INTERNATIONAL ATOMIC ENERGY AGENCY
UNITED NATIONS EDUCATIONAL, SCIENTIFIC AND CULTURAL ORGANIZATION

INTERNATIONAL CENTRE FOR THEORETICAL PHYSICS
34100 TRIESTE (ITALY) - P.O.B. 586 - MIRAMARE - STRADA COSTIERA 11 - TELEPHONES: 224281/2/3/4/5/6
CABLE: CENTRATOM - TELEX 460392-I

SMR/99- 4

AUTUMN COURSE ON MATHEMATICAL ECOLOGY

(16 November - 10 December 1982)

MODELS OF POPULATION DISPERSAL

S.A. LEVIN

Section of Ecology & Systematics
Cornell University
Ithaca, New York
U.S.A.

MODELS OF POPULATION DISPERSAL

Simon A. Levin

Section of Ecology and Systematics
Cornell University
Ithaca, New York

I. INTRODUCTION

The spatiotemporal structure of environment, and its effect upon the movement patterns of individuals, are central issues in ecological theory. A knowledge of plant and animal dispersal patterns is fundamental to an understanding of the outbreaks of pest populations, of the recovery of disturbed areas after periods of stress, and of the optimal spatial design of agricultural systems to minimize herbivore effects. Similarly, seed and pollen dispersal, together with the germination of dormant seeds and the released growth of understory plants, can play important roles in the secondary successional patterns of forest communities following disturbance. Mathematics has an important role to play in the description of movement patterns, and in an understanding of their evolution.

There are several distinct approaches to modelling populations in heterogeneous environments; the appropriate choice depends upon the system under investigation, upon the types

ISBN 0-12-148360-6

of questions being asked, and upon the scales of interest. The most general development, and that most familiar to mathematicians, is built upon the theory of diffusion equations.

II. DIFFUSION MODELS

Random walk models have had a rich history in population biology. Okubo,(1980), [59], who has written the state-of-the-art text on the subject, traces their origin back to early work of Pearson and Blakeman, (1906), [63], in evolutionary theory and Brownlee's, (1911), [4], work on epidemics. In population genetics, the theory of the wave of advance of an advantageous allele prompted a number of fundamental theoretical papers (e.g. Fisher, (1937), [19], Kolmogorov et al. 1937, [36]), and important early experiments by Dobzhansky and Wright, (1943), [15], began to quantify the dispersal capabilities of *Drosophila*.

The basic equation of diffusion and growth utilized in those early papers was of the form

$$\frac{\partial n(\underset{\sim}{x},t)}{\partial t} = D\nabla^2 n(\underset{\sim}{x},t) + f(n(\underset{\sim}{x},t)), \qquad (1)$$

in which $n(\underset{\sim}{x},t)$ is the population density at position $\underset{\sim}{x}$ at time t. Equation (1) was advanced in an ecological context by Skellam, (1951), [70], and by Kierstead and Slobodkin, (1953), [34]; those papers have been cornerstones in the later development of the subject. Since their appearance, diffusion equations have been widely applied to describe movement, and

they have formed the basis of most mathematical investigations. However, comparatively few experiments have been carried out which would allow an evaluation of the validity of such models.

Kareiva, (1981a,b), [28],[29], in studying the movement of flea beetles among collard plants, designed experiments to critically evaluate the applicability of diffusion models by means of mark and recapture experiments. In homogeneous environments, he found remarkable agreement between observation and the predictions of diffusion models (see discussion in Levin, (1981), [45]). A comprehensive survey of the literature concerning the foraging movements of phytophagous insects (Kareiva (1981a),[28]) showed that seven of the eleven cases examined were compatible with constant coefficient diffusion models.

