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# DISPERSION AND POPULATION INTERACTIONS*

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The distribution of a species over its range of habitats is a fundamental and inseparable aspect of its interaction with its environment, and no complete study of population dynamics can afford to ignore it. This point was emphasized over 20 years ago by Skellam (1951) and Hutchinson (1951); and yet, until recently, the mathematical theory of population dynamics has largely ignored spatial considerations. The rise of the theory of island biogeography has given rise, however, to a renewed interest in such questions, particularly with reference to the coexistence of species in a patchwork environment of similar habitats (Cohen 1970; Levins and Culver 1971; Horn and MacArthur 1972; Slatkin, in preparation). The general approach of these investigators is to focus attention simply on the number of patches in which each species is found, intentionally ignoring both the densities of the species within individual patches and the identities of occupied patches. Horn and MacArthur (1972) extend the approach of Levins and Culver (1971) to consider competition between two species over a mosaic of patches of two habitat types, labeled 1 and 2, developing for that purpose the equations

$$\begin{aligned}\frac{dq_1}{dt} &= q_1[(m_{11} - e_1) - m_{11}q_1 - c_1p_1] + m_{21}q_2(1 - q_1)\\ \frac{dq_2}{dt} &= q_2[(m_{22} - e_2) - m_{22}q_2 - c_2p_2] + m_{12}q_1(1 - q_2)\end{aligned} \tag{1}$$

for the respective fractions, $q_1$ and $q_2$, of available patches actually occupied by species 2. Analogous equations apply for species 1 and its occupation fractions, $p_1$ and $p_2$. Here, $m_{ij}$ is a coefficient governing the rate of colonization of habitat $j$ by individuals coming from patches of habitat $i$, so that, for example, $m_{12}q_1$ $(1 - q_2)$ is the rate of colonization of patches of habitat 2 by individuals from habitat 1. Further, $e_i$ is the rate of local extinction in type $i$ patches in the absence of interspecific competition, and $c_ip_i$ the increase in that rate due to competition. Horn and MacArthur (1972) introduce $c_i$ through the statement "species 1 outcompetes species 2 in a fraction $c_1$ of the habitats of type 1 that both species co-occupy," and later identify $c_1 = 1$ with the situation when species 2 always loses in habitat 1. This some-

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* This manuscript is dedicated to the memory of the late Robert H. MacArthur, whose ingenious efforts in stimulating the development of a mathematical ecology were unsurpassed. He will be sorely missed.

what misstates $c_1$'s true role, as a decay rate which must bear reference to a time scale, but the confusion is not central to their main points.

Horn and MacArthur (1972) further restrict their attention to the case

$$m_{22}m_{11} = m_{12}m_{21}, \tag{2}$$

since their model is based on random colonization of patches. Little would be lost, however, in extending their results to the more general case when there is no restriction on the $m_{ij}$ or when, say, colonization of type $i$ patches might conceivably be most likely to occur by colonists from type $i$ patches. In the latter case, the weakened restriction becomes simply

$$m_{11}m_{22} \geqslant m_{12}m_{21}. \tag{3}$$

Such a relaxation of the model would be particularly relevant if the patches were not randomly intermingled but tended to be clumped according to type. Similarly, habitat selection in a coarse-grained environment would necessitate a condition such as (3) in place of (2).

The model discussed above ignores direct reference to the sizes of the individual colonies or the numbers of habitable patches, these variables by implication exerting their influence through the various colonization and extinction parameters.

The main result of the work of Horn and MacArthur (1972) is the criterion for species 2 to be able to invade a patchwork in which species 1 is already present in equilibrial occupancy fractions $\hat{p}_1$ and $\hat{p}_2$. That condition is given as the inequality

$$\frac{m_{11}}{e_1 + c_1\hat{p}_1} + \frac{m_{22}}{e_2 + c_2\hat{p}_2} > 1. \tag{4}$$

If either term on the left exceeds unity by itself, species 2 could invade a habitat made up entirely of patches of the one corresponding type; but otherwise, it is the existence of both sets of patches which permits the invasion.

Note that the potential coexistence does not depend on the fact that there are two *types* of patches. What condition (4) requires is simply that the colonization coefficients $m_{11}$ and $m_{22}$ be sufficiently high with respect to $e_1 + c_1\hat{p}_1$ and $e_2 + c_2\hat{p}_2$. Indeed, in an environment in which there is no ecological distinction between the two types of patches and the labeling is an arbitrary classification which labels half of the patches type 1 and half type 2, it will be the case that $m_{11} = m_{22}$, $e_1 = e_2$, and $c_1 = c_2$. Assuming $\hat{p}_1 = \hat{p}_2$, (4) becomes simply $m_{11} > \frac{1}{2}(e_1 + c_1\hat{p}_1)$, whereas the appropriate condition when only the type 1 patches are habitable is the more stringent $m_{11} > e_1 + c_1\hat{p}_1$. Since type 1 patches are ecologically identical to type 2 patches, the only altered ingredient when type 2 patches are present is that there are twice as many patches. What this means is that coexistence may become possible simply due to a doubling of the number of patches, leading to a doubling of the colonization rates through a doubling of the number of potential colonists. There is no real connection to the existence of two types of patches. The result is more a kind of Allee effect (Allee 1939) in that invasion of a region is only possible if sufficient numbers of supportive colonies of the species are present to reinforce and replace colonies lost to extinction. When the species is low in numbers, growth is slow because recolonization is slow. As it expands, so does the recolonization rate and hence the overall growth rate.

Condition (4) appears at first glance to be independent of the inter-type colonization coefficients $m_{12}$ and $m_{21}$; but this is an artifact caused by assumption (2). Without (2), (4) is replaced by the condition that either $m_{11}/(e_1 + c_1\hat{p}_1) > 1$ or $m_{22}/(e_2 + c_2\hat{p}_2) > 1$ (species 2 can persist in one patch type alone) or else

$$\frac{m_{11}}{e_1 + c_1\hat{p}_1} + \frac{m_{22}}{e_2 + c_2\hat{p}_2} > 1 + \frac{m_{11}m_{22} - m_{12}m_{21}}{(e_1 + c_1\hat{p}_1)(e_2 + c_2\hat{p}_2)}. \tag{5}$$

Thus, if inter-type colonization for the invader (species 2) is reduced without a corresponding increase in intra-type colonization, invasion becomes more difficult, again due to a reduction in the overall recolonization rates. Condition (5) is however not dependent on condition (3).

Note that a general lowering of the barriers to migration for both species will not necessarily make the task easier for an invader, since it is to be expected that such a lowering of the barriers would lead to an increase in the equilibrial values $\hat{p}_1$ and $\hat{p}_2$. Success in invasion by species 2 is thus indirectly related to differential colonization, that is, to the colonization rate of species 2 relative to that of species 1.

