the water column migrating vertically past a predator), yielding an effective encounter velocity v_e in the coordinate reference frame centered on the predator when prey enter its detection radius d_e . Encounter velocity thus varies with position of encounter on the detection semicircle (with the angle θ). Because all prey are moving from right to left, no detection occurs to the left of the predator. **C.** Prey have constant, uniform swimming speed but random direction relative to a fixed predator. Encounter velocity thus depends upon the angle of incidence (θ) of the prey with the predator's detection circle. In **B** and **C** prey not yet detected are shown in gray. Each of these two-dimensional geometries can be generalized to three dimensions by rotating the respective figures about the axes of symmetry labeled a .

This formula works equally well for a benthic (= bottom-dwelling) predator that sits still and captures prey brought past by a steady current; v_d is simply reinterpreted as the relative speed of the predator and its prey field.

A slight complication of Eq. 3.1—that gives the identical result—adds more physical insight into the process of encounter and generalizes far more easily to more complex (than circular or spherical) encounter geometries and situations in which both predator and prey move. Its difference and advantage is that it makes the geometry of encounter explicit. Consider d_e to be a radius scribed about the

predator to form a semicircle in the direction of its swimming (Fig. 3.1B). Take the origin fixed at the center of the radial field defined by the position of the predator, so that prey move with respect to it. Prey with no component of motion toward the origin cannot be encountered, leading to the inutility of one-half of the perimeter of the circular detection field. (By the arguments of optimal foraging theory, then, if detection is expensive energetically this swimming predator species probably will lose evolutionarily the ability to detect prey rearward of its direction of motion.) Prey will cross the leading half of the detection circle at a speed proportional to the cosine of the incidence angle θ of Fig. 3.1B. The areal density term, N_y , thus remains the same, but both the (mean) speed and perimeter terms of Eq. 3.1 are altered:

$$E = (\pi d_e)(N_y) \left(\frac{1}{\pi} \int_{-\frac{\pi}{2}}^{\frac{\pi}{2}} v_y \cos \theta d\theta \right) . \quad (3.2)$$

The fraction immediately preceding the integral uses the definition of the mean in dividing the integral by the length of a semicircle on the unit circle. The solution of this equation is the right side of Eq. 3.1, noting that v_d and v_y can be interchanged.

Now add the seeming complication of prey individuals moving with a fixed, uniform speed, but with a random or uniform distribution of directions among individuals (Fig. 3.1C). The full detection perimeter (of length $2\pi d_e$) is effective in encounter, but one-half of the prey trajectories in each quadrant are of no use to the predator because they have no component in the direction of the origin (center of mass of the predator), effectively reducing the prey density by one-half. Prey incident on the encounter perimeter can have trajectories ranging from tangential ($\theta = \pm\pi/2$ to normal ($\theta = 0$) with respect to the encounter circle. The rate of encounter thus becomes:

$$E = (2\pi d_e) \left(\frac{N_y}{2} \right) \left(\frac{1}{\pi} \int_{-\frac{\pi}{2}}^{\frac{\pi}{2}} v_y \cos \theta d\theta \right) , \quad (3.3)$$

which again (after exchanging v_d and v_y) simplifies to the same solution (Eq. 3.1).

Each of these three equations has a homolog in three dimensions that can be written and solved by the contrivance of rotating the respective two-dimensional figures about an axis of symmetry (indicated as a in each part of Fig. 3.1). The areal density of prey in two dimensions becomes a volumetric density [$N \text{ L}^{-3}$]. One can conceive the detection sphere as sweeping out a cylinder of the same radius as the sphere:

$$E = (2\pi d_e^2)(N_y)(v_d) . \quad (3.4)$$

The semicircle of Fig. 3.1B becomes a hemisphere (composed in the unit sphere of circles of radius $\sin \theta$) upon rotation, and to calculate the mean encounter speed thus requires division by the area of a unit hemisphere (2π):

$$E = (2\pi d_e^2)(N_y) \left(\frac{1}{2\pi} \int_0^{\frac{\pi}{2}} v_y \cdot \cos \theta \cdot 2\pi \sin \theta \, d\theta \right) . \quad (3.5)$$