With one exception, the deviations from the simplest model showed distributions in point-release mark-recapture experiments which were leptokurtic rather than normal (Kareiva, (1981a),[28]). Normality would be predicted on the basis of (1) with $f \equiv 0$; leptokurtic distributions are more peaked. Dobzhansky and Wright,(1943),[15], also found leptokursis in their experiments and suggested heterogeneity of either population or habitat as being responsible. The probable importance of population heterogeneity in these earlier experiments was borne out by later work (Dobzhansky and Powell, (1974), [14]) with more homogeneous populations; in those studies, leptokursis did not arise.

The problem of habitat heterogeneity is of profound importance in understanding the movements of individuals under natural circumstances. In deriving the appropriate modification of (1), it is critical to understand the mechanisms and the factors that control movement. The most familiar model for incorporating heterogeneity simply allows the diffusion coefficient to depend on spatial position, and (with $f \equiv 0$) takes the form

$$\frac{\partial n}{\partial t} = \nabla\cdot(D\nabla n), \tag{2}$$

where $\underline{D}$ depends on position. Under homogeneous boundary conditions, the steady states of such models are spatially uniform, and this is a hint that something may be wrong with (2) as a description of population movements. In general, in heterogeneous environments one expects to see accumulations of individuals in more favorable environments, and this implies non-uniform distributions; this is what is observed under natural conditions (Kareiva,(1981c),[30], Kareiva,(1981 b,c, [29] [30]). If one passes to the continuous limit from a random walk model in which emigration is locally determined, then in place of (2) one obtains (Patlak,(1943),[62], Dobzhansky et al (1979),[14], Okubo,(1980),[59])

$$\frac{\partial n}{\partial t} = \nabla^2(Dn), \tag{3}$$

which supports steady states in which $\underline{n}$ is inversely related to $\underline{D}$. This is in better agreement with data in experimental situations, as has been reemphasized by Lapidus and Levandowsky,(1981),[38], with regard to models of chemotaxis. Lapidus and Levandowsky discuss the parallels between the distinction made above and that made between the Stratonovich and Ito stochastic calculi.

The model (3) was discretized and used by Dobzhansky et al (1979),[14], as a basis for describing dispersal in heterogeneous environments, and similar discrete models were utilized by Kareiva (1981 b),[29] and DeAngelis, (1978),[11]. Kareiva's is the only work which provides the basis for a test of model validity, and even in his work any such test must be incomplete.

The relationship between (2) and (3) can be understood by expanding (3), which is then seen to be equivalent to the model

$$\frac{\partial n}{\partial t} = \nabla\cdot(D\nabla n) + \nabla\cdot(n\nabla D), \tag{4}$$

in which vector $\underset{\sim}{v} = \nabla \underline{D}$ is an advective influence driving the population towards environments with lower $\underline{D}$. Equation (4) is seen to be a special case of a more general class of models in which advective factors are added to (2). Alternative forms are discussed in Okubo,(1980),[59].

In one experiment described by Kareiva,(1981 a),[28], platykursis rather than leptokuris is found, and the likely explanation lies in density-dependent influences upon dispersal. The potential importance of density dependence is also illustrated in the work of Morisita (1950,1954),[52],[53], Ito (1952,[26], Kono (1952),[37], Watanabe et al.(1952),[75], and Taylor (1977),[71]. Appropriate variants on (3) in which $\underline{D}$ is allowed to depend explicitly on $\underline{n}$ have been intensively studied recently by mathematicians (Gurney and Nisbet (1976),

[51], Newman and Sagan (1981),[57]). A somewhat different model has been put forward by Cohen and Murray (1981),[9].