Slatkin (in preparation), in reconsidering the problem analyzed by Levins and Culver (1971), has made points which apply equally well to model (1). He points out that the model assumes the probability of extinction, say, of species 2 in patches of a particular type to be related to interspecific competition directly through the fraction $p$ of patches of that type occupied by species 1. Slatkin argues correctly that a more appropriate scheme is an extension of Cohen's approach (Cohen 1970), which considers four possible states for each patch: with or without species 1 and with or without species 2.

It is worthwhile to rephrase and examine in more detail the point raised by Slatkin. Denote by $(i, j)$ the four possible states of a patch, where $i, j = 0$ or 1. [Here, (1, 0) indicates the presence of species 1 alone; (0, 1), only species 2; (1, 1), both; (0, 0), neither.] Slatkin's objection would not be important if the covariance $D = E(ij) - E(i)E(j)$ were zero. In general, however, this is not the case, and such an assumption, in fact, is not consistent with the premises of the model. Hence, the objection cannot be easily dismissed. Indeed, $D$ is undergoing directed change and may be expected to stabilize in the negative region, facilitating coexistence. Model (1) is valid for the consideration of invasion, the case of most interest to Horn and MacArthur (1972), since the random colonization hypothesis implies that initially $D = 0$. For the question of coexistence, however, a modified description is necessary which includes consideration of the $D$ values for the two habitats. The problem suggests very strongly an analogy with the population genetics problem of the consideration of two-locus gametic frequencies, with, for example, the "gamete" $Ab$ corresponding to patches in state (1, 0). In the context of this general approach, the fraction of patches with both species present will be $pq + D$, species 1 alone $p(1 - q) - D$, species 2 alone $q(1 - p) - D$, neither species $(1 - q)(1 - p) + D$. The existence of two types of patches as in the Horn and MacArthur (1972) model, of course, would add a further minor complication.

When the modifications suggested are made, the general approach described above presents some striking potential advantages. For example, it allows one to confront the question of extinction, a stochastic event at the level of the individual patch, and to treat it deterministically by consideration of a large aggregate of patches. Thus, whereas individual patches may be constantly entertaining new tenants, including "fugitives" whose survival depends on rapid dispersal and effective recolonization, the overall species densities for the mosaic should be more predictable and may indeed reach steady state. These ideas are not restricted to the fugitive from competition, such as the insect *Corixa dentipes* cited by Hutchinson (1959). They apply equally well in other contexts, for example, to the "fugitive" prey mites in Huffaker's laboratory predator-prey system (Huffaker 1958) or to the prickly pear *Opuntia* in its flight from the herbaceous moth *Cactoblastis cactorum* (Dodd 1940, 1959; Nicholson 1947). Huffaker's experiments provide a classic example of the role of differential dispersal abilities in allowing two species to coexist.

Although the coexistence described above is based on a balance between local extinctions and recolonizations, complete obliteration of local demes is not a requirement. The essential element is the temporal fluctuation of local population densities, which translates into fluctuation in the environment facing the various species. Moreover, it is not a concept restricted to discrete environments, being equally relevant in continuous ones. The only analytical modification necessary when local fluctuations, rather than extinctions, provide the means for coexistence is the replacement of the gross "occupancy fraction" by some more general spatial average. The fugitive survives simply due to its ability to take advantage of local fluctuations in interspecies pressures, fluctuations which the fugitive's own movements may help maintain. A spatially uniform "equilibrium" would mean extinction of the fugitive.

In the patch occupancy models, population density variations within a patch are ignored. Indeed, what is being assumed is that over the short run, the densities within each patch will reach an equilibrium which can be entirely characterized by the presence or absence of the various species. On the slower time scale, equilibrium is viewed as a balance between colonization and extinction. The technique, when valid, simplifies what may be a very complicated mathematical problem when population densities are considered. For example, when one is dealing with fugitive species, consideration of the equations which are directed to the "fast" time scale, and thus to the transient dynamics of the intrapatch densities of the individual species, must involve the difficult search for stable nonconstant solutions (e.g., limit cycles). On the slower time scale, however, equilibrium can be attained in terms of the *fraction* of patches occupied, although the specific dispersion patterns will necessarily vary with time. For such cases, therefore, this approach has real advantages. It has apparent advantages as well for the consideration of invasion by introduced species, especially in situations where the sizes of individual colonies are relatively unimportant. When, however, the specific dispersal pattern is crucial, as would be the case if migration rates between patches depended on geographical proximity, a different approach is mandated. This might not be a difficulty for the type of epidemic problems considered by Cohen (1970) where individuals (or perhaps families or communes) are highly mobile patches without fixed geographical position. However, for infestation problems as posed for example by the gypsy moth, the geographical spread is of essential importance.

The migration-extinction approach is similarly not adequate when the possible equilibrium colonies may have more than the limited number of characterizations indicated, nor obviously when interest must be focused on the fast time scale. Moreover, even when the approach is valid, it represents a simplification of the full equations, that is, those which allow for consideration of intrapatch densities. For all of these reasons, I now discuss the full equations.

## GENERAL FORMULATION

The approach described in this section is the classical one used in dealing with "diffusion-reaction" systems in many applied contexts; and similar "diffusion equations" may be found in Skellam's work (Skellam 1951). Further, the understanding of the integration of spatial and temporal organization is one of the central problems of theoretical biology and the subject of much current research (e.g., Goodwin and Cohen 1969; Keller and Segel 1970; Othmer and Scriven 1971, 1973; Karlin and McGregor 1972; Gierer and Meinhardt 1972). Much current work (Keller and Segel 1970; Othmer and Scriven 1971, 1973; Gierer and Meinhardt 1972) has taken inspiration from the seminal paper of Turing (1952), which was an attempt to explain the breakdown of symmetry in morphogenesis.

In the form developed by Othmer and Scriven (1971), the equations are very general and serve as a starting point for the development given here. Consider $n$ species distributed over an interconnected network of $m$ patches. The density of species $i$ ($i = 1, \ldots, n$) in patch $\mu$ ($\mu = 1, \ldots, m$) is denoted $x_i^\mu$. Within patch $\mu$, ignoring migrations between patches, the overall growth rate of species $i$ is labeled $f_i^\mu(\boldsymbol{x}^\mu)$, where $\boldsymbol{x}^\mu$ is the vector $(x_1^\mu, \ldots, x_n^\mu)$ of densities of all species in patch $\mu$. The functions $f_i^\mu$ are arbitrary, except that they are assumed to be defined and continuously differentiable on an open set containing the biologically realistic region $R(x_i^\mu \geqslant 0$ for all $i)$, and further that on $R$, $f_i^\mu(\boldsymbol{x}^\mu) \geqslant 0$ if $x_i^\mu = 0$. The last condition is common sense, stating simply that a nonexistent species is in no danger of declining. Migrations into the patch from outside the network, however, might establish the species there, so that $f_i^\mu(\boldsymbol{x}^\mu)$ need not be zero. The net migration of species $i$ from other patches to patch $\mu$ is denoted $J_i^\mu$.

