



A Mathematical Model of Coevolving Populations

Simon A. Levin, J. Daniel Udovic

American Naturalist, Volume 111, Issue 980 (Jul. - Aug., 1977), 657-675.

Stable URL:

<http://links.jstor.org/sici?sici=0003-0147%28197707%2F197708%29111%3A980%3C657%3AAMMOC%3E2.0.CO%3B2-%23>

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

American Naturalist is published by The University of Chicago Press. Please contact the publisher for further permissions regarding the use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/ucpress.html>.

American Naturalist

©1977 The University of Chicago Press

JSTOR and the JSTOR logo are trademarks of JSTOR, and are Registered in the U.S. Patent and Trademark Office. For more information on JSTOR contact jstor-info@umich.edu.

©2002 JSTOR

A MATHEMATICAL MODEL OF COEVOLVING POPULATIONS

SIMON A. LEVIN AND J. DANIEL UDOVIC

Section of Ecology and Systematics, Cornell University, Ithaca, New York 14850;
and Department of Biology, University of Oregon, Eugene, Oregon 97403

Interactions between populations have both demographic and evolutionary consequences. Although this point has been made by many authors beginning with Darwin, the interaction between demographic and evolutionary variables has been until recently largely ignored in the development of theory concerning population interactions. In this paper we construct and analyze a model for the coevolution of two populations. The results suggest that the interaction between demographic and genetic variables has significant implications for both community theory and evolutionary theory. Our interest is in changes in genotypic frequencies and is complemented by phenotypic studies such as those of Lawlor and Maynard Smith (1976), Rocklin and Oster (1976), and Rosenzweig (1973), as well as by the rather different optimization approach to genetic equilibrium by Roughgarden (1976a).

Consider two genetically heterogeneous populations which are interacting either through competition, exploitation (e.g., predation, parasitism, or herbivory), or mutualism (we will use the term mutualism in the broad sense, synonymous with protocoeperation). A thorough investigation of this system requires an analysis of the six basic kinds of interactions between variables represented by arrows in figure 1.

Loop 1 represents the effect of the density of a population on its own growth rate (density dependence) and loop 3 represents (intraspecific) frequency-dependent selection (e.g., Kojima 1965, 1971; Petit and Ehrman 1969; Cockerham et al. 1972). Our usage of "frequency dependence" is somewhat broader than that conventional in population genetics; we use the term to refer to any dependence of absolute fitnesses on gene frequency. This extension seems to us logical and essential for populations which vary in density. In most cases, it is impossible to distinguish mechanisms which lead to relative frequency dependence (the more usual notion) from those which lead to absolute frequency dependence. We identify these interactions (1 and 3) in order to emphasize their interdependence with each other and particularly their interdependence with the interspecific components of figure 1. For example, frequency dependence and density dependence within a population may often be caused by interactions with other populations (Clarke 1962; Rosenzweig 1969; Ayala 1971; Udovic 1974).

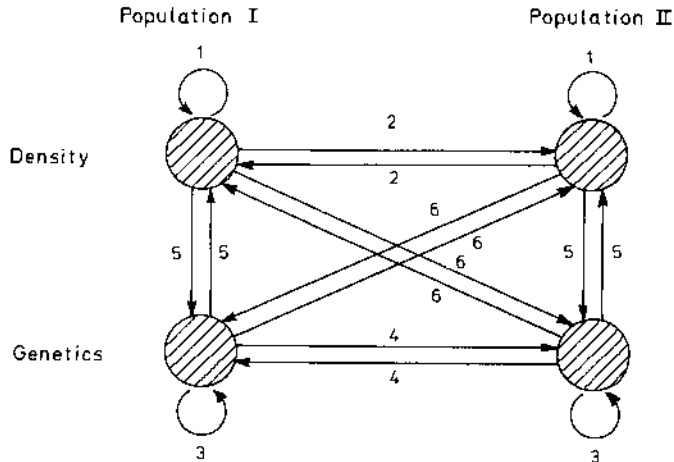


FIG. 1.—The basic kinds of interactions between densities and genetic frequencies for two interacting populations.

Arrow 2, which represents the effects of the density of each population on the growth rate of the other population and entirely ignores genetic variables, is exemplified by classical Lotka-Volterra theory (see review by Maynard Smith, 1974). Arrow 4 considers only the interaction between genetic variables and ignores density. The recent coevolution models of Mode (1958), Jayakar (1970), and Yu (1972) concentrate on this interaction.

Arrows 5 and 6 involve both density and genetic structure. Models of density-dependent selection (e.g., MacArthur 1962; Charlesworth 1971; Roughgarden 1971; Clarke 1972) focus on the interaction between the density and genetic structure of the same population (5), while the genetic feedback models (Pimentel 1961; Levin 1972) are directed to the interaction between the density of one population and the genetic structure of the second population (6). Despite the obvious differences between genetic feedback and density-dependent selection, there is an inherent similarity in structure. Both involve selection dependent on density, and both involve a "genetic" feedback loop. Either one could be referred to as "density-dependent genetic feedback." Indeed, Pimentel's original usage of genetic feedback in competitive systems was probably in this broader sense (Pimentel 1961).

To summarize, the arrows in figure 1 may be labeled as follows: (1) intraspecific density-dependent regulation of population growth rates, (2) interspecific density-dependent regulation of population growth rates, (3) density-independent selection (either frequency-dependent or independent), (4) density-independent co-selection, (5) intraspecific density-dependent selection, (6) genetic feedback (interspecific density-dependent selection and reciprocal interspecific frequency-dependent regulation of population growth rates). Wallace's "soft-selection" (Wallace 1975) would combine (3) and (5).

To our knowledge there are only three models of coevolution of sexual populations in the literature which incorporate all four variables in figure 1.

Stewart (1971) developed a model for coevolution of a predator and prey, and Léon (1974) developed a model for the coevolution of two competitors. Léon's model is based on the Lotka-Volterra equations and the models of density-dependent selection developed by Roughgarden (1971) and Charlesworth (1971). He assumes that there is no intraspecific or interspecific frequency-dependent selection. Stewart (1971) also used a modified logistic equation as the basis for his model, but argued that his results were not qualitatively dependent on the linearity assumptions of the logistic. Both Stewart and Léon derived conditions for the stability of an equilibrium at which both coevolving populations were polymorphic. Stewart was able to show that in predator-prey systems polymorphic equilibria may be stable even if the loci involved show complete dominance. Léon showed that heterozygote superiority in both populations was a necessary condition for stability of a doubly polymorphic equilibrium in his competition models. Neither Stewart nor Léon considered stability conditions for equilibria not involving polymorphisms for both populations. In related papers, Roughgarden (1976*a*, 1976*b*) considers a more general formulation, but still assumes frequency independence.