Other modifications of the basic model may also be necessary in other situations, and a variety of approaches have been taken. Jones et al. (1980),[27], develop a discrete simulation model to describe butterfly foraging movements in which the probability of leaving a grid unit in a particular direction is related to the direction in which the individual entered the unit. In earlier work, Patlak (1953),[62], developed a variant on (4) (with an additional advection term imposed) to describe, in inhomogeneous environments, movement in which there is correlation between successive steps. Under somewhat different assumptions (and in a homogeneous environment), Goldstein (1951),[20], derived the telegraph equation

$$\frac{\partial n}{\partial t} = D\,\frac{\partial^2 n}{\partial x^2} - \frac{1}{2}\,T\,\frac{\partial^2 n}{\partial t^2}\,, \qquad (5)$$

in which (Okubo (1980),[59]) T is the characteristic time of step correlation. Numerous other authors have considered simulations in which individuals move typically in fixed directions, but with the possibility of "turning" in response to cues. Taxis, in which individuals follow gradients of one sort or another, is an important biological complication, and has been dealt with for example by Keller and Segel (1971 a,b) [32],[33], and Lapidus and Levandowsky (1981),[38].

Swarming, schooling, and other group responses have been examined by various authors (Sakai (1973),[38], Okubo and Chiang (1974),[60], Okubo et al. (1977),[61]); but, in general, uncertainty as to the exact behavioral mechanisms by which individuals orient to each other or to each other's movements makes it difficult to develop definitive models for grouping behavior. There remain a number of important mathematical questions, in particular regarding the exact forms of the equations and the nature of the theoretical population "fronts" such models would predict.

III. NON-UNIFORM STATIONARY SOLUTIONS IN MODELS OF DISPERSAL AND GROWTH

The mathematical investigation of diffusion-reaction models, even within the context of population models, is voluminous, and no attempt will be mode to survey it in this short paper (see however Levin (1976 a,b), [40],[41],(1978),[42], (1979),[43]; Fife (1979),[17]; Okubo (1980),[57]). Models of diffusion and reaction arise, as extensions of (1), when populations disperse and interact. Extensions to allow for age-dependent effects, delays and other historical effects, and genetic structure have been widely used (see for example Webb, and Green and Stech, this volume).

Two classes of problems have received the most extensive study in regard to such systems. The first, which has been examined primarily within the context of population genetics theory and, to a lesser extent, the spread of epidemics (e.g. Ludwig et al. (1979),[49]), concerns the existence of wave or pulse solutions; related work of considerable importance exists within the literature regarding signal transport along axons (see Rinzel (1978), [64]). There is a substantial recent mathematical literature concerning such problems (Evans (1972),[24]; Aronson and Weinberger (1975),[2],(1978),[3]; Conley (1975),[10]; Carpenter (1977 a,b), [5],[6]: Hadeler (1977),[24]; Fife (1979),[17]).

The second class of problems, the existence of non-uniform stationary solutions, has been of interest in a wide variety of biological situations, but especially regarding developmental pattern formation, and the existence of clines (see for example Nagylaki (1975),[54]) and other non-uniform distributions in gene frequencies and in ecological dispersion.

The problem of the existence of non-uniform stationary solutions under homogeneous Neumann boundary conditions has been a problem of great interest to mathematicians, and is reviewed in Levin (1979),[45]. Chafee (1975),[8] demonstrated that the problem

$$\frac{\partial u}{\partial t} = f(u) + D\frac{\partial^2 u}{\partial x^2} \tag{6}$$

cannot possess stable non-uniform stationary solutions (NUSSes), and Casten and Holland (1978),[7] extended this result to convex regions in several dimensions. However, Matano (1979),[50] demonstrated by example that this result depended critically on convexity, and gave sufficient conditions that stable NUSSes could exist for two-dimensional extensions of (6). The major ingredients of his examples were bistability, that is the existence of two homogeneous stable states for (6) with $\underline{D} = 0$, and constrictions ("bottlenecks") in the regions of interest. Although the existence of such solutions was an

open question until Matano's work, in retrospect it should have been intuitively clear by analogy with known results for spatially discrete systems in both continuous time (Levin (1974),[39],(1979),[43]) and discrete time (Karlin and McGregor (1972),[31]). The constrictions on the region necessary in Matano's scheme effectively render the regions approximations to discrete ones, in which mixing within convex subsets (for example) will be much more effective than flow between them. This suggested (Levin (1979),[43]) that for convex regions (indeed, even in one dimension) such NUSSes are possible if flow is severely restricted in suitable portions of the region, and this has been demonstrated by Fife and Peletier (1980),[18] by reduction to a problem involving constant diffusion but spatially varying growth. In this form, the problem is similar to ones involving the existence of clines in population genetics (e.g. Nagylaki (1978),[55]). Stable stationary solutions when dispersal is density dependent have been investigated by Namba (1980),[52] and Shigesada (1980),[68].

