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LETTERS TO THE EDITOR

Coexistence of Two Competitors on One Resource

In a recent paper, Koch (1974*b*) presented a computer simulation showing that two predator species can coexist on a single prey species in a spatially homogeneous and temporally invariant environment. This result was then interpreted in the context of Levin's extended exclusion principle (Levin, 1970). In this note we offer a different interpretation of the relation of Koch's work to Levin's and relate both to the classical work of Volterra (1928).

Volterra (1928) was apparently the first to use a mathematical model to demonstrate that under certain conditions it is impossible for two species to coexist indefinitely while using the same resource. Volterra first assumed that the growth of the competing species could be described by a system of differential equations. He then postulated the existence of two species N_1 and N_2 competing for the same resource R and assumed that the specific growth rate of each of the competing species increases linearly with the amount of resource present; that is, he assumed competitor equations of the form

$$\begin{aligned} \frac{1}{N_1}\cdot\frac{\mathrm{d}N_1}{\mathrm{d}t} &= \gamma_1 R-\sigma_1 \\ \frac{1}{N_2}\cdot\frac{\mathrm{d}N_2}{\mathrm{d}t} &= \gamma_2 R-\sigma_2. \end{aligned} \tag{1}$$

Volterra next assumed that the amount of resource available to any competitor at time t is diminished in proportion to the densities of the competitors so that

$$R = R_{\max}-F(N_1, N_2), \tag{2}$$

where F is an increasing unbounded function of N_1 and N_2. Substituting (2) into (1) and replacing $\gamma_i R_{\max}-\sigma_i$ by ε_i, we obtain Volterra's original equations:

$$\begin{aligned} \frac{\mathrm{d}N_1}{\mathrm{d}t} &= N_1[\varepsilon_1-\gamma_1 F(N_1, N_2)] \\ \frac{\mathrm{d}N_2}{\mathrm{d}t} &= N_2[\varepsilon_2-\gamma_2 F(N_1, N_2)]. \end{aligned} \tag{3}$$

Volterra showed that if $\varepsilon_1/\gamma_1 > \varepsilon_2/\gamma_2$ and $N_1(0) \neq 0$, then $N_2(t) \to 0$ as $t \to \infty$. Thus N_2 is eliminated by N_1 in competition for the single resource R.

In addition to the many ecological simplifications, which have been discussed extensively elsewhere (Hutchinson, 1961; Haigh & Maynard Smith, 1972; Stewart & Levin, 1973; Koch, 1974*a*), Volterra's model contains two restrictions on the mathematical form of the equations used: (a) the resource available at time t is a function of the population densities of the competitors at time t, and (b) the specific growth rate of each competitor is a linear function of R. By relaxing both of these assumptions simultaneously, Koch (1974*b*) was able to show by computer simulation that even in a spatially homogeneous and temporally invariant environment the stable coexistence of two predators on a single undifferentiated resource is possible, although this coexistence is not at fixed densities.

We have been investigating the properties of models similar to those used by Koch (1974*b*) and have developed a rigorous proof that the coexistence of two predators on one resource is indeed possible. The details of this proof are too involved to be presented in this note; they will be the subject of a later communication. Our proof complements and confirms Koch's result: that n species can coexist on fewer than n resources. We differ with Koch, however, regarding the implications of this result for the validity of Levin's (1970) proposition that n species cannot coexist on fewer than n "limiting factors". We explore this point more fully below.

The models employed by Koch (1974*b*) and by us (McGehee & Armstrong, 1976) are of the form

$$\begin{aligned}\frac{dN_1}{dt} &= N_1[-m_1+c_1Rp_1(R)]\\ \frac{dN_2}{dt} &= N_2[-m_2+c_2Rp_2(R)]\\ \frac{dR}{dt} &= R[g(R)-N_1p_1(R)-N_2p_2(R)].\end{aligned} \tag{4}$$

Here the resource R is a prey species on which the two competitors N_1 and N_2 prey. The constants m_1 and m_2 are mortality rates of the predators in the absence of prey. The specific growth rate of the prey in the absence of both predators is $g(R)$. For the ith predator the predation rate per predator is the function $Rp_i(R)$ of the prey density. The constants c_1 and c_2 describe the calorific or numerical conversion of prey into predator, depending on the units chosen.

Except in the unlikely case where $-m_1+c_1Rp_1(R)$ and $-m_2+c_2Rp_2(R)$ are both zero for the same value of R, there will be no simultaneous solution of the three equations

$$\frac{dN_1}{dt} = 0,$$

$$\frac{dN_2}{dt} = 0,$$

and

$$\frac{dR}{dt} = 0$$

with N_1 and N_2 both positive. Therefore the two competitors cannot in general coexist at constant population densities.

It can be shown, however, that in a class of equations of the form of equations (4) the solution trajectories forever remain bounded away from the planes $N_1 = 0$, $N_2 = 0$ and $R = 0$ (McGehee & Armstrong, 1976). Thus neither predator can ever approach extinction; the predators coexist indefinitely, though not at fixed densities.

This result reflects directly upon the validity of Levin's (1970) extension of the competitive exclusion principle. In developing his idea, Levin replaces "resources" with more abstract quantities he terms "limiting factors". Levin introduces the following model:

$$\begin{aligned} \frac{dx_k}{dt} &= x_k f_k(z_1, \ldots, z_p), \qquad k = 1, \ldots, n \\ z_j &= z_j(x_1, \ldots, x_n), \qquad j = 1, \ldots, p. \end{aligned} \tag{5}$$

Here x_k represents the population of the kth species, and z_j is the jth limiting factor. The specific growth rate of the kth species is f_k, assumed by Levin to be a linear function of the limiting factors. Given the linearity restriction on the f_k, Levin (1970) showed that stable coexistence cannot occur if $p < n$. On the basis of this result Levin proposed an extended exclusion principle: that n species cannot coexist if they are limited by fewer than n independent "factors".

Levin's proof, however, depends critically on the linearity of the functions $f_1, \ldots f_n$. To see this, consider equations (4) and make the following substitutions:

$$x_1 = N_1, \quad x_2 = N_2, \quad x_3 = R$$

$$z_1(x_1, x_2, x_3) = x_3$$

$$z_2(x_1, x_2, x_3) = g(x_3) - x_1 p_1(x_3) - x_2 p_2(x_3)$$

$$f_1(z_1, z_2) = -m_1 + c_1 z_1 p_1(z_1)$$

$$f_2(z_1, z_2) = -m_2 + c_2 z_2 p_2(z_1)$$

$$f_3(z_1, z_2) = z_2.$$

Equations (4) are then transformed to the form of equations (5) with $p = 2$ and $n = 3$. Since there exists a class of systems of the form of equations (4) in which stable coexistence does occur (Koch, 1974*b;* McGehee & Armstrong, 1976), n species can indeed coexist when limited by fewer than n factors.

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