In this paper, we develop more general models incorporating all of the interactions represented by arrows in figure 1. We extend the results of Léon and Stewart by considering coevolution in competitive, exploiter-victim and mutualistic systems, by considering nonlinear relationships between the densities of the populations and fitnesses of individual genotypes, by incorporating the possibility of intra- and interspecific frequency-dependent selection, and by considering the stability conditions for various boundary equilibria, such as equilibria involving one polymorphic population and one monomorphic population. We are able to simplify the interpretation of our results by introducing the concept of intrinsic stability, which allows us to separate the criteria for stability of an equilibrium into two categories: those relating to the intrinsic properties of the system, and those relating to its response time. Models of density-dependent selection, soft selection (Wallace 1975), genetic feedback and interspecific frequency-dependent selection are all special cases of the model presented here (Udovic and Levin, unpub.).

BASIC FRAMEWORK

We recognize that there are serious limitations to a theory of population genetics which is constructed essentially as an extension of one-locus, two-allele models (Slatkin 1971; Lewontin 1974). However, such models have served a highly suggestive role in classical theory and no comparable multilocus theory has been developed to take their place. On the other hand, extension to many alleles is relatively straightforward. As such, we begin our study of coevolution by considering evolution at a single autosomal locus in each of two interacting diploid sexual populations which we label X and Y . Some primitive extensions to multiple loci are considered in Pimentel et al. (1975).

We also realize that two-population coevolutionary situations represent only a very restricted class, and that the problems of scaling such models up to whole

communities are substantial. Indeed, the community situation may require an entirely novel approach. On the other hand, particularly in the case of interactions between host and parasite and between model and mimic, two-species coevolution is of real importance.

Population X is of density N , and is segregating at a single autosomal locus with alleles A_1 and A_2 ; population Y is of density M with alleles B_1 and B_2 . Mating in both populations is assumed random, generations discrete and non-overlapping, and the populations large enough to justify the use of a deterministic model. Selection is assumed to occur after the formation of zygotes, so that zygotic frequencies can be determined from allelic frequencies by binomial expansion.

For simplicity of discussion, we assume that both populations have the same generation time, which will be equal to the time step in our model. This approach extends easily to situations where the time step may be conveniently taken to be an integral multiple of the generation time of each species, although interpretation of parameters must be modified. For example, if one species has a 6-month generation time and the other a 12-month one, the 1-year period may be used and the equations for the first species represent a two-generation jump. It may be shown that the basic equations remain valid.

Generalizing the approach of Charlesworth (1971), we define W_{ij} and V_{ij} as the expectations of offspring (of all possible genotypes) of zygotes carrying, respectively, alleles A_i and A_j (in population X) and alleles B_i and B_j (in Y). As with all parameters in the model, W_{ij} can vary from generation to generation, but we assume that this variation is completely determined by the population densities and the allelic frequencies (because these determine the zygotic frequencies). Let p_i be the frequency of A_i and q_i the frequency of B_i in the current zygotic populations. Then, modifying only slightly the standard notation of Wright (1955), we may describe the overall dynamics of the system by a set of four difference equations for the values (denoted by primes) of p_i , q_i , N , and M after one time interval:

$$\begin{aligned} p'_1 &= p_1 W_{1.} / \bar{W}, & q'_1 &= q_1 V_{1.} / \bar{V}, \\ N' &= N \bar{W}, & M' &= M \bar{V}, \end{aligned} \quad (1)$$

in which

$$\begin{aligned} W_{j.} &= \sum_i p_i W_{ij}, & V_{j.} &= \sum_i q_i V_{ij}, \\ \bar{W} &= \sum_j p_j W_{j.} = \sum_i p_i p_j W_{ij}, & \bar{V} &= \sum_j q_j V_{j.} = \sum_i q_i q_j V_{ij}. \end{aligned} \quad (2)$$

Here \bar{W} represents the mean fitness for population X , \bar{V} for Y . Moreover, $W_{ij} = W_{ij}(p_1, q_1, N, M)$, $V_{ij} = V_{ij}(p_1, q_1, N, M)$, where W_{ij} and V_{ij} are continuously differentiable on $N \geq 0$, $M \geq 0$, $0 \leq p_1 \leq 1$, $0 \leq q_1 \leq 1$. Clearly population X will grow if $\bar{W} > 1$ and decline if $\bar{W} < 1$; for population Y , the condition for growth is $\bar{V} > 1$.

The above description can accommodate emigration or immigration as well

as births and deaths. If population X is a predator upon population Y , for example, emigration due to the undesirability of the prey or their low abundance is indistinguishable from predator death due to toxicity or starvation.

An alternative representation of (1) is useful. Following and modifying Lewontin (1958), we introduce the quantities $a = W_{11} - W_{12}$, $b = W_{22} - W_{12}$, $c = V_{11} - V_{12}$, $d = V_{22} - V_{12}$. Our basic system can now be written

$$\begin{aligned} N' &= \bar{W}N, \\ M' &= \bar{V}M, \\ p_1' &= p_1 + p_1(1 - p_1)(W_{11} - W_{12})/\bar{W} \\ &= p_1 + p_1(1 - p_1)[(a + b)p_1 - b]/\bar{W}, \\ q_1' &= q_1 + q_1(1 - q_1)(V_{11} - V_{12})/\bar{V} \\ &= q_1 + q_1(1 - q_1)[(c + d)q_1 - d]/\bar{V}. \end{aligned} \quad (3)$$

Here \bar{W} , \bar{V} , a , b , c , and d are variable, and

$$\begin{aligned} \bar{W} &= W_{12} + ap_1^2 + b(1 - p_1)^2, \\ \bar{V} &= V_{12} + cq_1^2 + d(1 - q_1)^2. \end{aligned} \quad (4)$$

Alternatively, we may write

$$\begin{aligned} \Delta N &= (\bar{W} - 1)N, \\ \Delta M &= (\bar{V} - 1)M, \\ \Delta p_1 &= p_1(1 - p_1)[(a + b)p_1 - b]/\bar{W} = p_1 f(p_1, q_1, N, M), \\ \Delta q_1 &= q_1(1 - q_1)[(c + d)q_1 - d]/\bar{V} = q_1 g(p_1, q_1, N, M). \end{aligned} \quad (5)$$

Our objective is to determine the long-term (asymptotic) behavior of this system for various functional relationships. Under what conditions will this system possess the potential for regulation of both populations at fixed levels (or more generally, between fixed nontrivial bounds)? Under what conditions will regulation depend upon the interactions with one or both genetic systems? Does the interaction between populations or the dependence of fitness values on density and gene frequency enhance or reduce the potential for maintaining polymorphisms? The equally important task of determining the effects of various biological factors on the functional relationships expressed in system (3) or (5), and thus on the stability criteria, is only briefly discussed.

Our analysis centers on the local asymptotic stability properties of the various equilibria of system (3) or (5), which may be investigated using the properties of certain linearization matrices. We do not discuss in this paper the stability of time-varying solutions, but we shall discuss these solutions further for certain special cases in a subsequent paper.

INTRINSIC STABILITY

The criteria for the stability of an equilibrium will be of two types: those which depend on the overall time scale of response of the system, and those which do not. The first set is related fundamentally to the discrete nature of the

system, while the second provides the necessary and sufficient criteria for the stability of the analogous equilibrium in the system of differential equations

$$dN/dt = (\bar{W} - 1)N \quad (6a)$$

$$dM/dt = (\bar{V} - 1)M \quad (6b)$$

$$dp_1/dt = p_1(1 - p_1)[(a + b)p_1 - b]/\bar{W} = p_1f \quad (6c)$$

$$dq_1/dt = q_1(1 - q_1)[(c + d)q_1 - d]/\bar{V} = q_1g. \quad (6d)$$

This system has the same equilibrium points as (5) (May 1973a).

