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PATTERN GENERATION IN SPACE AND ASPECT*

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Abstract. A survey is presented of theories for the generation and maintenance of spatial pattern in reaction-diffusion equations and their generalizations. Applications are selected from the biological sciences and physical chemistry. Special emphasis is placed on nonlocal interaction, as manifested by the inclusion of terms involving higher derivatives or integrals. It is stressed that traditional ideas of spatial pattern generation can usefully be extended to the study of pattern in general descriptive ("aspect") variables, particularly in understanding ecological diversity and heterogeneity.

Key words. pattern formation, reaction-diffusion, diffusion, mathematical biology, population ecology

1. Introduction. Striking spatial patterns are found in a variety of physical systems. We review here some aspects of pattern formation in such systems, and then extend our scope to include the biological sciences, with particular applications to problems in ecology.

By "spatial pattern" we mean spatial inhomogeneity with a degree of regularity. (We hence exclude turbulent or chaotic phenomena from our present discussion.) Hence we recognize explicitly the contrast and tension that are embodied in the appearance of irregularity at a local scale and regularity on a more global scale.

Thus a natural way to approach the study of pattern generation is to investigate the fate of an initial small inhomogeneity in an otherwise uniform state. This approach is advantageous because in many cases it mimics the "ontogeny" of pattern, and because more generally we may draw on the techniques of stability theory to provide a powerful method of estimating whether the small disturbance will evolve into a pattern. In many cases, we even can gain insight into the nature of the pattern which emerges.

Consider, then, a small disturbance to uniformity. To aid our exposition, we will assume that the disturbance is confined to a small region of space. Two questions then arise: (i) If we confine our attention to that region alone, what type of intensification or diminution of the disturbance will we observe? (ii) How and to what extent will the local disturbance make its effect felt at distant points? These questions involve the concepts of local interaction and global redistribution, which underlie and determine pattern formation. However, in some of the examples which we shall present later, the line between these is blurred. In these, action at a distance is important; but such action can be thought of as the product of the processes of movement of information or individuals and of localized dynamics.

In many ways, chemical reactions are the simplest model system for the study of pattern formation. In these models, global redistribution occurs simply by the independent random walk of each particle, as manifested phenomenologically by the process of

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diffusion. The local feedback comes from chemical reactions, which can supply a rich variety of behaviors.

Pattern in such reaction-diffusion systems forms a particularly natural starting point for our discussion, because both diffusive movement and local “mass action” can, to some extent, represent realistic ecological situations. This contrasts with the patterns in the Bénard and Taylor fluid flow problems, for which there is no obvious ecological counterpart of the underlying physics except perhaps for the phenomenon of bioconvection (Childress, Levandowsky and Spiegel (1975)).

We begin then with a brief look at the current state of “classical” reaction diffusion theory as applied to spatial pattern formation. (See Fife (1979) for a general mathematical overview of reaction-diffusion theory.) We then examine extensions of the classical theory in which reaction is generalized to interaction, and in which diffusion is replaced by more general mechanisms of transport, including nonlocal redistribution. We further extend the notion of pattern in space to pattern in more general “aspect” space, and show that in many cases, the same basic mechanisms are at work in generating and maintaining pattern.

Among the major stimuli for the current interest in reaction-diffusion theory are the reports by Belousov (1959) and Zhabotinskii (1973) on dynamic colored patterns in certain chemical reactions, and work by Turing (1952) on biological development. Sections 2 and 3 are concerned with these two related lines of research and their extensions. Our attention then turns to the field of ecology, where the major portion of our exposition is centered.