Similarly, if prey have randomly or uniformly distributed swimming directions but uniform speeds, the solution becomes:

$$E = (4\pi d_e^2) \left(\frac{N_y}{2} \right) \left(\frac{1}{2\pi} \int_0^{\frac{\pi}{2}} v_y \cdot \cos \theta \cdot 2\pi \sin \theta \, d\theta \right) . \quad (3.6)$$

Again Eq. 3.5 and 3.6 reduce to Eq. 3.4 when v_d of Eq. 3.4 is exchanged for v_y in the other two.

Frequently, both predators and prey move. If their speeds are fixed at constant, predator- and prey-specific values, but direction of swimming varies evenly or randomly, then the law of cosines in two dimensions and analogous rotational manipulation can be used to solve for the mean speed of encounter (Fig. 3.2, adopting for derivational convenience the convention that v_f refers to the faster and v_s to the slower of the two species):

$$\bar{v}_e = \frac{1}{4\pi} \int_0^{\pi} \sqrt{v_f^2 + v_s^2 - 2v_f v_s \cos \theta} \cdot 2\pi \sin \theta \, d\theta = v_f + \frac{v_s^2}{3v_f} . \quad (3.7)$$

Gerritsen and Strickler (1977) came to an identical solution in a different manner. For this case, then:

$$E = (4\pi d_e^2) \left(\frac{N_y}{2} \right) \left(v_f + \frac{v_s^2}{3v_f} \right) . \quad (3.8)$$

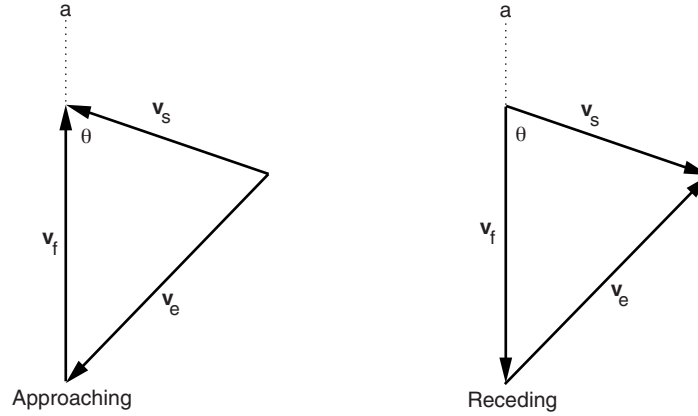


Fig. 3.2 Encounter geometries for predator and prey when each swims with a constant speed but direction of swimming is evenly or randomly distributed (all angles θ being equally likely) among individuals. Encounter speed v_e thus depends on the scalar components of the velocity vectors of the faster (v_f) and slower (v_s) swimming of the two species and on the encounter angle (θ). One-half of the prey individuals (receding), however, have no component of velocity toward the predator. Directions of the encounter velocity vectors v_e are selected arbitrarily. The full suite of equiprobable three-dimensional possibilities for v_e is generated by letting θ range from $-\pi/2$ to $\pi/2$ while rotating about the axis labeled a to produce a sphere of end points of v_e centered on the intersection of v_f with v_s .

Evans (1989) pointed out that this mean is very near (within 6%) the solution for v_e when $\theta = \pi/2$ (i.e., to $\sqrt{v_d^2 + v_y^2}$) the scalar sum of the vectors at the mean angle of incidence rather than the mean scalar sum of vectors. Given the oversimplified geometry (e.g., the perfectly spherical detection perimeter) it hardly seems worth carrying the added complexity of Eq. 3.8. Evans (1989) also pointed out that the simpler solution is more accurate than Eq. 3.8 for \bar{v}_e when predator and prey speeds show well-behaved stochastic variation about their respective mean values. If turbulent velocity fluctuations are added to the picture, and one assumes that turbulence-induced motions of prey and predator are independent with mean speed v_t , then \bar{v}_e becomes $\sqrt{v_d^2 + v_y^2 + 2v_t^2}$ (Evans 1989).