When systems of equations of the form (1) are considered ($\underset{\sim}{n}$ is then a vector), it is well known that non-uniform patterns can arise as *dissipative* structures, bifurcating from uniform solutions as the result of differential diffusion rates. Such ideas were first put forth by Turing (1952),[74] within the context of developmental biology, and the nonlinear consequences were explored by Segel and Levin (1976),[67]. Within an ecological context, such *diffusive instabilities* have been studied as regards predator-prey systems (Segel and Jackson (1972),[66], Levin (1974),[39], Okubo (1974),[58], Levin and Segel (1976),[47], Levin and Segal (1976),[67]). It is also the case, as a simple linearization analysis will show, that such bifurcation when diffusion rates are increased cannot take place when all species have identical diffusion rates; in this case the effect of increasing diffusion is simply to shift the spectrum of the linear operator uniformly to the left in the complex plane.

However, the possibility remains that NUSSes could exist which are far from equilibrium, and which would not arise by bifurcation from feasible homogeneous solutions as diffusion rates were varied. Indeed, Matano's method immediately provides trivial examples (not involving interaction) of such NUSSes for systems, and it is clear that numerous more complicated examples could be constructed for non-convex regions. For convex regions, a conjecture is that NUSSes cannot be stable if all species have identical diffusion coefficients. This remains open, although Kishimoto (1981),[35] has recently proved nonexistence results for competitive systems of a particular form, for regions which are parallelepipeds.

Other recent work extends the above considerations by allowing reaction terms to depend on spatial position, the analogue of the clinal problem (e.g. Hodgson, this volume,[25]), or by allowing diffusion to depend on position in analogy with (3) (Shigesada *et al*. (1979),[69], Mimura (1981),[51]). Shigesada *et al*. (1979),[69] demonstrated numerically the existence of NUS solutions in the bistable case of the Lotka-Volterra competition equations, but also assuming an underlying environmental heterogeneity. Mimura (1981),[51] considered the same equations, but under the assumption that a stable solution involving both species exists in the absence of diffusion. For computational convenience, Mimura assumes a partial symmetry, and considers the equations

$$\begin{aligned} \frac{\partial u}{\partial t} &= \beta(R_1 - au - bv)u + \{(1+av)u\}_{xx}, \\ \frac{\partial v}{\partial t} &= (R_2 - av - bu)v + \varepsilon^2 v_{xx}, \end{aligned} \tag{7}$$

and shows the existence of non-uniform stationary solutions satisfying homogeneous Neumann conditions when β and/or ε are sufficiently small and

$$\frac{a}{b} > \frac{R_1}{R_2} > \frac{b}{a} \tag{8}$$

Mimura was unable to resolve analytically the problem of the stability of the non-uniform solutions, although simulations showed an apparent trend to a NUSS.

IV. GENERALIZATIONS AND CONCLUSIONS

The models considered in this paper are basically all variants on diffusion-reaction equations, and these have certainly formed the bulk of the mathematical literature. However, important alternatives exist, and are necessary when assumptions vary from those applicable above.