The explanation of observed patterns in space and hierarchy represents one of the most fundamental problems in ecology. Patterns that we can see, e.g. morphological and geographical patterns, constitute the most obvious examples; but the issues of speciation, of community and ecosystem definition, and of functional hierarchies and repeatable functional organization among ecosystems represent other phenomena demanding explanation. In general, we may expect to see such patterns emerge from the inevitable interaction among those forces that oppose uniformity (positive feedback mechanisms—Levin (1981), DeAngelis et al., to appear) and those that stabilize (negative feedback). Problems of this sort arise at every level of biological investigation, from molecular evolution (Eigen and Schuster (1977), (1978)) to the evolution of the biosphere and of biogeochemical cycles (Lovelock (1979)). How can we understand the emergence and stabilization of pattern, repeatable in form across diverse systems, from knowledge of only a few smaller scale interactions?

Section 4 briefly reviews largely classical results concerning pattern formation in ecology and cellular biology. Section 5 shows how considerations regarding classical spatial pattern can be generalized to a discussion of pattern in the distribution of a variable describing the “aspect” of an organism. Here, for example, assortative mating (modelled by an integral operator) can serve to stimulate inhomogeneity, while “search image” can act to restrain and stabilize. The particular example discussed describes a somewhat special situation, but its general features can be played out on many different stages.

When one observes similar phenomena over a range of conditions, one naturally seeks to abstract and generalize in order to discover the features that are at the core. Interaction-redistribution systems provide a convenient and general framework for this quest.

In §5 we develop an illustrative example, and in §6 we present some previously unpublished ideas; thus our exposition becomes more discursive. We revert to the

conventional review style in §7, where we mention further biological contexts wherein pattern can be generated by long-range interactions. In §8, we present our summary and conclusions.

2. Chemical, biochemical and physico-chemical patterns. The spatial patterns associated with the Belousov–Zhabotinskii (B–Z) chemical reaction scheme have been of immense interest both intrinsically and because they serve as models for patterning in biology (Winfree (1980)) and other areas. With regard to their intrinsic interest, there is a parallel to be found in earlier theoretical research on soap bubbles. Viewed strictly as physical phenomena, both soap bubbles and B–Z patterns could be regarded as of somewhat marginal concern. But if one seeks sources of challenging mathematical problems, it is hard to surpass the multitudinous static equilibrium patterns of soap films or the expanding, spiraling, colliding colored waves of the B–Z chemicals.

B–Z theory analyzes suitable special cases of the reaction diffusion system

$$(2.1) \quad \frac{\partial C_i}{\partial t} = R_i(C_1, \dots, C_n) + D_i \nabla^2 C_i, \quad i = 1, \dots, n.$$

An excellent review is that of Tyson (1976). Representative of later work on B–Z models are Field and Troy’s (1979) proof of the existence of a solitary wave solution and Tyson and Fife’s (1980) study of target patterns.

The B–Z phenomena have spurred theoretical research on pattern in general reaction-diffusion systems, for example Erneux’s (1981) study of rotating waves. Kernevez (1980) provides a comprehensive mathematical treatment of immobilized enzyme systems, for which theoretical and experimental work on spatio-temporal pattern have been intertwined especially productively. Experiments by Avnir, Kagan and Levi (1983) and Avnir and Kagan (1983) have broadened greatly the class of chemical systems in which B–Z-like structures can be found.

Winfree and Strogatz (1983) have carried out an investigation of possible three-dimensional wave structures that satisfy constraints both of topology and of continuities required by the nature of chemical reaction. Mathematical progress toward an understanding of the bifurcation structure implicit in reaction-diffusion equations is illustrated by the work of Fujii, Mimura, and Nishiura (1982).

Within reaction-diffusion theory, an area of particular interest is that dealing with excitable systems. These are systems whose homogeneous versions are globally asymptotically stable, but which give a large transient response to super-threshold perturbations. For analysis of possible wave solutions in the inhomogeneous case, see for example Keener (1980), Ermentrout and Rinzel (1981), and Britton (1982). Carpenter (1977) analyzes wave propagation in an excitable reaction-diffusion system that includes as a special case the classical Hodgkin–Huxley equations for nerve transport. Excitable systems as generators of spiral patterns have been studied by Greenberg and Hastings (1978), who also cite earlier relevant references; an independent later investigation was carried out by Madore and Freedman (1983).