In the simplest case, the net exchange from patch $\nu$ to patch $\mu$ is proportional to $x_i^\nu - x_i^\mu$, a passive migration with nonnegative constant of proportionality $D_i^{\nu\mu}$ ($D_i^{\mu\mu}$ is arbitrarily defined as zero for all $\mu$). With this simplification, $J_i^\mu$ takes the form

$$J_i^\mu = \sum_{\nu=1}^{m} D_i^{\nu\mu}\,(x_i^\nu - x_i^\mu). \tag{6}$$

More generally, if for example predators do not diffuse randomly, but rather in response to a prey gradient, or if fugitive species do not colonize randomly, but are able to seek out unoccupied areas, then a different form of (6) would result (see [8] and [9]). This would similarly be true in the important case when emigration is density-dependent. However, if (6) were to be employed, the governing equations for the system would become

$$dx_i^\mu/dt = F_i^\mu(X, D) = f_i^\mu(\boldsymbol{x}^\mu) + J_i^\mu = f_i^\mu(\boldsymbol{x}^\mu) + \sum_{\nu=1}^{m} D_i^{\nu\mu}(x_i^\nu - x_i^\mu), \tag{7}$$

where $i = 1, \ldots, n$ and $\mu = 1, \ldots, m$, and where

$$X = (\boldsymbol{x}^1, \boldsymbol{x}^2, \ldots, \boldsymbol{x}^m)$$

and

$$D = (D_1^{11}, \ldots, D_1^{m1}, \ldots, D_1^{1m}, \ldots, D_1^{mm}, \ldots, D_n^{mm}).$$

Thus, the form of the equations denotes the dependence of the growth rates not only on the species densities but on the parameters $D_i^{\nu\mu}$ as well. The analogous discrete versions were considered by Karlin and McGregor (1972); results obtained below are continuous analogues of their results.

More generally, the governing equations of the system are given compactly by

$$dx_i^\mu/dt = F_i^\mu(X, D), \tag{8}$$

where $F_i^\mu(X, 0) = f_i^\mu(\boldsymbol{x}^\mu)$. Here 0 is the zero vector in the $nm^2$ parameter space. Note further that the assumptions previously made on the functions $f_i^\mu$ and the nonnegativity of the elements of $D$ guarantee that

$$F_i^\mu(X, D) \geqslant 0 \text{ if } x_i^\mu = 0 \text{ and } X \in R, \tag{9}$$

and the $F_i^\mu$ are continuously differentiable.

Equations (8) and (9) summarize the essential properties of the dynamics. Moreover, as indicated earlier, (8) and (9) describe a much more general framework not tied, for example, to the colonization assumptions underlying (6).

Using this framework, two questions of biological interest are assessed in succeeding sections: (i) To what extent does the spatial component of the environment lead to the coexistence of species which could not coexist within a single patch? (ii) To what extent is the behavior of the system affected by migration rates?

## COMPETITION IN PATCHY ENVIRONMENTS

The outcome of interspecies interactions may not be completely determinate but may depend in an essential way on initial densities (Park 1962; Slobodkin 1961). Species which are able to reach and colonize areas first may be able to establish themselves and thereby resist invasions by species that might otherwise exclude them. Indeed, the possibility of such a situation is inherent in even the simplest of competition models, provided only that parameters are properly chosen. It occurs, for example, in the Lotka-Volterra competition equations, rewritten as

$$dx/dt = x(R - ax - by),$$
$$dy/dt = y(S - cx - dy),$$

provided interspecific competition outweighs intraspecific:

$$a/c < R/S < b/d. \tag{10}$$

Here $x$ and $y$ represent species densities. Note that in this formulation, the "saturation values" (Slobodkin 1961) are $R/a$ and $S/d$ respectively, and the "coefficients of competition" are respectively $b/a$ and $c/d$. The situation is also present in much more general models and, indeed, will occur whenever the defining equations are of the form

$$dx_i/dt = f_i(x), \qquad i = 1, \ldots, n \tag{11}$$

and possess more than one stable equilibrium (or, more generally, more than one stable attractor).

Consider then a network of $m$ initially identical patches, in each of which considered alone one or more of the $n$ species would become extinct but in each of which every species has the potential to survive given a sufficient lead. Then, for any specified collection of species, there exists a number $N$ such that, if the number of patches $m$ exceeds $N$ and if there is no migration between patches, a stable configuration is possible with all of those species present. (Below I show that the "no migration" condition can be relaxed.) In particular, if $m > N$, then a stable arrangement would be possible with, say, species 1 (and perhaps other species) established in patch 1 (and perhaps elsewhere), species 2 in patch 2, etc.

If some migration is now allowed between patches ($D \neq 0$ but $D$ "close to" 0), a perturbation theorem (Appendix 1) applies and a new equilibrium results with all species present. In this case, the equilibrium number of species in the mosaic is dependent on initial densities and the connectedness $D$ of the network. In particular, if the matrix $\Delta_i = (d_i^{\mu\nu})$ is *irreducible* (Gantmakher 1959), then species $i$ will at equilibrium be represented in every patch. In general, in a patchy environment, individual patches (or islands) may be expected to vary substantially in their species lists (Simberloff and Wilson 1969, 1970; Root 1973; Paine, personal communication).

The above results correspond to similar results derived in the discrete time system by Karlin and McGregor (1972).

Assuming that extinctions of local populations due to external factors occur on a slower time scale than that of intrapatch dynamics, the individual patches may be reasonably regarded as "equilibrium patches," in equilibria which track the changes in external factors, and a colonization-extinction approach to the expected equilibrium number of species becomes relevant. The theory presented in this section may be considered as directed to the fast time scale and would be complemented by a colonization-extinction approach to the colonization-extinction equilibrium. Such an approach in general would have to consider the distributions in sizes and relative geographic locations (through $D$) of the various equilibrium patches and would seek the correlation between communities as a function of distance, as did Kimura and Weiss (1964), Weiss and Kimura (1965), and others in considering stepping-stone models of genetic correlation.

In summary, coexistence is made possible in a patchy environment because of a scenario whereby initially identical patches subject to random colonization diverge in species lists, through a kind of founder principle, culminating in a "linked" joint equilibrium in which a much higher diversity results than would be possible in a single patch. Diversity (number of species) generally increases as the number of patches increases until it reaches its maximum possible value. However, since in some sense perfect mixing (equivalently, a single homogeneous patch) is the limiting case as the interpatch elements of $D$ become infinite, diversity eventually may be expected to decrease as migration increases beyond some critical threshold. This result needs to be made more precise, however, and computer studies of the relation of the equilibrium number of species to $D$ would be very enlightening.