One important class of models arises when transport may be long-range. In discrete time, for example, the model

$$u_{t+1}(x) = \int m(x-y)g(u_t(y))dy \qquad (9)$$

has been treated in the theory of epidemics and in genetics (see for example Thieme (1977),[72], Diekmann (1978),[12], Weinberger (1980),[77]; and a continuous version

$$\frac{\partial u(x,t)}{\partial t} = -s(x,t)u(x,t) + \int_{-\infty}^{\infty} \Psi(x,y)u(y,t)s(y,t)dy \qquad (10)$$

was utilized by Levin and Segel (1981),[48] to describe switching behavior in predator search image. $u(x,t)$ is the density function of individuals with search image x, and s defines the switching rate. For simplicity of presentation, only transport is shown in (10); appropriate growth terms can be added. An age-structured version was introduced by Levin, Cohen, and Hastings (1981),[46] (see Levin (1980),[44]) to describe seed dispersal in temporal habitats.

Transport models are playing an increasingly important role in biological investigations, and a growing number of field studies are being developed to test and to quantify them. Quantification of dispersal is of both theoretical and applied importance, with applications ranging from analysis of the northern advances of forest species following glaciations to investigations of the evolutionary adaptations of annual plants and marine invertebrates, to the control of forest and agricultural pest species. As partnerships between mathematicians and biologists increase, such studies will also increase in number; and there is little doubt that the role of mathematics will grow in such investigations. The past decade has seen important theoretical advances of a general nature, and the maturation of the subject can be seen by even a casual reading of Okubo's 1980 survey. The general theory has laid the basic foundations, and the advances now will come from the development of more special versions and variations more closely tuned to the needs of particular biological problems and situations. In this quest, the need for and challenge to mathematics in the development of the appropriate theory will be even greater than it has already been.

ACKNOWLEDGMENTS

I am pleased to acknowledge the support of the National Science Foundation under grant MCS-8001618. This paper is dedicated to the memory of my friend and colleague, Sol Rubinow, whose ability to enlist the power of mathematics in the solution of substantive biological problems was ever an inspiration, and always in the best sense of mathematical biology.

REFERENCES

[1] Aronson, D. G. (1980), "Density-dependent interaction diffusion systems", Pages 161-176 in Dynamics and Modelling of Reactive Systems. Academic Press, New York.

[2] Aronson, D.G. and H.F. Weinberger (1975), "Nonlinear diffusion in population genetics, combustion, and nerve propagation", Pages 5-49, in J. Goldstein (ed.), Partial Differential Equations and Related

Topics. Lecture Notes in Mathematics 446. Springer-Verlag, Heidelberg.

[3] Aronson, D.G. and H.F. Weinberger (1978), "Multidimensional nonlinear diffusion arising in population genetics", Adv. Math. 30:33-76.

[4] Brownlee, J. (1911), "The mathematical theory of random migration and epidemic distribution", *Proc. Roy. Soc.*, Edinburgh 31:262-289.

[5] Carpenter, G. A. (1977a), "A geometric approach to singular perturbation problems with applications to nerve impulse equations", *J. Diff, Eq.*, 23:335-367.

[6] Carpenter, G. A. (1977b), "Periodic solutions of nerve impulse equations", *J. Math. Anal. Appl.*, 58:152-173.

[7] Casten, R. G. and C. J. Holland (1978), "Instability results for reaction-diffusion equations with Neumann boundary conditions", *J. Diff. Eq.*, 27:266-273.

[8] Chafee, N. (1975), "Asymptotic behavior for solutions of a one-dimensional parabolic equation with homogeneous Neumann boundary conditions", *J. Diff. Eq.*, 180:111-134.

[9] Cohen, D. S. and J. D. Murray, (1981), "A generalized diffusion model for growth and dispersal in a population", *J. Math. Biol.*. In press.

[10] Conley, C.C. (1975), "Traveling wave solutions of nonlinear diffusion equations", in P.F. Hilton, (ed.), Proc. Conf. Structural Stability, Catastrophe Theory, and Their Applications in the Sciences", Springer-Verlag, New York.

[11] DeAngelis, D. L. (1978), "A model for the movement and distribution of fish in a body of water", Publ. 1173, Environmental Sciences Division, ORNL, Oak Ridge, Tennessee.