We will call an equilibrium of (5) intrinsically stable whenever that equilibrium is stable in the homologous differential equation system (6). The only features which may destabilize an intrinsically stable equilibrium relate to the overall rate of response of the system. Stability in the differential equation system insures the existence of a corresponding discrete system with response rapid enough to insure stability (May 1973a). Thus any stable equilibrium in a discrete system is intrinsically stable, but the reverse is not true. The concept of intrinsic stability is convenient in our analysis, because it simplifies the biological interpretation of the stability conditions by dividing them into two distinct categories with very different interpretations.

ANALYSIS

We distinguish two sets of models: one which assumes that fitnesses are independent of gene frequency and one which incorporates frequency-dependent fitnesses. In each case we will first consider the stability characteristics of equilibria of system (5) which are polymorphic in both species; then we will consider the stability of various equilibria which do not correspond to two polymorphic species (boundary equilibria). Boundary equilibria in this case are of substantial interest because it is important to determine not only when the structure of a coevolving system leads to the maintenance of polymorphisms in both species, but also when this structure leads to one polymorphic population and one monomorphic population, or to two monomorphic populations. It is also important to determine under what circumstances coevolution will lead to the extinction (at least on a local level) of one or both populations or allow for invasion.

We will not attempt to catalog necessary and sufficient conditions for the existence of either doubly polymorphic equilibria or boundary equilibria. Such a catalog may be easily provided, but provides few insights. However, one characteristic of doubly polymorphic equilibria is easily obtained: at the equilibrium, each heterozygote must be either superior to both homozygotes or inferior to both. Léon (1974) obtained this result for two coevolving competitors when the fitness functions were linearly related to density. We extend his results to nonlinear fitness functions, and to exploiter-victim and mutualistic systems. Note that there may be several polymorphic equilibria, and the following con-

siderations are valid for each one. From the first two equations in (5), we see at once that such equilibria satisfy the equations

$$\begin{aligned} p_1 &= (W_{22} - W_{12})/(W_{11} + W_{22} - 2W_{12}) = b/(a + b), \\ q_1 &= (V_{22} - V_{12})/(V_{11} + V_{22} - 2V_{12}) = d/(c + d). \end{aligned} \quad (7)$$

These equations have the form which is familiar from classical theory; but this is to some extent misleading because the W_{ij} and V_{ij} values are not constants but depend, among other things, on p_1 and q_1 . The relations thus do not determine p_1 and q_1 explicitly, but are implicit relations and must be solved in conjunction with the equations $\bar{W} = 1$ and $\bar{V} = 1$. For simplicity, we ignore the special case $W_{11} = W_{12} = W_{22}$, or $V_{11} = V_{12} = V_{22}$ at equilibrium, ensuring that denominators in (7) are not zero. Equations (7), together with the restraints $0 \leq p_1 \leq 1$ and $0 \leq q_1 \leq 1$, lead immediately to the condition that neither heterozygote can be intermediate in fitness at a doubly polymorphic equilibrium. Thus a necessary condition for the existence of a doubly polymorphic equilibrium is the existence of a region in the four-dimensional state-space in which neither heterozygote is intermediate. A necessary and sufficient condition is that this region overlap the intersection of the surfaces $\bar{W} = 1$ and $\bar{V} = 1$. A special case of this is proved by Léon (1974).

Asymptotic stability of the equilibrium (Goldberg 1958; Levin 1972, 1973; May 1973a) depends on the eigenvalues of the matrix

$$J = \begin{pmatrix} 1 + N \partial \bar{W} / \partial N & N \partial \bar{W} / \partial M & N \partial \bar{W} / \partial p_1 & N \partial \bar{W} / \partial q_1 \\ M \partial \bar{V} / \partial N & 1 + M \partial \bar{V} / \partial M & M \partial \bar{V} / \partial p_1 & M \partial \bar{V} / \partial q_1 \\ p_1 \partial f / \partial N & p_1 \partial f / \partial M & 1 + p_1 \partial f / \partial p_1 & p_1 \partial f / \partial q_1 \\ q_1 \partial g / \partial N & q_1 \partial g / \partial M & q_1 \partial g / \partial p_1 & 1 + q_1 \partial g / \partial q_1 \end{pmatrix}.$$

The equilibrium will be stable provided all of the eigenvalues of this matrix are less than 1 in magnitude, and unstable if any has magnitude greater than 1.

When fitnesses are independent of gene frequencies, a number of simplifications occur:

- i) a , b , c , and d are independent of p_1 , q_1 .

A somewhat less restrictive situation is relative frequency independence, in which only a/b and c/d are frequency independent. In particular, f and g depend only on relative frequencies. Genetic feedback models of the simplest kind still retain the assumption that relative fitnesses are independent of gene frequencies, but the "absolute fitness" in one population (which happens to be fixed genetically) depends on the gene frequencies in the other population.

- ii) Because $\bar{W} = W_{12} + ap_1^2 + b(1 - p_1)^2$,
 $\partial \bar{W} / \partial p_1 = 2p_1[ap_1 - b(1 - p_1)] = 2p_1[(a + b)p_1 - b]$,
 $\partial \bar{W} / \partial q_1 = 0$.

Thus, at equilibrium, $\partial \bar{W} / \partial p_1 = \partial \bar{W} / \partial q_1 = 0$.
 Similarly, $\partial \bar{V} / \partial p_1 = \partial \bar{V} / \partial q_1 = 0$.

$$\text{iii) } \partial f / \partial q_1 = \partial g / \partial p_1 = 0.$$

iv) At equilibrium,

$$\begin{aligned} \partial f / \partial p_1 &= (1 - p_1) \cdot (a + b) = (1 - p_1)(W_{11} + W_{22} - 2W_{12}) \\ \partial g / \partial q_1 &= (1 - q_1) \cdot (c + d) = (1 - q_1)(V_{11} + V_{22} - 2V_{12}). \end{aligned}$$

Utilizing this information, we find that two of the eigenvalues of J are $1 + p_1(1 - p_1)(W_{22} + W_{11} - 2W_{12})$, and $1 + q_1(1 - q_1)(V_{22} + V_{11} - 2V_{12})$, and the other two are the eigenvalues of

$$\begin{pmatrix} 1 + N \partial \bar{W} / \partial N & N \partial \bar{W} / \partial M \\ M \partial \bar{V} / \partial N & 1 + M \partial \bar{V} / \partial M \end{pmatrix}.$$

Using lemma 1 of Levin (1973) (see also Goldberg 1958; Léon 1974) and ignoring the borderline case when the dominant eigenvalue has magnitude equal to one, we obtain the conditions for stability:

- i) $-2 < p_1(1 - p_1)(W_{22} + W_{11} - 2W_{12}) < 0$
- ii) $-2 < q_1(1 - q_1)(V_{22} + V_{11} - 2V_{12}) < 0$
- iii) $|2 + N \partial \bar{W} / \partial N + M \partial \bar{V} / \partial M| - 2 < N \partial \bar{W} / \partial N + M \partial \bar{V} / \partial M + NM[(\partial \bar{W} / \partial N)(\partial \bar{V} / \partial M) - (\partial \bar{W} / \partial M)(\partial \bar{V} / \partial N)] < 0.$

Of these, the most interesting and transparent subset is comprised of the conditions for intrinsic stability:

$$W_{22} + W_{11} - 2W_{12} < 0 \quad (8a)$$

$$V_{22} + V_{11} - 2V_{12} < 0 \quad (8b)$$

$$N \partial \bar{W} / \partial N + M \partial \bar{V} / \partial M < 0 \quad (8c)$$

$$(\partial \bar{W} / \partial N)(\partial \bar{V} / \partial M) - (\partial \bar{W} / \partial M)(\partial \bar{V} / \partial N) > 0; \quad (8d)$$

the other conditions necessary for satisfying (i), (ii), and (iii) specify in essence that the time scale be sufficiently rapid.

Because the heterozygotes cannot be of intermediate fitness, conditions (8a) and (8b) will hold if and only if the heterozygote is the most fit genotype in each population.

Conditions (8c) and (8d) are identical in form to stability conditions obtained from analysis of general models of species interactions ignoring evolution (May 1973b). Condition (8c) is satisfied whenever the growth rate (average fitness) of each population decreases as that population increases in density. It is also satisfied whenever the negative-density-dependent effects (e.g., intraspecific competition) on one population "outweigh" the positive-density-dependent effects (e.g., Allee effects) on the other. Positive density dependence is a substantial possibility, particularly in an exploiter-victim relationship where the exploitation rate per victim may be a decreasing function of victim density (Watt 1959; Rosenzweig 1969). Condition (8d) depends upon the nature of the

relationship between the coevolving populations. The expression $(\partial \bar{W}/\partial M) \times (\partial \bar{V}/\partial N)$ will always be negative in an exploiter-victim relationship, and will always be positive in a competitive or mutualistic relationship. If intraspecific competition in both populations results in negative density dependence, then $(\partial \bar{W}/\partial N)(\partial \bar{V}/\partial M)$ will be positive. Exploiter-victim relationships satisfying this last criterion will always satisfy condition (8d). For competing populations condition (8d) is essentially the condition that intraspecific competition outweigh interspecific competition, while for mutualistic populations condition (8d) requires that intraspecific competition outweigh the effects of their mutualistic interaction. Positive-density-dependent effects alter these interpretations of condition (8d), reducing the possibility for a stable equilibrium in exploiter-victim systems, and eliminating the possibility in competitive and mutualistic systems.

In summary, in the absence of (interspecific or intraspecific) frequency-dependent fitnesses and positive density dependence, the necessary and sufficient conditions for the intrinsic stability of a doubly polymorphic equilibrium are: (1) heterozygote advantage in both populations; (2*a*) for exploiter-victim relationships, negative density dependence in at least one of the populations, and (2*b*) for mutualistic and competitive relationships, negative intraspecific density-dependent effects should outweigh the effects of interspecific interactions. Léon (1974) obtained similar results for his logistic model of coevolving competitors.

With regard to the introduction of new mutant alleles, an equilibrium stable in the above sense will be "evolutionarily stable" (in the sense of Lawlor and Maynard Smith [1976]) provided that the mean fitness of the heterozygotes which the mutant forms with the resident alleles (weighted according to their gene frequencies) is less than 1. Lawlor and Maynard Smith (1976) require a somewhat different condition which is technically appropriate only for asexual populations. In their approach, a homozygote with fitness greater than 1 would be sufficient to destabilize, but in a randomly mating population this clearly is not technically correct.

BOUNDARY EQUILIBRIA

In this section we will examine the stability of some important boundary equilibria with regard to unrestricted perturbations and with regard to perturbations which are restricted to the same boundary. For example, an equilibrium with one population fixed for one allele and the other population polymorphic may be stable to density fluctuations and fluctuations in the allelic frequencies of the polymorphic population (stable in the restricted sense), but not to the introduction of the absent allele in the other population (unstable in the unrestricted sense). Unrestricted stability can usually be examined using conventional linear stability analysis, while restricted stability can be examined by reducing the system by one or more dimensions and using linear stability analysis on the reduced system.

Both Species Present, One Species Polymorphic

Because it would be redundant to consider more than one of the four possible kinds of equilibria of this sort ($p_1 = 0$, $p_1 = 1$, $q_1 = 0$, or $q_1 = 1$), we consider only the canonical form $0 < p_1 < 1$, $q_1 = 0$, $N > 0$, $M > 0$. (For the case $q_1 = 1$, eq. [5d] must be replaced by the equation for $1 - q_1$.) Repeating earlier procedures for examining criteria for the existence of an equilibrium, we find that the heterozygote of the polymorphic population (in this case, population X) cannot be intermediate in fitness at the equilibrium. The unrestricted stability conditions can be obtained by examining the eigenvalues of the linearization matrix of the four-variable system at the equilibrium. This linearization matrix is not the same as J , but has the form:

$$\hat{J} = \begin{pmatrix} & & N \frac{\partial \bar{W}}{\partial q_1} \\ & J_1 & M \frac{\partial \bar{V}}{\partial q_1} \\ & & p_1 \frac{\partial f}{\partial q_1} \\ 0 & 0 & 0 & 1 + g \end{pmatrix}$$

where J_1 is the linearization matrix for the reduced, three-variable system, p , N , and M :

$$J_1 = \begin{pmatrix} 1 + N \frac{\partial \bar{W}}{\partial N} & N \frac{\partial \bar{W}}{\partial M} & N \frac{\partial \bar{W}}{\partial p_1} \\ M \frac{\partial \bar{V}}{\partial N} & 1 + M \frac{\partial \bar{V}}{\partial M} & M \frac{\partial \bar{V}}{\partial p_1} \\ p_1 \frac{\partial f}{\partial N} & p_1 \frac{\partial f}{\partial M} & 1 + p_1 \frac{\partial f}{\partial p_1} \end{pmatrix}.$$

The eigenvalues of \hat{J} are $1 + g$ plus the three eigenvalues of J_1 , and for unrestricted stability each eigenvalue must have a modulus less than one. On the other hand, the condition for restricted stability is that the three eigenvalues of J_1 have moduli less than one. Thus the equilibrium will be stable in the unrestricted sense whenever it is stable in the restricted sense and in addition $-2 < g < 0$. The condition $-2 < g$ results from the discrete nature of the system, and is not a necessary condition for intrinsic stability. The condition $g < 0$ simply states that at equilibrium $V_{12} < V_{22} = 1$. Intuitively this means that if the B_1 allele is introduced into a monomorphic population fixed for the B_2 allele, it will increase in frequency only if $V_{12} > V_{22} = 1$; that is, if the heterozygote (B_1B_2) is more fit than the homozygote (B_1B_2) at the equilibrium. Again, this corresponds directly to the notion of evolutionarily stable strategy (Lawlor and Maynard Smith 1976) with the modification discussed earlier. A population fixed for B_2 is "evolutionarily stable" unless for some mutant allele B_1 , the relevant heterozygote has superior fitness.

