CONTRIBUTION TO THE MATHEMATICAL THEORY OF CAPTURE. I. CONDITIONS FOR CAPTURE

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The equations for a simple biological system comprising one *prey* species and one *predatory* species, the latter consuming the former for food, have been given by the writer (1920, 1923, 1925), and, independently, by Volterra (1926) in the form

$$\frac{dX_1}{dt} = aX_1 - kX_1X_2$$
$$\frac{dX_2}{dt} = kk'X_1X_2 - bX_2, \quad (1)$$

where X_1, X_2 are, respectively, the total masses of the two species S_1 and S_2; or, with slight and obvious change in the argument and in the physical significance of the coefficients, X_1 and X_2 may be taken to represent the number of individuals in the two species. We shall here read them in this latter sense. The coefficients a, k, k', b, may, in first approximation, and especially for small ranges of variation of X_1 and X_2, be regarded as constants; or, in more exact treatment of the problem, these coefficients are themselves functions of X_1 and X_2 (Lotka, 1923; Volterra, 1926).

The purpose of the present communication is to single out for further discussion the term $kk'X_1X_2$ in (1), and, in particular, the coefficient k. The physical significance of this coefficient depends on the particular physical process by which individuals of the species S_2 "consume" those of species S_1. We shall here consider the case in which this takes place by pursuit and capture, an individual S_1 being killed, at capture, by an individual S_2, and consumed in whole or in part. The further resolution of the coefficient k is the analytical counterpart of the further resolution of the physical process of capture.

Influence of Topography: Distributed Refuges.—Now capture can take place in various ways, as, for example, by simple pursuit until the pursuer overtakes the pursued. In such case capture *can* take place only if the velocity of the pursuer exceeds that of the pursued; and *must* take place, in that event, provided sufficient time is given. But this is not the typical situation in nature. What usually happens is that the pursued runs to *cover*, i.e., to a *refuge*, and escapes if it reaches effective cover before being overtaken.

Cover can be of various kinds. In the case of a bird, for example, rising from the ground affords effective refuge from terrestrial enemies. But a case of particular interest is that in which cover is presented by features of the topography. The problem of the frequency of capture in this case resolves itself into a triangular study of the relations between three classes of factors, namely,

1. Properties of the individuals S_1.
2. Properties of the individuals S_2.
3. Properties of the topography over which the two species operate.

Preserving the essential characteristics of typical organisms, but reducing them to their simplest terms for the purpose of achieving a first approach to the problem, we shall conceive the process of capture as follows:

1. *Random Motion between Encounters.*—Every individual S_1 and S_2 moves "in random manner" over the topography so long as it is not "in encounter" with an individual of the other species. As a first approximation we shall assume that the random motion is rectilineal, the azimuth changing at each encounter, all azimuths being equally frequent, and with no correlation between azimuths before and after encounter.

2. *Encounters, First Phase: The "Stalk."*—About each individual S_2 a field can be described, which we shall speak of as the *field* of *influence* of S_2. In general this field might have various shapes, and might be a function of the topography; but still restricting ourselves to the simplest case, we shall suppose that the field is a circle of radius r_2 and center attached to S_2. This field of influence has the following property: As soon as an individual S_1 enters this field r_2, the motion of S_2 is, *in a fraction* ψ *of such cases*, no longer random, but follows a "curve of pursuit" defined as a characteristic property of the species S_2. The fraction ψ measures the *observability* (*visibility*) of S_1 with respect to S_2. This observability depends, in a manner which we shall not here seek to analyze further, (*a*) on features of the environment; and (*b*) on features of the prey species (coloration, mimicry, camouflage, etc.).

3. *Encounter, Second Phase: The Pursuit or Flight.*—The motion of S_2 continues as stated under (2) above, until in turn S_2 enters the field of influence of S_1. For simplicity we shall here assume that this also is circular, with radius r_1 and center at S_1. From the moment that S_2 enters into the field of S_1, e.g., as soon as the prey senses (sights) the pursuer, the motion of S_1, which until then may have had any random character, follows, in a fraction χ of such cases, *a curve of flight* characteristic of the species S_1. The fraction χ measures the observability (visibility) of S_2 with respect to S_1.