As pointed out elsewhere (Levin 1970), stable coexistence is only possible provided the effective number of limiting factors is as great as the number of species. When, for example, two species are limited by a single resource, no stable equilibrium exists. A patchy environment may, however, increase the number of limiting factors, say by increasing the number of resource or prey species, and further by making relevant local densities within patches rather than overall densities. Though the environment may have been uniform initially, it becomes heterogeneous (in the sense of Smith [1972]) as a result of what may be random initial disturbances. Obviously, this scenario depends neither on the initial uniformity nor on the randomness of disturbances. What is striking is that it can occur even in the face of these.

Note that in this example coexistence occurs because of the spatial component of the environment but is not dependent on fluctuations in local densities. Further, higher migration rates tend to homogenize the system and to reduce the potential for coexistence. This contrasts with coexistence due to fugitive strategies, where high migration rates do not homogenize (quite the contrary) and coexistence is the result of sustained fluctuations in the environment. Patchiness does not require the existence of multiple types of patches. The above results were derived under the assumption that all patches were identical, precisely to emphasize this point. If, however, patches are of a variety of types, the perturbation theorem still applies; that is, small amounts of migration do not destabilize an arrangement which is stable without migrations. To quote Karlin and McGregor (1972), "complex systems when combined with slight migration between them produce even more complex systems with more possibilities and representations of stable polymorphisms."

## COMPETITION BETWEEN TWO SPECIES OVER TWO PATCHES

To exemplify the general results just given, this section deals with the simplest case, two species in competition in two patches which differ only with regard to the species densities. For simplicity of illustration, the dynamics introduced earlier,

$$\begin{aligned} dx/dt &= x(R - ax - by), \\ dy/dt &= y(S - cx - dy), \end{aligned} \tag{12}$$

are assumed within each patch. (Again, the qualitative results do not depend on such oversimplified equations.) Equivalence of the two patches means that the same parameters $R$, $S$, $a$, $b$, $c$, and $d$ apply in each patch. Assume further that $a/c < R/S < b/d$, condition (10). This means that coexistence is not possible within a single patch but that either species can establish itself given a sufficient lead.

As is well known, the system (12) has four equilibria (fig. 1), stable ones at $(R/a, 0)$ and $(0, S/d)$ and unstable ones at $O = (0, 0)$ and

$$U = \left( \frac{Rd - Sb}{ad - bc}, \frac{-Rc + Sa}{ad - bc} \right).$$

When the two patches are considered together, and migration is passive, the corresponding equations take the form

$$\begin{aligned} dx_i/dt &= x_i(R - ax_i - by_i) + D_x(x_j - x_i), \\ dy_i/dt &= y_i(S - cx_i - dy_i) + D_y(y_j - y_i), \quad i, j = 1, 2; i \neq j, \end{aligned} \tag{13}$$

where $D_x$ and $D_y$ are the species-specific migration rates between patches.

In the completely symmetric case, when the species behave identically except for the (symmetric) effects of interspecific competition, $R = S$, $a = d$, $b = c$, and $D_x = D_y$. Congeneric species might reasonably be ex-

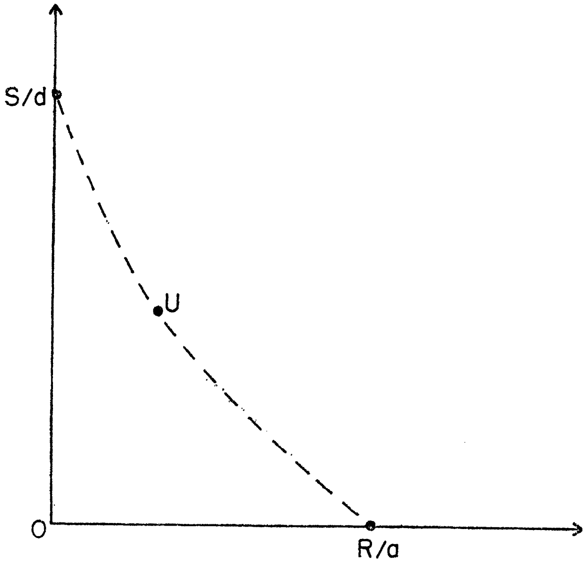

FIG. 1.—The four equilibria for the system (12)

pected to approximate this behavior, if sufficiently close, but the choice is made here simply for ease of illustration. In this case, the system becomes

$$dx_i/dt = x_i(R - ax_i - by_i) + D(x_j - x_i),$$
$$dy_i/dt = y_i(R - bx_i - ay_i) + D(y_j - y_i), \quad i, j = 1, 2; \quad i \neq j, \tag{14}$$

where the subscript on $D$ has been dropped. Equation (10) becomes simply

$$a < b. \tag{15}$$

For small D, the qualitative behavior of (14) is the same as that for (13), but the symmetry makes arithmetic calculation a great deal simpler. Hence, (14) will be analyzed in closer detail.

Note first that the uncoupled equations

$$dx/dt = x(R - ax - by)$$
$$dy/dt = y(R - bx - ay)$$

have four possible equilibria (see fig. 2):

$$\begin{aligned} \text{I}&: x = 0, \ y = 0, && (0) \\ \text{II}&: x = 0, \ y = R/a, && \\ \text{III}&: x = R/a, \ y = 0, && \\ \text{IV}&: x = R/(a+b), \ y = R/(a+b). && (U) \end{aligned}$$

In light of (15), only II and III are stable, and correspond to the exclusion of one or the other species. Moreover, almost every solution tends either to state II or to III, depending on which species is initially more abundant.

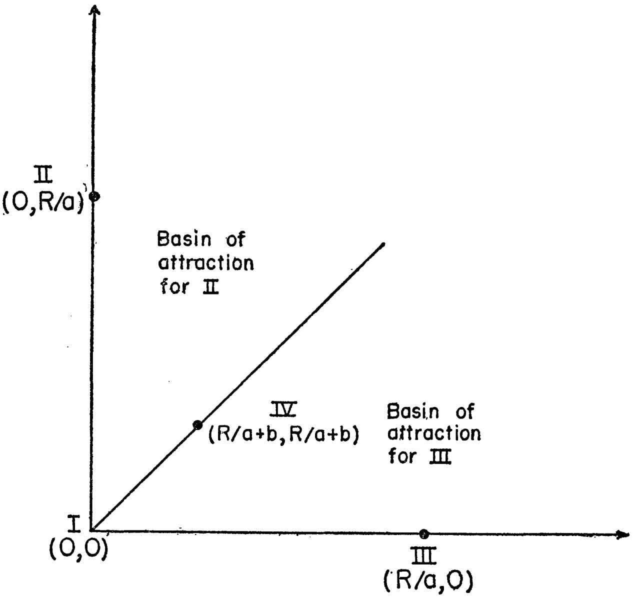

FIG. 2.—The four possible equilibrium states for the system $\dot{x} = x(R - ax - by)$, $\dot{y} = y(R - bx - ay)$, with basins of attraction shown.