Specializing to the frequency-independent case, we find the conditions for restricted intrinsic stability to be identical to conditions (8a), (8c), and (8d), and may be given the same interpretation. (8b) is removed as a requirement.

Both Species Present, Neither Polymorphic

The canonical case is $p_1 = 0$, $q_1 = 0$, $N > 0$, $M > 0$. This case must be examined more carefully because it involves a corner of state space. One must

be assured that an eigenvector (or combination of eigenvectors) corresponding to any destabilizing eigenvalue (or pair of complex ones) has nonnegative p_1 and q_1 coordinates. The linearization matrix is

$$\begin{pmatrix} 1 + N \frac{\partial \bar{W}}{\partial N} & N \frac{\partial \bar{W}}{\partial M} & N \frac{\partial \bar{W}}{\partial p_1} & N \frac{\partial \bar{W}}{\partial q_1} \\ M \frac{\partial \bar{V}}{\partial N} & 1 + M \frac{\partial \bar{V}}{\partial M} & M \frac{\partial \bar{V}}{\partial p_1} & M \frac{\partial \bar{V}}{\partial q_1} \\ 0 & 0 & 1 + f & 0 \\ 0 & 0 & 0 & 1 + g \end{pmatrix}.$$

The eigenvalues include those of the matrix

$$\begin{pmatrix} 1 + N \frac{\partial \bar{W}}{\partial N} & N \frac{\partial \bar{W}}{\partial M} \\ M \frac{\partial \bar{V}}{\partial N} & 1 + M \frac{\partial \bar{V}}{\partial M} \end{pmatrix}$$

with the corresponding eigenvectors taken to have zero coordinates in the p_1 and q_1 positions; $1 + f$, with eigenvector $(0 \ 0 \ 1 \ 0)^T$; and $1 + g$, with eigenvector $(0 \ 0 \ 0 \ 1)^T$. Thus, no problems arise due to the corner, and the equilibrium is intrinsically stable provided A_2A_2 is more fit than A_1A_2 , B_2B_2 is more fit than B_1B_2 , and as in the previous two cases: $N \frac{\partial \bar{W}}{\partial N} + M \frac{\partial \bar{V}}{\partial M} < 0$ and $(\frac{\partial \bar{W}}{\partial N})(\frac{\partial \bar{V}}{\partial M}) > (\frac{\partial \bar{V}}{\partial N})(\frac{\partial \bar{W}}{\partial M})$. These last two conditions are the conditions for restricted intrinsic stability, and are the familiar conditions for co-existence of two genetically homogeneous populations.

One Population Absent

The canonical case is $M = 0$. The significance of equilibria of this kind should be clearly understood. Although it makes little sense to discuss the gene frequency of a nonexistent population, it is important to examine any boundary equilibria with $M = 0$, $0 < q_1 < 1$, because the system may tend toward such an equilibrium (i.e., as the population heads towards extinction, its gene frequency tends toward q_1), or because of the potentiality for invasion and the relevant restrictions on the requisite genetic makeup for invasion.

For any equilibrium with $M = 0$ the linearization matrix of the system (5) is

$$\begin{pmatrix} 1 + N \frac{\partial \bar{W}}{\partial N} & N \frac{\partial \bar{W}}{\partial M} & N \frac{\partial \bar{W}}{\partial p_1} & N \frac{\partial \bar{W}}{\partial q_1} \\ 0 & \bar{V} & 0 & 0 \\ p_1 \frac{\partial f}{\partial N} & p_1 \frac{\partial f}{\partial M} & 1 + p_1 \frac{\partial f}{\partial p_1} & p_1 \frac{\partial f}{\partial q_1} \\ q_1 \frac{\partial g}{\partial N} & q_1 \frac{\partial g}{\partial M} & q_1 \frac{\partial g}{\partial p_1} & g + q_1 \frac{\partial g}{\partial q_1} \end{pmatrix}.$$

Because \bar{V} is an eigenvalue of the matrix, if $\bar{V} > 1$ any such equilibrium point will be unstable. That is, population Y will grow if introduced in small numbers.

If $\bar{V} < 1$, the conditions for intrinsic stability hinge on the eigenvalues of the matrix

$$J_2 = \begin{pmatrix} 1 + N \frac{\partial \bar{W}}{\partial N} & N \frac{\partial \bar{W}}{\partial p_1} & N \frac{\partial \bar{W}}{\partial q_1} \\ p_1 \frac{\partial f}{\partial N} & 1 + p_1 \frac{\partial f}{\partial p_1} & p_1 \frac{\partial f}{\partial q_1} \\ q_1 \frac{\partial g}{\partial N} & q_1 \frac{\partial g}{\partial p_1} & g + q_1 \frac{\partial g}{\partial q_1} \end{pmatrix}.$$

We consider two canonical cases: (a) $q_1 = 0$, and (b) $0 < q_1 < 1$. In case (a), the intrinsic stability conditions reduce to $g < 0$ (that is, $V_{22} > V_{12}$) plus the restricted conditions for intrinsic stability, that both eigenvalues of

$$\begin{pmatrix} N \partial \bar{W} / \partial N & N \partial \bar{W} / \partial p_1 \\ p_1 \partial f / \partial N & p_1 \partial f / \partial p_1 \end{pmatrix}$$

have negative real parts. The latter is also the condition for intrinsic stability of polymorphic equilibria in the case of density-dependent selection (Charlesworth 1971). In another paper (Udovic and Levin, unpub.) we analyze these conditions in detail. Here we only point out that in the frequency-independent case, $N \partial \bar{W} / \partial p_1$ is zero at equilibrium. The intrinsic stability conditions thus reduce to (i) $N \partial \bar{W} / \partial N < 0$ (negative density dependence), and (ii) $p_1 \partial f / \partial p_1 < 0$ (heterozygote superiority).

Case (b) is more complicated. It is a special case of the situation where both populations are evolving, but one is fixed in density (in this case, fixed at $M = 0$). In the frequency-independent case, the matrix J_2 then reduces to:

$$\begin{pmatrix} 1 + N \partial \bar{W} / \partial N & 0 & 0 \\ p_1 \partial f / \partial N & 1 + p_1 \partial f / \partial p_1 & 0 \\ q_1 \partial g / \partial N & 0 & 1 + q_1 \partial g / \partial q_1 \end{pmatrix}.$$

The intrinsic stability conditions are simply negative density dependence in population X and heterozygote superiority in both populations X and Y .