In these formulations (Eqs. 3.1–3.6) there is only one explicit spatial scale, d_e . An implicit spatial scale, however, is at least as important if these equations are to be approximately correct. Namely, all these velocities must hold steady over the mean separation distance between points on the encounter boundary and approaching prey (and hence over the time to travel this distance). Assuming that prey are substantially more abundant than predators and that the detection distance d_e is much smaller than the average distance between prey, this mean separation distance is of order $\sqrt[3]{N_y^{-1}}$ (but see Chapter 10 for a more accurate and less restrictive Poisson approximation of separation distance and see Chapter 14 for relaxation of

other assumptions of particle-particle encounter). A further stricture for this parameterization of the effects of turbulence, then, is that velocity fluctuations at separation distances of $\sqrt[3]{N_y^{-1}}$ be strictly independent (move predator and prey independently). For several reasons, this formulation of encounter speed must be considered an upper bound. It is clearly in the prey's best interests to reduce the encounter speed (yet the above parameterization takes no account of the prey's sensory or escape responses). As separation distances of interest fall below the smallest scales of turbulence, fluid-imposed relative velocity plummets to levels produced by laminar shear. Eqs. 3.3 and 3.6 further use the oversimplification of perfect isotropy both of swimming and of turbulent motion.

At the opposite extreme of starting assumptions for calculating encounter rates is that prey or predator motions are entirely diffusive over their characteristic separation distance. Movement may be by turbulent velocity fluctuations in the fluid, by active swimming with frequent directional changes produced either spontaneously or by collisions with other individuals, by Brownian motion in the case of small prey individuals, or by molecular diffusion in the case of dissolved "prey" molecules. Assuming that in any of these cases prey movement relative to the origin defined by a predator can be characterized by a diffusion coefficient, D_y [$L^2 T^{-1}$], then the problem becomes one of diffusion in spherical coordinates:

$$\frac{\partial N_y}{\partial t} = D_y \frac{1}{r^2} \frac{\partial}{\partial r} \left(r^2 \frac{\partial N_y}{\partial r} \right), \quad (3.9)$$

where r is radial distance from the predator.

Assume that prey density initially ($t = 0$) is uniform at N_{y0} for all $r > d_e$, that the predator consumes all prey entering the sphere enclosed by d_e ($N_y = 0$ for $t > 0$ and $r \leq d_e$), and that the predator is unable to affect the far-field concentration of prey ($N_y = N_{y0}$ for $t \geq 0$ and $r \rightarrow \infty$). Solving Eq. 3.9 with these boundary conditions yields (Friedlander 1977):

$$N_y = N_{y0} \left[1 - \frac{d_e}{r} \left(\operatorname{erf} \frac{r - d_e}{2\sqrt{D_y t}} \right) \right], \quad (3.10)$$

where $\operatorname{erf} x$ is defined as $\frac{2}{\sqrt{\pi}} \int_0^x e^{-w^2} dw$. From Fick's first law the flux, J , per unit of area of the sphere is

$$J = D_y \left(\frac{\partial N_y}{\partial r} \right)_{r = d_e}. \quad (3.11)$$

Combining Eqs. 3.10 and 3.11 gives

$$J = \frac{D_y N_{y0}}{d_e} \left(1 + \frac{d_e^2}{\pi D_y t} \right). \quad (3.12)$$