Distribution of Cover or Refuges.—In the most general case the topography of the system may be complex, and may require, for its complete definition, a map indicating the character of the terrain at every point, as a function of the coördinates of position. For the present, however, we shall restrict ourselves to features of the topography which can be defined in statistical terms, and, in particular, we shall consider the influence of *cover* or *refuge* upon the course of events. In general refuges may be distributed in any manner over the topography, with a density δ per unit area, and the entire field may be divided into separate domains, one domain for each refuge, such that every point within a domain is nearer to the refuge (considered as a point) of that domain, than to any other refuge. So, for example, in figure 1, the points P_1, P_2... represent refuges. Each is contained within a polygon whose sides are formed by the perpendicular bisectors of the joins of adjacent refuge points. For example, the point Q_1 is nearer to P_1 than to any other refuge.

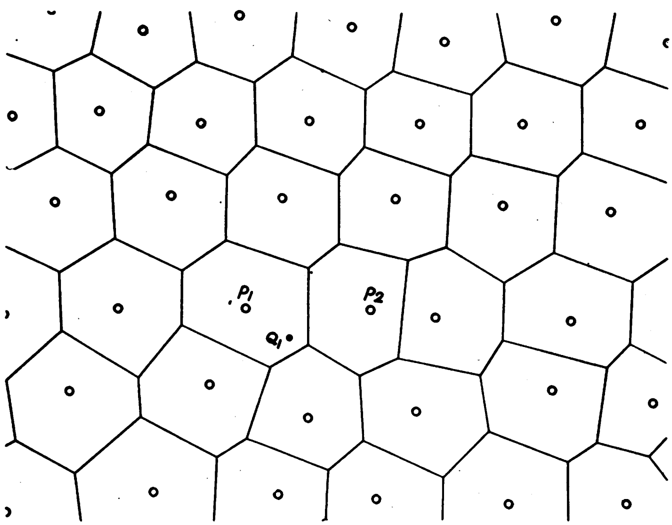

FIGURE 1

The perfectly general case of distribution of refuges may be narrowed down in various ways; for example, the refuge density, though variable over small areas, may be (in the limit) uniform, provided a sufficiently large area is observed. For a restricted patch, of area A, the frequency $f(\Delta)$ of the deviation Δ of the actual density from the mean taken over a large field, may be defined by some such law as

$$f(\Delta) = ke^{-\varphi(A)\,\Delta^2} \qquad (2)$$

where $\varphi(A)$ becomes very large when A is not small, so that for larger areas there are practically no deviations of the average density, from the mean over the entire terrain. This suggestion is here thrown out by the way of a hint for further generalization.

For the present we shall restrict our discussion to cases in which the *distribution pattern* does not materially affect our results, or to conventionalized cases in which the distribution pattern is simple, as will be indicated more in detail later. But first we must isolate for examination a single element of the general process under discussion. It is to this that the following section is devoted.

Single Refuge, Single Encounter: Conditions for Capture.—It will be convenient, in the following development, to consider first the simpler case in which $\psi = \chi = 1$, that is, in which every individual (prey or predator) that comes within the radius of observation of its opponent, is actually observed by that opponent (predator or prey).

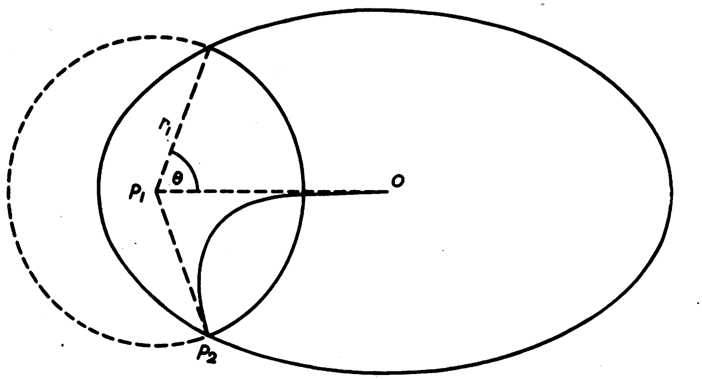

FIGURE 2

Consider first, then, a single refuge located at the point O in figure 2. Let P_1, P_2, respectively, be the positions of S_1, S_2 at the beginning of the *second* phase (flight) of an encounter between them. Then S_1 immediately flees toward O along P_1O, with velocity v_1, while S_2 pursues it with a velocity v_2 directed always toward S_1, that is, toward the moving point P_1. The point P_2 then traces a curve of the kind known as a *curve of pursuit*. In figure 3 a family of such curves of pursuit, all terminating in the point O, are shown. These correspond, then, to paths traced by S_2 in the limiting case that capture occurs just as S_1 reaches the refuge.