FREQUENCY-DEPENDENT SELECTION

The assumption of frequency-independent fitness values is quite restrictive. It seems unlikely that fitnesses which depend on population density do not depend on gene frequency as well (Clarke 1972; Bulmer 1974; Udovic and Levin, unpub.). Furthermore, there is substantial evidence in support of frequency-dependent fitnesses (see review by Ayala and Campbell 1974), including some evidence that the interaction between populations may be a causal factor (Clarke 1962; Ayala 1971; Udovic 1974). In addition, the frequency-independent model has also eliminated the possibility that gene frequencies in one population could influence the relative or absolute fitness values of genotypes in the other population. It seems unreasonable to assume that each population is responding evolutionarily to the density of the other population, but not to the quality of that population. There seems to be ample evidence against this assumption in the literature on plant-insect coevolution; the experimental results of Pimentel et al. (1963) show that the fitness values of wasp parasites can be influenced differentially by the level of host resistance.

The addition of either intra- or interspecific frequency dependence substantially alters the results of the model. The intrinsic conditions for the stability of a doubly polymorphic equilibrium can be obtained from examination of the matrix $J - I$. All eigenvalues of this matrix must have negative real parts. Utilizing the Routh-Hurwitz criteria (Brauer and Nohel 1969), we find that the eigenvalues of a 4×4 matrix satisfy these criteria if and only if: (i) the trace T ,

the sum of the diagonal elements, is negative, (ii) the sum Q of principal minors of order two is positive, (iii) the sum R of principal minors of order three is negative, (iv) the determinant D is positive, and (v) $D < [(QT - R)R]/T^2$. In the frequency-independent case these conditions simplify to yield the four conditions in expression (8). In the frequency-dependent case, expressing these conditions as conditions on the parameters of the model is a tedious task and the results are difficult to interpret within such a general framework.

Rather than emphasizing the restrictions on individual parameters which are required for stability, we point out the vast array of possibilities which exist with this model in comparison to the frequency-independent model. Any of the conditions given in expression (8) may be violated. Indeed, a stable equilibrium is possible even if none of these conditions is satisfied. This means that doubly polymorphic coevolutionary equilibria can be stable even if one or both heterozygotes is inferior at the equilibrium, and/or the demographic interaction between the two species appears unstable. For example, consider two competing populations which are at equilibrium but which do not satisfy conditions (8c) and (8d). From generalized (discrete) versions of the Lotka-Volterra equations and from all of the frequency-independent models discussed in this paper, we would expect such an equilibrium to be intrinsically unstable. But (Udovic and Levin, unpub.) the destabilizing forces which would be expected to result in competitive exclusion may be counteracted by stabilizing evolutionary forces in a manner similar to that suggested by Pimentel (1968). The results of our analysis indicate that this can only occur if absolute fitnesses are dependent on gene frequencies. Note that relative fitnesses may still be frequency independent, as in the case of genetic feedback. However, in general this is unlikely to be the case.

A more general but very simple example is useful in illustrating the potential stabilizing effects of frequency dependence. We demonstrate the existence of a polymorphism in one population; it is trivial to extend this to a doubly polymorphic example.

Suppose that the two species compete for space, and that their densities are governed by equations of the form $\Delta N = N[a - b \cdot (N + M)]$ and $\Delta M = M[a - c \cdot (N + M)]$; that is, they have identical maximal growth rates (a), but possibly differ in their sensitivities to crowding (b, c). If a, b , and c are constant, no stable coexistence is possible. Species X will win in competition if $b < c$ and lose if $b > c$; if $b = c$, the balance between X and Y will be metastable, resulting by drift in the ultimate extinction of one species or the other.

Suppose now that species X has an allelopathic capability by which it can gain a competitive advantage over Y . If production of the allelochemical is genetically controlled at a single locus (with p the allele frequency of the controlling gene A), then it is intuitively clear that a polymorphism can result. In particular, let b and c depend upon p (as well as upon $R = N/M$, because the relative proportions of N and M will also affect the levels of allelochemicals). Assume that b and c both increase with increasing p or R , but that c is more severely affected. We summarize this mathematically by writing $b = b(p, R)$, $c = c(p, R)$; $\partial p/\partial b > 0$, $\partial b/\partial R > 0$, $\partial c/\partial p > 0$, $\partial c/\partial R > 0$; $\partial b/\partial p < \partial c/\partial p$,

$\partial b/\partial R < \partial c/\partial R$. Under these conditions (and assuming $b > c$ when p and R are small), we would expect A to be selected for when it is rare and R is small, but its advantage to decrease as R increases. In particular, writing $\Delta p = pf$, we assume $f = f(p, R)$ where $\partial f/\partial R < 0$ for all p .

In analyzing this system, it is convenient to introduce an expression for the total population $S = N + M$, and to rewrite the equations as $\Delta S = S[a - (bN + cM)] = S\{a - bS + [(b - c)S/(1 + R)]\}$, $\Delta R = RS(c - b) \cdot M/(M + \Delta M) = RS(c - b) \cdot \{1/[1 + (a - cS)]\}$, $\Delta p = pf(p, R)$. A polymorphic equilibrium can occur only if $b = c$ and $S = a/b$, and the intrinsic stability is determined by the eigenvalues of the matrix

$$\begin{pmatrix} -bS & \frac{\partial(\Delta S/S)}{\partial R} & \frac{\partial(\Delta S/S)}{\partial p} \\ 0 & RS \frac{\partial(c - b)}{\partial R} & RS \frac{\partial(c - b)}{\partial p} \\ 0 & p \frac{\partial f}{\partial R} & p \frac{\partial f}{\partial p} \end{pmatrix}$$

evaluated at equilibrium, and hence by the eigenvalues of

$$\begin{pmatrix} RS \frac{\partial(c - b)}{\partial R} & RS \frac{\partial(c - b)}{\partial p} \\ p \frac{\partial f}{\partial R} & p \frac{\partial f}{\partial p} \end{pmatrix}.$$

Intraspecific frequency dependence is manifest both in the term $\partial b/\partial p$ and in $\partial f/\partial p$; interspecific frequency dependence appears in $\partial c/\partial p$.

Intrinsic stability requires not only that $\partial f/\partial p$ be negative (which can be achieved either through overdominance or frequency dependence), but also that the stabilizing effects of the off-diagonal terms be sufficiently large. Thus stability requires at the very least the dependence of $c - b$ on p , which means inter- or intrafrequency dependence.

Hence the polymorphism in species X is an essential ingredient for the stable balance between X and Y . Further, intraspecific frequency dependence can overcome both the absence of overdominance and the absence of the conditions for demographic equilibria.

DISCUSSION

An important implication of our results is that frequency-dependent selection should not be ignored in coevolution models. If the major premise of these models, that selection coefficients depend on population densities, is accepted, then it is reasonable to assume that selection coefficients will also depend on the genetic structure of populations. The only plausible reason for assuming frequency independence in models of coevolution is to simplify analysis. However, there are significant differences between results of analyses assuming

frequency independence and results obtained including the potential for frequency dependence, from which we conclude that the former are not robust. In the frequency-independent case the conditions for the stability of a doubly polymorphic equilibrium in our models of coevolution of two populations can be divided into three independent components: (1) criteria for the stability of equilibrium densities for the two populations which are equivalent in form to criteria obtained from generalized versions of the Lotka-Volterra equations (May 1973*b*); (2) criteria for the maintenance of a balanced polymorphism in population *X* which are equivalent in form to the criteria obtained in standard population genetics models for one population (Karlin and McGregor 1972); and (3) criteria analogous to (2) for population *Y*. The independence of these components essentially means that the stability criteria in the frequency-independent case are independent of the interaction between density and genetic structure. The interaction between these variables only influences stability because it influences the values of the parameters upon which stability depends; the criteria for evaluating the parameters remain unchanged. However, when either intraspecific or interspecific frequency-dependent selection is considered the stability criteria are not divisible into these three independent components. The whole is not the sum of its parts.