For $t \gg \frac{d_e^2}{D_y}$ the term in parentheses can be dropped. Multiplying by the surface area of a sphere to get the total encounter rate and inserting parentheses to separate the terms in the same manner as in Eqs. 3.1–3.6 gives

$$E = (4\pi d_e^2)(N_{y0}) \left(\frac{D_y}{d_e} \right). \quad (3.13)$$

Although the last term is the diffusive transfer velocity (inward radial component of instantaneous speed of prey crossing the detection threshold), it should be remembered that this velocity will not hold as a mean over the separation distance. The contrast can be emphasized by calculating under what conditions an encounter rate due to steady prey swimming (v_y) equals the encounter rate due to diffusive motion over the characteristic separation distance: This equivalence requires (from Eqs. 3.6 and 3.13) that

$$D_y = \frac{d_e v_y}{2}. \quad (3.14)$$

It is possible for both prey and predators to move or be moved diffusively. In effect the origin of the frame of reference (in my derivation centered on the predator) also diffuses. If prey and predators do so independently, then the effective diffusion coefficient, D_e , for predator and prey encounter is simply $D_y + D_d$ (Friedlander 1977). Thus if predator and prey are moved independently by turbulence or are of the same size and moved by Brownian diffusion, the effective diffusion coefficient for encounter is twice that measured for the diffusion of one component. All of the above encounter equations take the perspective of a single predator. If one wishes to calculate total predator–prey encounter rate rather than encounter rate per predator, then both sides of the encounter equations should be multiplied by N_d .

Functional responses

A predator may not capture, handle or digest prey at the rate of encounter. The kinetics of postencounter steps of prey processing by predators, however, are not as easy to generalize because there are many such steps. As a crude dichotomy, biological responses often are classified as due either to changes in individual behavior or to changes in numbers of individuals. The former are called functional responses, whereas the latter are called population responses. It is safe to say that some high encounter rate with prey will saturate any predator's ability to process

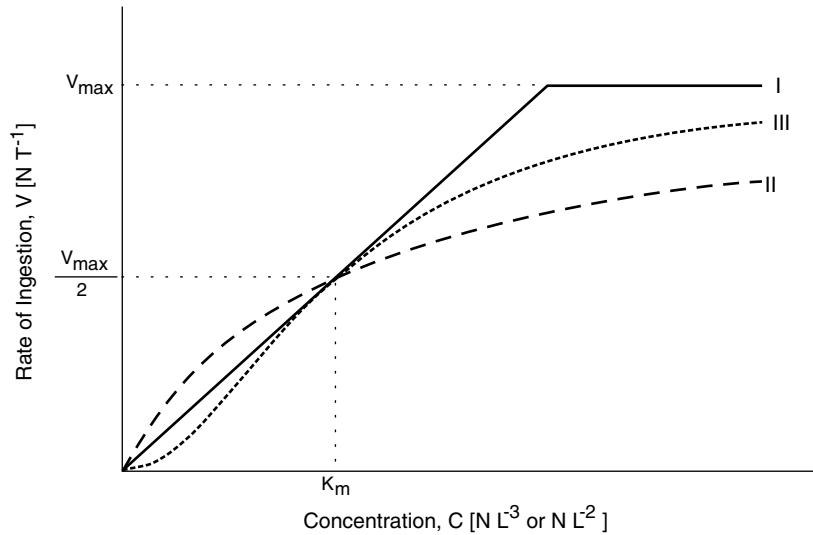


Fig. 3.3 Types of functional responses. Rate of ingestion is taken as the example, and concentration of prey is used as a surrogate for encounter rate. The simplest response (type I) is rectilinear and indicates an abrupt shift from overall rate limitation by encounter rate to limitation by some subsequent step. The hyperbolic curve (type II) shows very gradual saturation of post-encounter processing. A sigmoidal response (type III) suggests some inefficiency or behavioral change that reduces encounter or its effectiveness at low concentrations and yet saturates rapidly at high concentrations. Type I–III curves are roughly linear in concentration, respectively, right up to $(2K_m, V_{max})$, only well below K_m , and only near K_m . For purposes of illustration, all three curves are forced through the point $(K_m, V_{max}/2)$, where V_{max} is the maximal ingestion rate (reached asymptotically in curves of Type II and III). For further explanation of this choice of notation, see text.

them, and then density of prey within the encounter boundary will rise. This increase has no effect on encounter rate with later-arriving individuals in the formulations that contain only steady motion (Eq. 3.1–3.6), but it decrements encounter rate in the diffusive formulation (cf. boundary conditions) in proportion to the relative increase in prey density within the encounter sphere.