Greenberg and Hastings (1978) employ a relatively novel approach, built on a description in terms of finite automata, in which space is reticulated into cells. In their formulation, the state of a cell in any generation is determined by the sum of a local contribution, depending only on the state of that cell in the previous generation, plus an influence that spreads from neighboring cells. The local contribution models the cycling between excited, refractory and rest states, while the additional term permits the spread of excitation from neighbors to resting cells.

A number of researchers have used cellular automata to investigate pattern formation by working backwards: guessing rules that yield patterns close to those observed. In contrast, Greenberg and Hastings' (1978) paper exemplifies an approach that seems likely to be much more productive, namely the induction of simple rules that reflect the essence of the governing physics; Wolfram's recent review (Wolfram (1984)) illustrates the growing awareness of the value of this approach as a complement to other descriptions of pattern formation. In general, there is no single correct description of a particular phenomenon; understanding is better served when one has available a hierarchy of models, each providing insights at its own level of detail. To illustrate this point, let us suppose that one's interest is macroscopic viscous fluid flow. Then only in special circumstances is it worthwhile to derive via Boltzmann's equation the dependence upon state variables of constitutive coefficients in the Navier–Stokes equations. Similarly, if one's interest is the phenomenology of patterns in excitable media, automata models provide an independent caricature of the “true” physics, not just an approximation to the caricature that is embodied in the partial differential equations of reaction-diffusion theory. Automata theory approaches have been applied, for example, to the study of the highly filagreed forms of snowflakes, the details of which are difficult to capture in more conventional approaches.

An area of reaction-diffusion theory with important practical ramifications is the analysis of flames. In many circumstances, flame fronts can be regarded as wave-like solutions of systems of reaction-diffusion equations. Rather complex free boundary conditions apply, so that it was a considerable achievement when Sivashinsky (1979) reduced the reaction-diffusion problem for a disturbed spherical flame front to the following generic scalar equation for the surface perturbation:

$$(2.2) \quad \frac{\partial f}{\partial t} + 4\nabla^4 f + \nabla^2 f + \frac{1}{2}(\nabla f)^2 + 2R^{-1}f = 0, \quad R \text{ a constant.}$$

Sivashinsky demonstrated that as the radius of the front increases beyond a critical value, the smooth flame becomes unstable, giving way to a stable cellular structure. Numerical analysis showed that further increase in the radius leads to a gradual breakdown of regularity and the onset of turbulent motion. Recent trends in combustion theory can be represented by the work of Kapila, Matkowsky and van Harten (1983), in which propagating waves are studied in situations wherein both diffusion and convection of heat and reactant are important.

Diffusion theory (linear parabolic equations) is a classical arena for applied mathematicians. The progression to nonlinear reaction-diffusion equations and then to the more complicated partial differential equations of combustion represents a trend toward the treatment of more difficult and practically important problems. Other examples of this trend can be found in the analysis of the cellular structure found in the solidification of molten metals (e.g. Wollkind (1981)) and in electro-chemical boundary layer structures that stem from the breakdown of charge neutrality in the presence of large voltage gradients (e.g. Rubinstein (1984)).

The “Brussels school” has concentrated on reaction-diffusion pattern as a key to extending thermodynamics into nonequilibrium situations. Such pattern is impossible according to classical equilibrium thermodynamics, but patterned *dissipative structures* are indeed permitted when the state of an open system is sufficiently far from equilibrium (Nicolis and Prigogine (1977)). Another unifying approach is that of *synergetics* (Haken (1978)), which emphasizes the underlying similarity of patterning in many disciplines. From a mathematical point of view, the pattern can be regarded as the

outcome of bifurcation. A salient contribution here is Sattinger's (1979) application of group representation theory to the study of pattern formation.