This mathematical result has at least three significant biological implications. First, whereas in the frequency-independent models the coexistence of two coevolving populations requires satisfaction at equilibrium of the conditions obtained from generalized Lotka-Volterra equations, in the frequency-dependent case coexistence can occur even when those conditions are violated. Second, whereas in the frequency-independent models heterozygote superiority was a necessary condition for the maintenance of polymorphisms in each population (Léon 1974), stable disruptive-selection regimes (heterozygote inferiority) are possible in the frequency-dependent case. Thus coevolutionary interactions between populations may increase the potential for sympatric speciation (Mather 1955; Maynard Smith 1966; Dickinson and Antonovics 1973; Udovic, unpub.). Third, whereas in the frequency-independent models the average fitness for each population is maximized at equilibrium subject to the constraint that population densities are at equilibrium, it is difficult to determine what is optimized by natural selection in the frequency-dependent case. Our results suggest that the important assumption of many ecological and evolutionary models that natural selection produces optimal results unless constrained by history or by competing goals (Cody 1974; e.g., Levins 1968; Stearns 1976), may not always be valid.

Coevolution may either be a stabilizing or destabilizing force in community dynamics. Random assemblages of interacting species are not likely to be stable (May 1973*b*), and coevolution may have been an important factor in assuring that natural communities are not "random assemblages," but rather groups of species whose ecological interactions produce a relatively stable system. Léon (1974) had hoped to illustrate this point using the results of his models of coevolving competitors, but he felt that his results pointed the opposite way because doubly polymorphic equilibria seemed even less likely to be stable than

monomorphic equilibria. As we have already pointed out, and as Léon has suggested, including frequency-dependent selection in these models can alter results to permit stable coexistence of two polymorphic coevolving populations when otherwise impossible.

To focus attention upon stable doubly polymorphic equilibria, as Léon (1974) has done, is not sufficient. The relevant question is coexistence, and coevolution can facilitate this not only through doubly polymorphic equilibria, but also through time-varying solutions and through boundary equilibria (in which one or both populations are monomorphic). Finally, even stable boundary equilibria for which only one population is present may contribute to regional coexistence (Levin 1974), and monomorphic boundary equilibria to polymorphic regional patterns (Karlin and McGregor 1972).

Coevolution can also destabilize an otherwise stable relationship. If a boundary equilibrium is stable in the restricted sense, but unstable in the unrestricted sense, then introduction of a new allele may destabilize the old equilibrium.

The maintenance of disruptive selection regimes may result from stabilizing forces present in arrows 3, 4, 5, or 6 of figure 1 or some combination. All involve frequency-dependent selection, either directly, or indirectly through interaction with another variable. Arrow 3 involves direct intraspecific frequency-dependent selection. This may be due to mechanisms such as intragenotypic competition (Kojima and Tobari 1969; Huang et al. 1971; Clarke 1972), preferential mating with rare genotypes (Petit and Ehrman 1969), predator switching (Clarke 1962; Murdoch 1969), or strong predator preference for certain genotypes which results in increased predation pressure on those genotypes as they become rare (Udovic 1974). Note that the latter mechanism is destabilizing, because it places rare genotypes at a relative disadvantage. Arrows 4, 5, and 6 represent examples of indirect, or delayed, intraspecific frequency-dependent selection. Changes in gene frequency do not alter selection pressures directly, but influence the rate of change of some other variable, which in turn influences selection coefficients. Arrows 4 and 6 indicate that frequency-dependent selection may be caused by the coevolutionary interactions between populations. Whether or not arrows 4 and 6 represent negative (stabilizing) feedback loops which could overcome the destabilizing force of disruptive selection, or positive (destabilizing) feedback loops will depend on the parameters of each specific coevolving system.

Our results hinge on three major premises: (1) predation, competition, and mutualism are strong selective forces; (2) selection coefficients and therefore rates of evolution in natural systems are relatively high; and (3) selection pressures and rates of population growth are sensitive to changes in gene frequencies. Only the first premise is well established. An appropriate "test" of our model would be field investigations testing the validity of premises (2) and (3). If these premises are verified and if our models are robust, then our results, which are logical consequences of these premises and our simplifying assumptions, would also be verified. To determine the robustness of our models it is necessary to examine: (1) coevolution in the context of a larger community; (2) the effects of polygenic inheritance; (3) the effects of spatial heterogeneity; and (4) the effects of chance.

Our approach in this paper has been to consider general coevolutionary models which could serve as a framework for future investigations. Our most general model encompasses all of the interactions between variables designated by arrows in figure 1 for any pair of coevolving species which meets our assumptions concerning generation time. Although in this paper we have not attempted to analyze in detail any of the six arrows in figure 1, or the interaction between arrows, a paper in preparation will (Udovic and Levin, unpub.) analyze arrows 5 and 6, density-dependent selection, and genetic feedback. A thorough understanding of coevolution seems to require a detailed analysis of all arrows and their interactions. A comparative study of their influence in competitive, exploiter-victim, and mutualistic systems seems essential to understand how different kinds of population interactions influence the potential for population regulation and the maintenance of polymorphisms. Such explorations conducted within the theoretical framework presented may lead to hypotheses useful in assessing the validity of our approach.

SUMMARY

We present a general model for coevolution of two interacting populations which we believe can serve as a framework for theoretical investigations in this area. The model describes coevolution of two competitors, exploiter and victim, or two mutualistic species. The conditions on the parameters of the model which are required for local stability of various equilibria are derived. In order to simplify analysis the stability conditions are separated into those which are independent of the nature of the time response of the system (intrinsic conditions) and those which depend on the time response. For the most part, only intrinsic conditions are discussed. Because of the nature of the model the results of our analysis are stated only in general terms. Much of their significance will depend on the particular coevolutionary systems being analyzed. The results of our analysis indicate that coevolution may result in stable coexistence of two populations even when the stability conditions derived from generalized versions of the Lotka-Volterra equations are violated; that coevolution may also destabilize what appears to be a stable interaction between populations; and that coevolution may result in stable disruptive selection regimes.

Local stability has been the focus of this paper, but the local instability, say, of polymorphic equilibria does not exclude the possibility of time-dependent polymorphic solutions. We shall discuss such solutions in further detail in a subsequent paper.

ACKNOWLEDGMENTS

S. A. L. was supported by NSF grant GP33031. J. D. U. was supported by the Office of Scientific and Scholarly Research, University of Oregon.

We gratefully acknowledge valuable suggestions on the manuscript by Bryan Clarke, Joel Cohen, Peter Frank, Michael Gilpin, Robert May, Michael Torelli, and two referees, and numerous helpful conversations with David Pimentel.