Now it can be shown* that the *isochrone* through P_1, that is, the locus of points corresponding to equal times upon the several curves of pursuit terminating synchronously at O, is an ellipse of eccentricity $e = \frac{v_1}{v_2}$, with one focus at P_1 and its center at O. (See figures 2 and 3.) For this ellipse the polar equation, dated from P_2 as pole and P_1O as axis, is

$$\rho = \frac{Re}{1 - e^2}(1 - e \cos \theta) \qquad (3)$$

or

$$R = \frac{\rho(1 - e^2)}{e(1 - e \cos \theta)} \qquad (4)$$

where ρ is the focal distance P_1O, while θ is the phase or amplitude P_2P_1O in figure 2, and R is the radius vector P_2P_1.

But, at the beginning of the second phase (flight) of the encounter, P_2 is at a distance r_1 (the range of perception of S_1, the pursued species) from P_1. In other words, at that instant P_2 lies somewhere on a circle drawn about P_1 as center, with radius r_1. If it lies at the intersection of this circle with the ellipse (3), capture will just take place as S_1 reaches the refuge at O. If P_2, on the other hand, lies anywhere in the arc of the circle drawn in a sólid line in figure 3, the part within the ellipse, then, evidently, capture will occur before the refuge is reached; and on the contrary, if P_2 lies in the arc shown in a dashed line, the arc outside the ellipse, then S_1 will escape to the refuge, and there will be no capture.

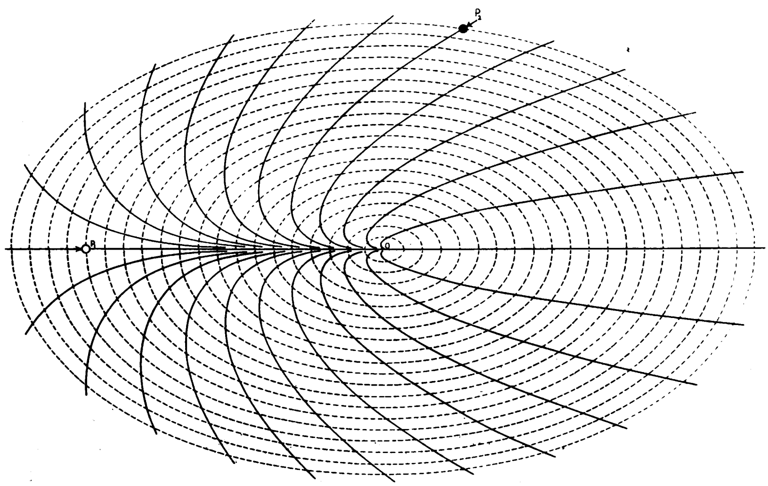

FIGURE 3

To sum up, capture will, or will not, take place, according as, at the moment pursuit begins, the pursuer lies within or lies outside an ellipse (3) of eccentricity $e = \frac{v_1}{v_2}$, drawn with the refuge O as center, and the initial position P_1 of S_1 as focus. Analytically this statement takes the form that capture will, or will not, take place, according as

$$r_1 \lessgtr R \qquad (5)$$

i.e., as

$$r_1 \lessgtr \frac{\rho(1 - e^2)}{e(1 - e \cos \theta)} \tag{6}$$

or, again, according as

$$\cos \theta \gtrless \frac{1}{e} - \frac{\rho(1 - e^2)}{r_1 e^2} \tag{7}$$

or, as

$$\theta \lessgtr \text{arc cos}\left\{\frac{1}{e} - \frac{\rho(1 - e^2)}{r_1 e^2}\right\}. \tag{8}$$