Only the thin ridge $x = y$ of initial conditions does not lead to II or III being perched precariously between the two basins of attraction.

When $D = 0$, the system (14) clearly has 16 possible equilibrium states, since it is still uncoupled and each patch has four possible equilibria. However, only four of these, denoted (II, II), (II, III), (III, II), and (III, III), are stable. When $D > 0$, the four homogeneous equilibrium states (I, I), (II, II), (III, III), and (IV, IV) remain and with the same stability characteristics as previously, respectively unstable, stable, stable, and unstable. The coupling destroys 10 of the other equilibria not under the protection of the perturbation theorem, since they were initially unstable, but the remaining two, (II, III) and (III, II), are the most interesting of all. Due to the symmetry, it suffices to consider just (II, III).

When there is no coupling, the system (14) as stated permits an equilibrium at (II, III), that is, at

$$x_1 = 0,\ y_1 = R/a,\ x_2 = R/a,\ y_2 = 0.$$

This equilibrium is shown in figure 3*a*, where *1* denotes the equilibrium in patch 1, *2* the equilibrium in patch 2; and again in figure 3*b*. In short, the equilibrium discussed is one in which species 2 alone prevails in patch 1, and species 1 in patch 2.

When $D > 0$ and is small, the perturbation theorem (Appendix 1) guarantees that the equilibrium (II, III) does not disappear. Rather, it moves slightly off the axes. To be precise, for

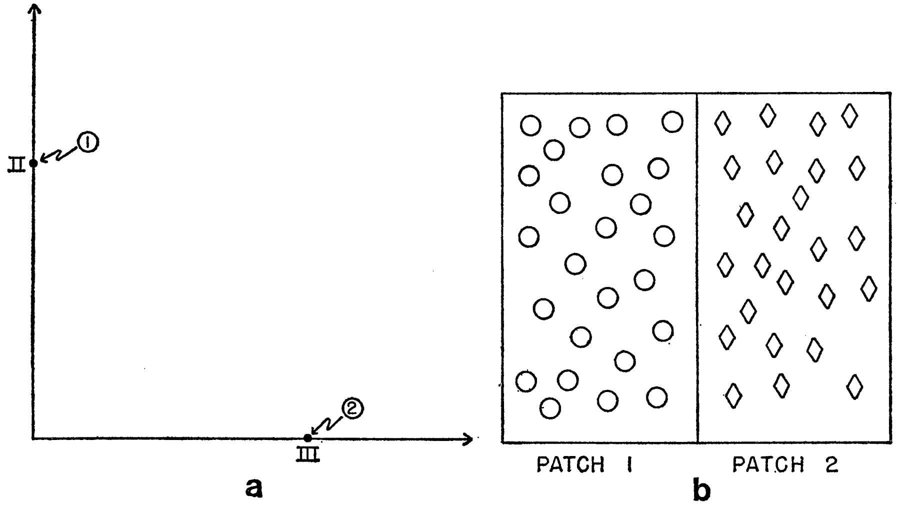

FIG. 3.—*a,* The equilibrium (II, III) for the system (14) when $D = 0$. *b,* An alternate representation of the equilibrium in *a.* Circles indicate individuals of species 2; diamonds, individuals of species 1.

$$0 \leqslant D \leqslant \frac{R}{2} \cdot \frac{b-a}{b+a}, \tag{16}$$

(14) has an equilibrium at

$$\begin{aligned} x_1 = y_2 &= \frac{R-2D}{2a} - \frac{1}{2a}\sqrt{\left(R-2D\right)\left(R-2D\frac{b+a}{b-a}\right)}, \\ x_2 = y_1 &= \frac{R-2D}{2a} + \frac{1}{2a}\sqrt{\left(R-2D\right)\left(R-2D\frac{b+a}{b-a}\right)}. \end{aligned} \tag{17}$$

It is easy to check, using (15) and (16), that these values are real and (for $D > 0$) positive. Furthermore, as $D$ tends to 0, the equilibrium clearly tends to (II, III), that is, to $x_1 = y_2 = 0$ and $x_2 = y_1 = R/a$, as predicted by the perturbation theorem. Finally, note that as $D$ tends to $(R/2) \cdot (b-a)/(b+a)$, the equilibrium tends to the homogeneous one (IV, IV), that is, to

$$x_1 = y_2 = x_2 = y_1 = R/(b+a),$$

which explains condition (16).

The perturbation theorem does not guarantee that (17) remains stable but only that it does so for $D$ small enough. Condition (16) is not sufficient to guarantee this, and in fact it may be shown (Appendix 2) that the equilibrium is stable for

$$0 \leqslant D < \frac{R}{2} \cdot \frac{b-a}{2b+a} \tag{18}$$

but unstable for

$$\frac{R}{2}\cdot\frac{b-a}{2b+a}<D\leqslant\frac{R}{2}\cdot\frac{b-a}{b+a}. \tag{19}$$

The entire situation is summed up in figure 4. In figure 4*a*, as $D$ increases from 0 toward the threshold value $(R/2)\cdot(b-a)/(b+a)$, the points $(x_1, y_1)$ and $(x_2, y_2)$, representing the equilibrium densities within the two patches, move symmetrically toward each other along the hyperbola

$$ax^2+2bxy+ay^2-Rx-Ry=0,$$

finally coalescing when $D$ hits the value $(R/2)\cdot(b-a)/(b+a)$. The joint equilibrium is stable only until $D$ reaches the value $(R/2)\cdot(b-a)/(2b+a)$, which corresponds to the equilibrium

$$x_1=y_2=\frac{R}{2a}\cdot\frac{b+2a}{2b+a}-\frac{R}{2a(2b+a)}\sqrt{b^2+2ab},$$

$$x_2=y_1=\frac{R}{2a}\cdot\frac{b+2a}{2b+a}+\frac{R}{2a(2b+a)}\sqrt{b^2+2ab}.$$

In summary, when there are at least two patches in the environment, coexistence of two species that would otherwise exclude each other is possible. Each establishes itself in one patch sufficiently to withstand invasion, and each is found in the other patch due to sustained migration from the favored territory. When the migration is too high (condition 19), mixing is rapid enough that there is effectively only a single patch, and coexistence is no longer possible.

Global analysis for this case has been performed by the author and L. E. Payne and will be published separately.