LITERATURE CITED

- Ayala, F. J. 1971. Competition between species: frequency dependence. *Science* 171: 820-824.
- Ayala, F. J., and C. A. Campbell. 1974. Frequency-dependent selection. *Annu. Rev. Ecol. Syst.* 5:115-138.
- Brauer, F., and J. A. Nohel. 1969. The qualitative theory of ordinary differential equations. Benjamin, New York. 314 pp.
- Bulmer, M. G. 1974. Density-dependent selection and character displacement. *Amer. Natur.* 108:45-58.
- Charlesworth, B. 1971. Selection in density-regulated populations. *Ecology* 52:469-474.
- Clarke, B. C. 1962. Balanced polymorphism and the diversity of sympatric species. In D. Nichols, ed. *Taxonomy and geography*. Systematics Assoc., Oxford.
- . 1972. Density-dependent selection. *Amer. Natur.* 106:1-13.
- Cockerham, C. C., P. M. Burrows, S. S. Young, and T. Prout. 1972. Frequency-dependent selection in randomly mating populations. *Amer. Natur.* 106:493-515.
- Cody, M. 1974. Optimization in ecology. *Science* 183:1156-1164.
- Dickinson, H., and J. Antonovics. 1973. Theoretical considerations of sympatric divergency. *Amer. Natur.* 107:256-274.
- Goldberg, S. 1958. Introduction to difference equations, with illustrative examples from economics, psychology and sociology. Wiley, New York. 260 pp.
- Huang, S. L., M. Singh, and K. Kojima. 1971. A study of frequency-dependent selection observed in the esterase-6 locus of *Drosophila melanogaster* using a conditioned media method. *Genetics* 68:97-104.
- Jayakar, S. D. 1970. A mathematical model for interaction between gene frequencies in a parasite and its host. *Theoret. Pop. Biol.* 1:140-164.
- Karlin, S., and J. McGregor. 1972. Polymorphisms for genetic and ecological systems with weak coupling. *Theoret. Pop. Biol.* 3:210-238.
- Kojima, K. 1965. The evolutionary dynamics of two-gene systems. Pages 197-220 in R. W. Stacey and B. Waxman, eds. *Computers in biomedical research*. Academic Press, New York.
- . 1971. The distribution and comparison of "genetic loads" under heterotic selection and simple frequency dependent selection in finite populations. *Theoret. Pop. Biol.* 2:159-173.
- Kojima, K., and Y. N. Tobari. 1969. Selective modes associated with karyotypes in *Drosophila ananassae*. II. Heterosis and frequency-dependent selection. *Genetics* 63: 639-651.
- Lawlor, L. R., and J. Maynard Smith. 1976. The coevolution and stability of competing species. *Amer. Natur.* 110:79-99.
- Léon, J. A. 1974. Selection in contexts of interspecific competition. *Amer. Natur.* 108: 739-757.
- Levin, S. A. 1972. A mathematical analysis of the genetic feedback mechanism. *Amer. Natur.* 106:145-164.
- . 1973. Erratum. *Amer. Natur.* 107:320.
- . 1974. Dispersion and population interactions. *Amer. Natur.* 108:207-228.
- Levins, R. 1968. *Evolution in changing environments*. Princeton University Press, Princeton, N.J. 120 pp.
- Lewontin, R. 1958. A general method for investigating the equilibrium of gene frequency in a population. *Genetics* 43:419-434.
- . 1974. *The genetic basis of evolutionary change*. Columbia University Press, New York. 346 pp.
- MacArthur, R. H. 1962. Some generalized theorems of natural selection. *Proc. Nat. Acad. Sci.* 48:1893-1897.
- Mather, K. 1955. Polymorphism as an outcome of disruptive selection. *Evolution* 9:52-61.
- May, R. M. 1973a. On relationships between various types of population models. *Amer. Natur.* 107:46-57.

- . 1973b. Stability and complexity in model ecosystems. Princeton University Press, Princeton, N.J. 235 pp.
- Maynard Smith, J. 1966. Sympatric speciation. *Amer. Natur.* 100:637-650.
- . 1974. Models in ecology. Cambridge University Press, London. xii + 146 pp.
- Mode, C. J. 1958. A mathematical model for the co-evolution of obligate parasites and their hosts. *Evolution* 12:158-165.
- Murdoch, W. W. 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecol. Monogr.* 39:335-354.
- Petit, C., and L. Ehrman. 1969. Sexual selection in *Drosophila*. In T. Dobzhansky, M. K. Hecht, and W. C. Steere, eds. *Evolutionary biology*. Vol. 3. Appleton-Century-Crofts, New York. 309 pp.
- Pimentel, D. 1961. Animal population regulation by the genetic feedback mechanism. *Amer. Natur.* 95:65-79.
- . 1968. Population regulation and genetic feedback. *Science* 159:1432-1437.
- Pimentel, D., S. A. Levin, and A. B. Soans. 1975. On the evolution of energy balance in some exploiter-victim systems. *Ecology* 56:381-383.
- Pimentel, D., W. P. Nagel, and J. L. Madden. 1963. Space-time structure of the environment and the survival of parasite-host systems. *Amer. Natur.* 97:141-167.
- Rocklin, S., and G. Oster. 1976. Competition between phenotypes. *J. Math. Biol.* 3:225-262.
- Rosenzweig, M. L. 1969. Why the prey curve has a hump. *Amer. Natur.* 103:81-87.
- . 1973. Evolution of the predator isocline. *Evolution* 27:84-94.
- Roughgarden J. 1971. Density dependent natural selection. *Ecology* 52:453-468.
- . 1976a. Resource partitioning among competing species—a coevolutionary approach. *Theoret. Pop. Biol.* 9:388-424.
- . 1976b. Coevolution in ecological systems. II. Results from "loop analysis" for purely density-dependent coevolution. In F. Christiansen and T. Fenchel, eds. *Symposium on the measurement of selection in natural populations: lecture notes in biomathematics*. Springer-Verlag, Heidelberg (in press).
- Slatkin, M. 1971. Selection and polygenic characters. *Proc. Nat. Acad. Sci.* 46:87-93.
- Stearns, S. C. 1976. Life history tactics: a review of the ideas. *Quart. Rev. Biol.* 51:3-47.
- Stewart, F. M. 1971. Evolution of dimorphism in a predator-prey model. *Theoret. Pop. Biol.* 2:493-506.
- Udovic, J. D. 1974. Evolution in predator-prey systems: some extensions of the genetic feedback models. Ph.D. thesis. Cornell University. 263 pp.
- Wallace, B. 1975. Hard and soft selection revisited. *Evolution* 29:465-473.
- Watt, K. E. F. 1959. A mathematical model for the effect of densities of attacked and attacking species on the number attacked. *Can. Entomol.* 91:129-144.
- Wright, S. 1955. Classification of the factors of evolution. *Cold Spring Harbor Symp. Quant. Biol.* 20:16-24.
- Yu, P. 1972. Some host parasite genetic interaction models. *Theoret. Pop. Biol.* 3:347-357.