It will be well to state the meaning of this relation in words. If at the beginning of the pursuit the pursued S_1 is at a distance ρ from the refuge, then *capture* will occur if the angle at which S_1 sights its pursuer S_2 is *less than* the critical angle arc $\cos\left\{\frac{1}{e} - \rho\frac{(1 - e^2)}{r_1 e^2}\right\}$, this angle being measured from the straight line P_1O drawn to the refuge, from S_1, as indicated in figure 3. Capture will *not* take place, but, on the contrary S_1 will escape, if the angle mentioned is *greater* than the critical angle of capture. Evidently, as ρ, the distance from the refuge, increases, θ, the critical angle within which capture is possible, increases also. These facts are brought out in the series of diagrams (Fig. 4).

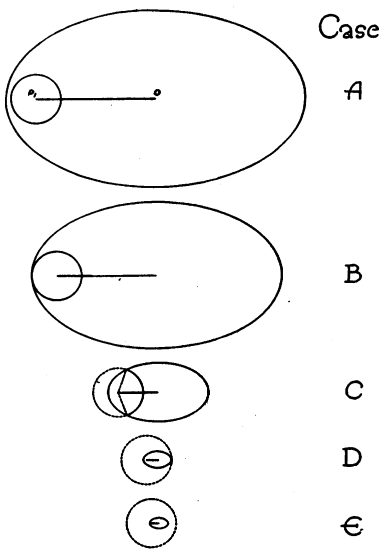

FIGURE 4

Five Types of Encounters, and Their Analytical Characteristics: Safe, Dangerous and Fatal Encounters; also Two Transition Types.—As has already been remarked, it is clear from figure 3 that of all possible azimuths of the position P_2 of S_2 with respect to P_1O at the beginning of the pursuit, those represented by the dashed portion of the circle result in escape, those represented by the fully drawn portion result in capture.

A number of different cases will present themselves, as follows:

Division of Entire Territory into Safe Field, Danger Zone and Fatal Field.

1. If $\rho < \frac{r_1 e}{1 + e}$ the ellipse lies wholly within the circle, without touching

it. In that case capture is impossible, escape is certain; S_1 is *safe*. (Fig. 4*E*.)

2. If $\rho > \frac{r_1 e}{1 - e}$, the circle lies wholly within the ellipse, and capture is certain; S_1 is in a *fatal* position. (Fig. 4*A*.)

3. If $\frac{r_1 e}{1 + e} < \rho < \frac{r_1 e}{1 - e}$, then the ellipse and the circle intersect. This is the case already mentioned, in which capture takes place for some azimuths, but not for others, namely, capture takes place whenever

$$\theta > \text{arc cos}\left\{\frac{1}{e} - \frac{\rho}{r_1}\frac{1 - e^2}{e^2}\right\}$$

Here S_1 is in *danger* of capture. (Fig. 4*C*.)

4. Limiting cases arise if

(*a*) $\rho = \frac{r_1 e}{1 + e}$; the ellipse is then internally tangent to the circle. Capture is possible (for azimuth exactly $\theta = 0$), but is infinitely improbable. (Fig. 4*D*.)

(*b*) $\rho = \frac{r_1 e}{1 - e}$; the circle is then internally tangent to the ellipse. Escape is possible (for azimuth exactly $\theta = \pi$), but is infinitely improbable. (Fig. 4*B*.)

These cases taken together evidently form a graded series, of which a few members are shown in figure 4 to illustrate these relations. If we consider a series of positions of P_1 successively nearer to the refuge, the ellipse, at first large and enclosing the circle, gradually shrinks, till there is contact at one point. On its further shrinking there is, first intersection at two closely neighboring points, so that the angle θ is small; with further approach of P_1 to the refuge the points of intersection spread farther apart, the angle θ increases, and with it the probability of escape. Finally, when the distance of P_1 from the refuge has fallen to $\frac{r_1 e}{1 + e}$, there is again only one point of intersection (contact), the angle θ is π, and escape is assured. On still further approach the ellipse shrinks into the interior of the circle.

* A. J. Lotka, *Am. Math. Month.*, p. 421, 1928. Quite recently the same result has been published independently by V. Lalan, *Compt. Rend.*, **192,** 468, 1931.