[12] Diekmann, O. (1978), "Thresholds and travelling waves for the geographical spread of infection", *J. Math. Biol.* 6:109-130.

[13] Dobzhansky, T. and J. R. Powell (1974), "Rates of dispersal of Drosophila pseudoobscura and its relations", *Proc. Roy. Soc.*, London B 187:281-298.

[14] Dobzhansky, T., J. R. Powell, C. E. Taylor, and M. Andregg, (1979) "Ecological variables affecting the dispersal behavior of Drosophila pseudoobscura and it relatives", *Am. Nat.* 114:325-334.

[15] Dobzhansky, T. and S. Wright (1943), "Genetics of natural populations. X. Dispersion rates in Drosophila pseudoobscura", *Genetics* 32:303-324.

[16] Evans, J. W. (1972), "Nerve axon equations III. Stability of the nerve impulse", *Indiana Math. J.*, 22:577-593.

[17] Fife, P.C. (1979), "Mathematical aspects of reacting and diffusion-systems", Lecture Notes in Biomathematics, 28, Springer-Verlag, Heidelberg.

[18] Fife, P. C. and L. A. Peletier (1980), "Clines induced by variable migration", Pages 276-278 in W. Jager, H. Rost, and P. Tautu (eds.), Biological Growth and spread, Lecture Notes in Biomathematics, 38, Springer-Verlag, Heidelberg.

[19] Fisher, R. A. (1937), "The wave of advance of advantageous genes", *Ann. Eugen. London* 7:355-369.

[20] Goldstein, S. (1951), "On diffusion by discontinuous movements, and on the telegraph equation", *Quart. J. Mech. Appl. Math.* 4:129-156.

[21] Green, D., Jr. and H. W. Stech (1982), "Diffusion and hereditary effects in a class of population models", This volume.

[22] Gurney, W. S. C. and R. M. Nisbet (1976), "A note on non-linear population transport", *J. Theor. Biol.* 56:249-251.

[23] Gurtin, M. E. and R. C. MacCamy (1977), "On the diffusion of biological populations", *Math. Biosci.* 33:35-49.

[24] Hadeler, K. P. (1977), "Nonlinear diffusion equations in biology", Proc. Conf. Partial Differential Equations, Dundee, Scotland (1976) in Lecture Notes in Mathematics. Springer-Verlag, Heidelberg.

[25] Hodgson, J. P. E. (1982), "Predator-prey systems with diffusion in non-homogeneous terrains", This Volume.

[26] Ito, Y. (1952), "The growth form of populations in some aphids, with special reference to the relation between population density and movements", *Res. Popul. Ecol.* 1:36-49 (Japenese with English Summary).

[27] Jones, R. E., N. Gilbert, M. Guppy and V. Nealis (1980) "Long distance movement of Pieris rapae", *J. Anim. Ecol.* 49:629-642.

[28] Kareiva, P. (1981a), "Dispersal as a passive diffusion: an analysis of field experiments involving herbivorous insects", Manuscript.

[29] Kareiva, P. (1981b), "Exclusion experiments and the competitive release of insects feeding on collards", Manuscript.

[30] Kareiva, P. (1981c), "The application of diffusion models to herbivore movement: plant spacing, plant quality, and consequent foraging discrimination", Manuscript.

[31] Karlin, S. and J. McGregor (1972), "Polymorphisms for genetic and ecological systems with weak coupling", *Theor. Pop. Biol.* 3:210-238.

[32] Keller, E. F. and L. A. Segel (1971a), Model for chemotaxis", *J. Theor. Biol.* 30:225-234.

[33] Keller, E. F. and L. A. Segel (1971b), "Traveling bands of chemotactic bacteria: a theoretical analysis", *J. Theor. Biol.* 30:235-248.