Then, at some encounter rate, postencounter processing becomes rate limiting. Ingestion rate is the postencounter functional response most often measured and is often plotted as a function of prey abundance. Prey abundance, in turn, is a surrogate for encounter rate. One of three patterns (Fig. 3.3) usually is found, and they often are denoted by Roman numerals as type I, II, and III, respectively. In the simplest rectilinear case, ingestion rate increases linearly with abundance until the saturation level is reached abruptly. The hyperbolic case results whenever some post-encounter step required before or for ingestion takes a fixed amount of time before the mechanism can be used to handle another item; it fits a wide array of ingestive

activities from enzymatic uptake of nutrients by plant cells, to ingestion of particles by protozoans, to capture of prey by much larger animals (Real 1977).

The most complex, sigmoidal curve has two frequent and related interpretations. One is that predators require some learning experience to handle prey effectively (and that they quickly forget what they learned when prey densities again drop) or that the handling mechanism for some mechanical reason becomes more efficient per prey item with increasing numbers of prey items handled at the same time (before it again becomes less efficient near saturation). The other interpretation is that at the lowest prey abundances the benefits do not repay the costs of foraging, but that the predator continues occasionally to sample the food environment at very low densities of prey to test whether conditions have changed. Recently, Mangel and Clark (1988) have suggested that a sigmoidal response will be typical of visual predators (those that use sight to locate their prey). At the lowest densities on average at any one time no prey can be seen. Therefore, ingestion rates are very low. Intermediate densities entail prey frequently sighted or continuously in view, and at the highest densities of prey the predator's processing (e.g., digestive) capabilities are saturated. Whatever the correct mechanistic interpretation for the functional response under discussion, this sigmoidal pattern of processing clearly is the least prone of the three to produce prey extinction since predation on a given prey type begins to drop so strongly when its abundance falls to low levels.

There is no standard notation for the parameters on the ordinates and abscissas of functional–response plots. To limit the diversity of notation introduced, to anticipate the section on osmotrophy (see Chapter 4), and to follow Real (1977) for Fig. 3.3 I have adopted symbols normally used in enzyme–substrate research. To emphasize shape differences and varying degrees of linearity, the functions chosen for curves I, II, and III are, respectively:

$$V = V_{max} \text{ for } C \geq 2K_m, \quad V = \frac{V_{max} C}{2K_m} \text{ for } C < 2K_m, \quad (3.15)$$

$$V = \frac{V_{max} C}{K_m + C}, \text{ and} \quad (3.16)$$

$$V = \frac{V_{max} C^2}{K_m^2 + C^2}. \quad (3.17)$$

Although the functional forms (if not the symbols) used for responses of type I and II are reasonably invariant, a great many alternative functional forms are roughly sigmoidal and occasionally are used to model responses of type III.

In practice, the scatter and dynamic range limitations of data frequently make it impossible to distinguish which of these alternative patterns holds. Often the

patterns have been considered characteristic of particular predators, but recent evidence shows that the same predator can change between type I and type II as a function of prey size (Rothhaupt 1990). Thus, the functional response should be considered characteristic of the predator–prey pair. A further difficulty with generalization and quantification and an important reason for the observed scatter is apparent time dependence of ingestion rate—due to recent feeding history. General application of the patterns presupposes rapid approach to a steady state defined by them. Predators cease feeding for various reasons and periods, however, and it is clearly possible to ingest material at more rapid rates for longer periods when the gut has been emptied recently. Thus one can expect more rapid feeding at a given food concentration when that concentration is approached from below rather than from above. Other generalizations about unsteady behavior are as yet difficult to draw. Hence most models of predator–prey interaction continue to use formulae that represent curves of type I, II or III without hysteresis, implicitly assuming steady state. Mangel and Clark's (1988) methods would appear to provide ideal means to retain mechanistic description of the feeding process and explore predator response to temporally and spatially varying prey abundances.

Further readings

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