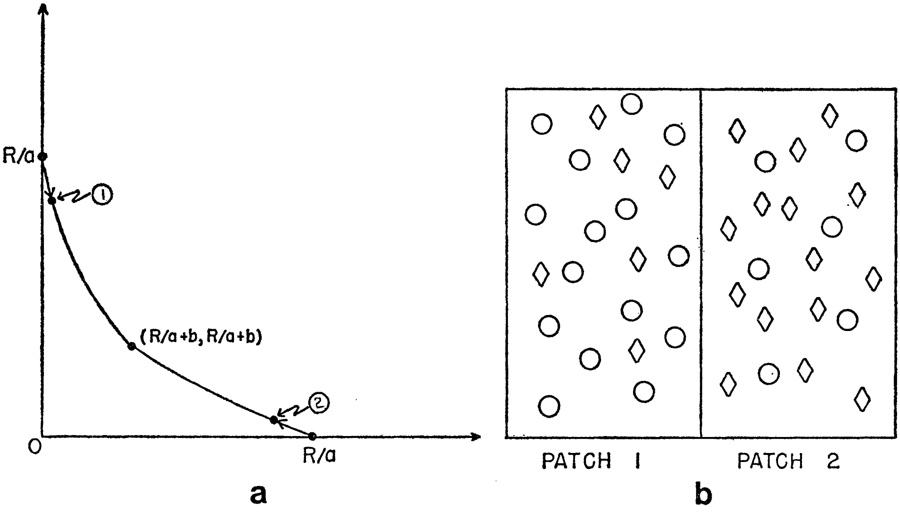

FIG. 4.—*a*, The nonhomogeneous competitive coexistence equilibrium for the system (14) when $D>0$ and is small. *b*, An alternate representation of the equilibrium in *a*. Circles indicate individuals of species 2; diamonds, individuals of species 1.

## THE DEVELOPMENT OF SPATIAL AND SPATIO-TEMPORAL PATTERNS

Opportunities for movement and habitat diversification provided by the spatial aspect of environment make possible in a variety of ways coexistence of species which could not otherwise survive together. If the environment is heterogeneous, different combinations of species are likely to be favored in the various local regions and maintained elsewhere principally by dispersal from more favored regions, and this will act to increase the overall species richness. This spatial heterogeneity in environment may be externally imposed, consisting principally of variation in weather, climate, edaphic factors, etc., or, as shown earlier, it may arise as a result of a divergence between subregions or patches due to an essentially random variation with respect to colonization. In any case, such spatial patterns are steady state, and are not related to temporal fluctuations in local densities.

When species life history patterns are such that local populations have periodic dispersal episodes, or when the environment varies in time, a premium is placed on how fast species can get to and utilize choice areas. In this case, opportunity exists for species which would otherwise become extinct to survive as fugitives, distributed according to spatio-temporal patterns involving consistently fluctuating local population densities. As with the steady-state strategy, the fugitive strategy can arise in an initially spatially uniform environment, since the spatio-temporal fluctuations in environment may be strongly coupled in a feedback relationship to the fluctuations in species densities. Such situations may be studied by seeking stable nonconstant solutions to (7) or continuous analogues of it, typically of the form

$$\frac{\partial x_i}{\partial t} = f_i(x, z) + \nabla \cdot (D_i \nabla x_i),$$

where $\nabla$ denotes the gradient with respect to the spatial variables, $z$. Such models, discrete or continuous, provide as well the starting point for the computation of the spatially nonuniform but steady-state distributions described previously. This computation is a difficult mathematical problem, but an elegant beginning to its solution may be found in Othmer and Scriven (1973).

Such spatial patterns, both steady state and temporally varying, may arise in a variety of ways. They may be, as stated earlier, determined by the patterns of initial colonization in newly available areas. Alternatively, they may arise simply due to invasion episodes of sufficient intensity to allow the invader to become established in some locale or through a fugitive strategy. Finally, they may arise through a change in either the species densities or in the basic interactions between species, when the change is sufficient to destabilize a previously uniform coexistence pattern. One particularly striking example, owing in motivation to Turing (1952), is that in which an increase in the ability to migrate by some species can destabilize the system. This phenomenon may be termed *diffusive* or *dissipative* instability (Segel and Jackson 1972). Many results discussed below parallel results discovered in the spatially continuous case by Segel and Jackson (1972). As with fugitive species, the lack of perfect mixing (over the spatial region) is responsible, since this effectively introduces a destabilizing time lag.

Basically, diffusive instabilities arise when diffusion or migration destabilizes an otherwise stable situation, in contrast to one's usual intuitions concerning the effects of diffusion. The theory has been explored by Turing (1952), Othmer and Scriven (1971, 1973), Keller and Segel (1970), Segel and Jackson (1972), and others, principally in developmental contexts. The effect of such instabilities is that, for example, a predator-prey relationship which permits stable coexistence when migration rates are low might become destabilized when the ability to migrate increases. The two species might still coexist, but in an oscillatory pattern similar to that caused by the fugitive species or in a steady-state but spatially nonuniform distribution such as discussed above. Although the prey could persist even without oscillations, there is clear advantage to individual prey to migrate to escape predation, and this may lead to evolutionary pressures toward destabilization. From the "viewpoint" of the predator population, increased migration becomes a necessity to stabilize an otherwise unstable situation and allow survival.

Diffusive instabilities do not arise in purely competitive systems. Further, they only arise in predator-prey systems when one species is rare enough that an Allee effect is applicable; that is, they arise only when the per capita rate of growth of the rare species is an increasing function of density due, say, to an increased ability to find mates. The Allee effect is inconsistent with stability in the purely competitive case.

By way of example, consider the interaction between an abundant prey and a rare predator, described near equilibrium by modified Lotka-Volterra equations:

$$dx/dt = x(K - ax - by),$$

$$dy/dt = y(-L + cx + dy).$$

These differ from the usual Lotka-Volterra predator-prey equations only in the sign of $d$, which reflects the Allee effect.

These equations permit a stable equilibrium at

$$x = \frac{Lb - Kd}{bc - ad}, \quad y = \frac{Kc - La}{bc - ad},$$

provided $ad < bc$ and

$$\frac{a}{c} < \frac{K}{L} < \frac{a}{d} \cdot \frac{b + d}{a + c} = \frac{a}{c} + \frac{a}{cd} \cdot \frac{bc - ad}{a + c}. \tag{20}$$

The corresponding system over two patches, with differential migration coefficients $\mu$, $\nu$ included,

$$\begin{aligned} dx_i/dt &= x_i(K - ax_i - by_i) + \mu(x_j - x_i), \\ dy_i/dt &= y_i(-L + cx_i + dy_i) + \nu(y_j - y_i), \; j \neq i, \end{aligned} \tag{21}$$

obviously permits the equilibrium

$$\bar{x}_1 = \bar{x}_2 = \frac{Lb - Kd}{bc - ad}, \quad \bar{y}_1 = \bar{y}_2 = \frac{Kc - La}{bc - ad},$$

but (Appendix 3) this equilibrium is unstable for large $\mu$ and small $\nu$, that is, for

$$\left(\mu + \frac{a\bar{x}_1}{2}\right)\left(\nu - \frac{d\bar{y}_1}{2}\right) < \frac{-bc\bar{x}_1\bar{y}_1}{4}.$$

This inequality defines a region in $(\mu, \nu)$-space with boundary the hyperbola

$$\left(\mu + \frac{a\bar{x}_1}{2}\right)\left(\nu - \frac{d\bar{y}_1}{2}\right) = \frac{-bc\bar{x}_1\bar{y}_1}{4}.$$

The regions of stability and instability are illustrated in figure 5.