[34] Kierstead, H. and L. B. Slobodkin (1953), "The size of water masses containing plankton blooms", *J. Mar. Res.* 12:141-147.

[35] Kishimoto, K. (1981), "Instability of non-constant equilibrium solutions of a system of competition-diffusion equations", *J. Math. Biol.*, In press.

[36] Kolmogorov, A., I. Petrovsky, and N. Piscounov (1937), "Étude de l'équation de la diffusion avec croissance de la quantité de matière et son application à un problème biologique, *Moscow Univ. Bull.*

[37] Kono, T. (1952), "Time dispersion curve: experimental studies on the dispersion of insects (2), *Res. Popul. Ecol.* 1:109-118, (Japanese with English Summary).

[38] Lapidus, I. R. and M. Levandowsky (1981) In M. Levandowsky and S. Hutner (eds.), Biochemistry and Physiology of Protozoa (2nd e.), Vol. IV., Academic Press, New York, Pages 235-260.

[39] Levin, S.A. (1974), "Dispersion and population interactions", *Am. Nat.* 108:207-228.

[40] Levin, S.A. (1976a), "Population dynamic models in Heterogeneous environments", *Annu. Rev. Ecol. Syst.* 7:287-310.

[41] Levin, S. A. (1976b), "Spatial patterning and the structure of ecological communities", Pages 1-35 in S. A. Levin (ed.), Some Mathematical Questions In Biology 7: Lectures on Mathematics in the Life Sciences 8. American Mathematical Society, Providence, Rhode Island.

[42] Levin, S. A. (1978), "Population models and community structure in heterogeneous environments", Pages 439-476 in S. A. Levin (ed.), Mathematical Association of America Study in Mathematical Biology II: Populations and Communities, Mathematical Association of America, Washington, D.C.

[43] Levin, S. A. (1979), "Non-uniform stable solutions to reaction diffusion equations: applications to ecological pattern formation", Pages 210-222, in H. Haken (ed.), Pattern Formation by Dynamic Systems and Pattern Recognition. Springer-Verlag, Heidelberg.

[44] Levin, S. A. (1980), "Some models for the evolution of adaptive traits", Pages 56-72, in C. Barigozzi (ed.), Vito Volterra Symposium on Mathematical Models in Biology, Lecture Notes in Biomathematics 39, Springer-Verlag, Heidelberg.

[45] Levin, S. A. (1981), "The role of theoretical ecology in the description and understanding of populations in heterogeneous environments", *Am. Zool.*, To appear.

[46] Levin, S. A., D. Cohen, and A. Hastings (1981), "Dispersal strategies in patchy environments", Manuscript.

[47] Levin, S. A. and L. A. Segel (1976), "An hypothesis for the origin of planktonic patchiness", *Nature* 259:659.

[48] Levin, S. A. and L. A. Segel (1981). "A model for the influence of predator pressure on aspect diversity in prey populations", Manuscript.

[49] Ludwig, D., D. G. Aronson, and H. F. Weinberger (1979), "Spatial patterning of the spruce budworm", *J. Math. Biol.* 8:217-258.

[50] Matano, H. (1979), "Asymptotic behavior and stability of solutions of semilinear diffusion equations", *Publ. Res. Inst. Math. Sci. Kyoto* 15:401-454.

[51] Mimura, M. (1981), "Stationary pattern of some density-dependent diffusion systems with competitive dynamics", Manuscript.

[52] Morisita, M. (1950), "Dispersal and population density of a water-strider, Cerris lacustris L.", Contrib. Phys. Ecol. Kyoto Univ. 65:1-149 (Japanese).

[53] Morisita, M. (1954), "Dispersion and population pressure: experimental studies on the population density of an ant-lion, Glenuroides japonicas M'L (2)", *Jap. J. Ecol.* 4:71-79, (Japanese with English Summary).

[54] Nagylaki, T. (1975), "Conditions for the existence of clines", *Genetics* 80:595-615.