Thus, an increase in mobility of the prey, expressed as increased migration $\mu$, will lead to a destabilization of the balance between predator and prey. However, no rate of migration by the prey is too great for the predator to overcome through increased ability to migrate on its own part. In particular, if $\nu > d\bar{y}_1/2$, the system is always stable.

This linear approach to the destabilization of the predator-prey system does not distinguish between the alternatives which result: (i) attainment of a new steady state, very possibly spatially nonuniform, (ii) limit cycle oscillations, in which predator and prey undergo their familiar coupled temporal oscillations, and (iii) extinction of the system. Moreover, it is not clear how common this phenomenon is in nature. It is, however, an intriguing possibility which lends itself to laboratory testing.

Finally, cooperative effects similar in effect to the Allee effect may be more common in prey than in predator, as increasing prey population size may decrease the per capita predation load (Rosenzweig and MacArthur 1963; Rosenzweig 1969). Results similar to those discussed in this section are found for systems in which these effects occur (Segel and Jackson 1972).

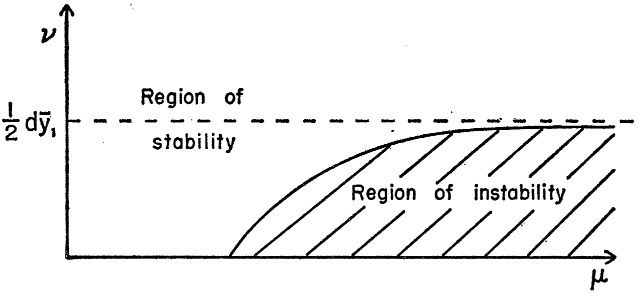

FIG. 5.—Stability diagram for the homogeneous equilibrium in the predator-prey system (21).

## SUMMARY

The spatial component of environment, often neglected in modeling of ecological interactions, in general operates to increase species diversity. This arises due to the heterogeneity of the environment, but such heterogeneity can arise in an initially homogeneous environment due to what may be random initial events (e.g., colonization patterns), effects of which are magnified by species interactions. In this way, homogeneous environments may become heterogeneous and heterogeneous environments even more so. In patchy environments, distinct patches are likely to be colonized initially by different species, and thereby a kind of founder effect results whereby individual patches evolve along different paths simply as a consequence of initial colonization patterns. Species which would be unable to invade may nevertheless survive by establishing themselves early and will moreover be found in lower densities in other areas as overflow from their "safe" areas. Spatially continuous environments may evolve toward essentially patchy ones by this kind of process. Overall species richness is expected to be higher in patchy environments but to decrease as the ability of species to migrate becomes large. These results are due to patchiness per se and do not depend on the existence of several kinds of patches, a situation which will tend to reinforce these effects.

Diversity is also increased in such environments with spatial extent due to the opportunities for fugitive-type spatio-temporal strategies. In these, local population oscillations provide the salvation for species which are for example competitively inferior or easy victims to predation but which can survive by superior migratory ability and (in patchy environments) talent for recolonization. Again, dependence is on spatial heterogeneity, in addition to temporal heterogeneity; again, this may be externally imposed or the result largely of internal processes.

Some gross statistics for these processes, principally patch occupancy fractions, may prove useful for a simplified treatment of colonization-extinction equilibria, as in the approaches of Cohen (1970), Levins and Culver (1971), Horn and MacArthur (1972), and Slatkin (in preparation). For such considerations, however, one cannot assume independence of distributions; and the approach of Cohen (1970) and Slatkin (in preparation), which allows for consideration of covariance, is favored.

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# APPENDIX 1

## PERTURBATION THEOREM

The theorem below is mathematically quite intuitive and is an analogue of one proved in Karlin and McGregor (1972) in the discrete time case. As they point out, its implications for population dynamics are substantial.

Theorem: *Assume that* $F_i^\mu(X, D) \geqslant 0$ *when* $x_i^\mu = 0$ *and* $X \geqslant 0$, *and that the system* $dx_i^\mu/dt = F_i^\mu(X, D_0)$ *has a stable equilibrium (the eigenvalues of the Jacobian matrix have negative real parts) at* $X = X_0 \geqslant 0$. *Then for* $D$ *sufficiently close to* $D_0$, *the system* $dx_i^\mu/dt = F_i^\mu(X, D)$ *has a stable equilibrium at some point* $X_D \geqslant 0$, *where* $X_D$ *tends to* $X_0$ *as* $D$ *tends to* $D_0$.

The notation $X \geqslant 0$ means that all components of $X$ are nonnegative. The quantity $F_i^\mu$ is assumed to be continuously differentiable in $X$ and $D$.

The proof of the perturbation theorem is given in Levin (in preparation) and rests on the condition $F_i^\mu(X, D) \geqslant 0$ when $x_i^\mu = 0$, which assures that trajectories do not cross the coordinate plane into the negative region.

# APPENDIX 2

## STABILITY ANALYSIS FOR (17)

Here I prove that (17) is stable if $D < (R/2) \cdot (b - a)/(2b + a)$ and unstable if $D > (R/2)\ (b - a)/(2b + a)$. For clarity, the bar notation denotes equilibrium values to free $x_1$, $y_1$, $x_2$, and $y_2$ for more general usage. Thus,

$$\bar{x}_1 = \bar{y}_2 = \frac{R - 2D}{2a} - \frac{1}{2a}\sqrt{\left(R - 2D\right)\left(R - 2D\frac{b + a}{b - a}\right)},$$

$$\bar{x}_2 = \bar{y}_1 = \frac{R - 2D}{2a} + \frac{1}{2a}\sqrt{\left(R - 2D\right)\left(R - 2D\frac{b + a}{b - a}\right)}.$$

Setting

$$\tilde{u} = \begin{pmatrix} x_1 - \bar{x}_1 \\ y_1 - \bar{y}_1 \\ y_2 - \bar{y}_2 \\ x_2 - \bar{x}_2 \end{pmatrix}$$

and linearizing (14) about the equilibrium, one obtains the system of equations

$$\frac{d\tilde{u}}{dt} = (I_2 \otimes J + DK \otimes K)\tilde{u} + \dots . \tag{22}$$

Here

$$I_2 = \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}, \quad K = \begin{pmatrix} 0 & 1 \\ 1 & 0 \end{pmatrix},$$

$$J = \begin{pmatrix} R - 2a\bar{x}_1 - b\bar{y}_1 - D & -b\bar{x}_1 \\ -b\bar{y}_1 & R - b\bar{x}_1 - 2a\bar{y}_1 - D \end{pmatrix}$$

$$= \begin{pmatrix} R - b\bar{x}_2 - 2a\bar{y}_2 - D & -b\bar{y}_2 \\ -b\bar{x}_2 & R - 2a\bar{x}_2 - b\bar{y}_2 - D \end{pmatrix},$$

and $\otimes$ denotes the tensor product of two matrices. (For an excellent introduction to this notation and the methods used in this Appendix, see Othmer and Scriven [1971].) Since the matrices $I_2$ and $K$ are self-adjoint with common spectral representation, a theorem of Friedman (1956) applies. The stability of (22) is determined by the eigenvalues of $\boldsymbol{I}_2 \otimes \boldsymbol{J} + D\boldsymbol{K} \otimes \boldsymbol{K}$, which are the eigenvalues of the matrices $\boldsymbol{J} \pm D\boldsymbol{K}$. But

$$\boldsymbol{J} \pm D\boldsymbol{K} = \begin{pmatrix} R - 2a\bar{x}_1 - b\bar{y}_1 - D & \pm D - b\bar{x}_1 \\ \pm D - b\bar{y}_1 & R - b\bar{x}_1 - 2a\bar{y}_1 - D \end{pmatrix}.$$

The four eigenvalues of these two matrices will all have negative real parts if and only if the (common) trace $T$ of these matrices is negative and the determinants positive. But

$$\begin{aligned} \mathrm{T} &= 2R - (2a + b)(\bar{x}_1 + \bar{y}_1) - 2D \\ &= 2R - (2a + b)\frac{R - 2D}{a} - 2D \\ &= -\frac{b}{a} \cdot R + \frac{2D}{a}(b + a) \\ &= \frac{2(b + a)}{a} \cdot \left[D - \frac{R}{2}\left(\frac{b}{b + a}\right)\right]. \end{aligned}$$

Thus, by (16), $T$ is always negative.

Finally, the determinants will be positive if and only if

$$(R - 2a\bar{x}_1 - b\bar{y}_1 - D)(R - b\bar{x}_1 - 2a\bar{y}_1 - D) > (D + b\bar{x}_1)(D + b\bar{y}_1),$$

that is, if and only if

$$[(R - 2a\bar{x}_1) - (b\bar{y}_1 + D)][(R - 2a\bar{y}_1) - (b\bar{x}_1 + D)] \\ > (D + b\bar{x}_1)(D + b\bar{y}_1).$$

This condition simplifies to

$$(R - 2a\bar{x}_1)(R - 2a\bar{y}_1) > (b\bar{x}_1 + D)(R - a\bar{x}_1) + (b\bar{y}_1 + D)(R - 2a\bar{y}_1),$$

and further to

$$R^2 - 2aR(\bar{x}_1 + \bar{y}_1) + 4a^2\bar{x}_1\bar{y}_1 > 2DR + \\ (Rb - 2aD)(\bar{x}_1 + \bar{y}_1) - 2ab(\bar{x}_1^2 + \bar{y}_1^2).$$

Simplifying further, one obtains

$$R(R - 2D) + [2aD - R(b + 2a)](\bar{x}_1 + \bar{y}_1) \\ > -2ab(\bar{x}_1 + \bar{y}_1)^2 + 4a(b - a)\bar{x}_1\bar{y}_1.$$

Substituting

$$\bar{x}_1 + \bar{y}_1 = \frac{R - 2D}{a}, \qquad \bar{x}_1\bar{y}_1 = \frac{D(R - 2D)}{a(b - a)},$$

one gets

$$R(R - 2D) + [2aD - R(b + 2a)]\frac{R - 2D}{a} \\ > -2ab\frac{(R - 2D)^2}{a^2} + 4D(R - 2D).$$

Since $R - 2D > 0$, this becomes

$$R + \frac{1}{a}[2aD - R(b + 2a)] > -2\frac{b}{a}(R - 2D) + 4D,$$

that is,

$$R\left(\frac{b - a}{a}\right) > D\frac{2(a + 2b)}{a}.$$

Thus, the equilibrium is stable if

$$D < \frac{R}{2} \cdot \frac{b - a}{a + 2b}$$

and unstable if

$$D > \frac{R}{2} \cdot \frac{b - a}{a + 2b}$$

## APPENDIX 3

### STABILITY ANALYSIS FOR PREDATOR-PREY EQUATIONS

The stability of the homogeneous equilibrium

$$\bar{x}_1 = \bar{x}_2 = \frac{Lb - Kd}{bc - ad}, \qquad \bar{y}_1 = \bar{y}_2 = \frac{Kc - La}{bc - ad} \tag{23}$$

for the system (21) depends on the eigenvalues having negative real parts for the equilibrium Jacobian matrix:

$$\boldsymbol{M} = \begin{pmatrix} -a\bar{x}_1 - \mu & -b\bar{x}_1 & \mu & 0 \\ c\bar{y}_1 & d\bar{y}_1 - \nu & 0 & \nu \\ \mu & 0 & -a\bar{x}_1 - \mu & -b\bar{x}_1 \\ 0 & \nu & c\bar{y}_1 & d\bar{y}_1 - \nu \end{pmatrix}$$

$$= \boldsymbol{I}_2 \otimes \begin{pmatrix} -a\bar{x}_1 & -b\bar{x}_1 \\ c\bar{y}_1 & d\bar{y}_1 \end{pmatrix} + \begin{pmatrix} -1 & 1 \\ 1 & -1 \end{pmatrix} \otimes \begin{pmatrix} \mu & 0 \\ 0 & \nu \end{pmatrix}.$$

Using the theorem of Friedman (1956) employed in Appendix 2, one finds that the eigenvalues of $\boldsymbol{M}$ are the eigenvalues of the matrices

$$\begin{pmatrix} -a\bar{x}_1 & -b\bar{x}_1 \\ c\bar{y}_1 & d\bar{y}_1 \end{pmatrix} \text{ and } \begin{pmatrix} -a\bar{x}_1 - 2\mu & -b\bar{x}_1 \\ c\bar{y}_1 & d\bar{y}_1 - 2\nu \end{pmatrix}.$$

By the stability of the equilibrium when $\mu = \nu = 0$, the criterion when $\mu, \nu \neq 0, 0$ reduces to

$$\left(\mu + \frac{a\bar{x}_1}{2}\right)\left(\nu - \frac{d\bar{y}_1}{2}\right) > \frac{-bc\bar{x}_1\bar{y}_1}{4},$$

as was to be proved.

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