[55] Nagylaki, T. (1978), "The geographical structure of populations", Pages 588-623 in S. A. Levin (ed.), Studies in Mathematical Biology II; Populations and Communities. Mathematical Association of America, Washington, D.C.

[56] Namba, T. (1980), "Density-dependent dispersal and spatial distribution of a population", *J. Theor. Biol.* 86:351-363.

[57] Newman, W. I. and C. Sagan (1981), "Galactic civilizations: population dynamics and interstellar diffusion", *Icarus*, To appear.

[58] Okubo, A. (1974), "Diffusion-induced instability in model ecosystems", Chesapeake Bay Institute, The John Hopkins Univ. Tech. Rep. 86.

[59] Okubo, A. (1980), "Diffusion and ecological problems: mathematical models", Biomathematics 10, Springer-Verlag, New York.

[60] Okubo, A. and H. C. Chiang (1974), "An analysis of the kinetics of swarming of Anarcte pritchardi Kim." Res. Popul. Ecol. 16:1-42.

[61] Okubo, A., W. Sakamoto, T. Inagaki, and T. Kuroki (1977), "Studies on the schooling behavior of fish. V. Note on the dynamics of fish schooling". *Bull. Jap. Soc. Sci. Fish.* 43:1369-1377.

[62] Patlak, C. S. (1953), "Random walk with persistence and external bias". *Bull. Math. Biophys.* 15:311-338.

[63] Pearson, K. and J. Blakeman (1906), "Mathematical contributions to the theory of evolution -XV. A mathematical theory of random migration". Draper's Company Research Mem. Biometric Series II. Dept. Appl. Math., Univ. College, Univ. London.

[64] Rinzel, J. (1978), "Integration and propagation of neuroelectric signals", Pages 1-66 in S. A. Levin (ed.), Studies in Mathematical Biology I: Cellular Behavior and the Development of Pattern. Mathematical Association of America, Washington, D.C.

[65] Sakai, S. (1973), "A model for group structure and its behavior". *Biophysics* 13:82-90.

[66] Segel, L. A. and J. L. Jackson (1972), "Dissipative structure: an explanation and an ecological example", *J. Theor. Biol.* 37:545-559.

[67] Segel, L. A. and S. A. Levin (1976), "Application of nonlinear stability theory to the study of the effects of diffusion on predator-prey interactions" Pages 123-152 in R. A. Piccirelli (ed.), Topics in Statistical Mechanics and Biophysics.

AIP Conf. Proc. 27, American Institute of Physics, New York.

[68] Shigesada, N. (1980), "Spatial distributions of dispersing animals", *J. Math. Biol.* 9:85-96.

[69] Shigesada, N., K. Kawasaki, and E. Teramoto (1979), "Spatial segregation of interacting species", *J. Theor. Biol.* 79:83-99.

[70] Skellam, J. G. (1951), "Random dispersal in theoretical populations", *Biometrika* 38:196-218.

[71] Taylor, L. R. and R. A. J. Taylor (1977), "Aggregation, migration, and population mechanics", *Nature* 265:415-421.

[72] Thieme, H. R. (1977), "A model for the spatial spread of an epidemic", *J. Math. Biol.* 4:337-351.

[73] Topoff, H. and J. Mirenda (1980), "Army ants on the move: relation between food supply and emigration frequency", *Science* 207(4435):1099-1100.

[74] Turing, A. M. (1952), "The chemical basis of morphogenesis", Phil. Roy. Soc. London B 237:37-72.

[75] Watanabe, S., S. Utida, and T. Yosida (1952), "Dispersion of insects and change of distribution type in its process: experimental studies on the dispersion of insects I.", *Res. Popul. Ecol.* 1:94-108 (Japanese with English Summary).

[76] Webb, G. F. (1982), "A genetics model with age dependence and spatial diffusion", This volume.

[77] Weinberger, H. F. (1980), "Long-time behavior of a class of biological models", Manuscript.