Traditional examples of pattern formation have been Bénard convection cells which can form in a fluid layer heated from below, and the toroidal Taylor vortices that can appear in the fluid between concentric rotating cylinders. Owing to a variety of reasons, work on such fluid patterns has been especially intense in the last few years. For reviews, see Meyer (1981), Swinney and Gollub (1981), and Schroeder (1982). A comprehensive recent treatment of pattern selection is that of Golubitsky, Swift and Knobloch (1984), who apply group theoretical methods to the problem.

Study of the Bénard problem has led to understanding of the types of pattern that appear in homogeneous planar domains when the uniform solution loses stability. (The dynamics of pattern formation is similar in other physical contexts.) Spatial patterns usually consist of repeating motifs of stripes ("rolls") or hexagons. The overall scale of such patterns typically emerges from a balance of two dominant processes, one providing positive and the other negative feedback to inhomogeneity, each having its greatest influence at a different length scale. The scale of pattern generally can be estimated by a linear stability analysis. By contrast, the form of the pattern can be regarded as the result of nonlinear processes of cooperation and competition among various modes. Rolls are prevalent because each Fourier mode exerts a damping effect on all its competitors. This damping may be coupled with a sufficiently strong mutual reinforcement among triads of modes so that a hexagonal pattern develops. Pattern imperfections move somewhat like dislocations in a crystal.

Pismen (1980) pointed out a comparative advantage of studying reaction-diffusion phenomena as models for pattern formation. The equations of fluids can be varied only slightly by changing physical conditions. On the other hand, if one can find interesting behavior for some class of terms R_i in (2.1), one can often identify a corresponding chemical reaction whose dynamics are similar. This gives an opportunity to test and apply one's ideas. Moreover, the relatively simple nature of the reaction-diffusion equations facilitates further development of the theory.

3. Pattern formation in developmental biology. A fundamental problem in developmental biology is understanding morphogenesis, the generation of form and pattern starting from a comparatively featureless initial state. In a seminal contribution to this problem, Turing (1952) studied pairs of reaction-diffusion equations (2.1). In his considerations, the reaction functions R_1 and R_2 were polynomials. However the fundamental results do not depend on such special forms; all that is required for the generation of pattern is some sort of nonlinear activator-inhibitor interaction. Turing also examined discrete analogues of (2.1) in which chemicals were regarded as passing from each "cell" to its neighbor at a net rate proportional to the concentration difference between the two. He showed that, under certain conditions, uniform solutions were unstable to small perturbations, and he demonstrated by numerical analysis that stable nonuniform spatial patterns could result. Turing thus demonstrated that reaction-diffusion instabilities could in theory lead to patterned distributions of chemicals and therefore that distributions of chemical "morphogens" might underlie the creation of biological pattern.

For a long time there were only scattered responses by biologists to Turing's work, for example the paper by Wardlaw (1955). However, the paper fascinated theorists, and inspired theoretical extensions such as Othmer and Scriven's (1971) treatment of interconnected compartmental networks, and Segel and Jackson's (1972) physical explanation of how diffusion, normally thought to be a smoothing mechanism, could in fact

generate inhomogeneity. Stuchl and Marek (1982) recently reported on experimental efforts to confirm predictions from discrete Turing models.

Interest among developmental biologists increased following the studies of Gierer and Meinhardt (1972), who advanced Turing-like ideas without at first being aware of Turing's work. Gierer and Meinhardt stressed that the key ingredient in the generation of diffusive pattern was the combination of short-range activation and long-range inhibition. They pointed out that gradients of morphogens, which many developmental biologists had invoked as underlying pattern generation, did not require pre-arranged sources and sinks; they could arise from instability or from the "firing" of preset slight inhomogeneities (as are found for example in fertilized eggs). Above all, they used their general ideas in computer simulations that suggest solutions to many specific problems of developmental biology, in particular, the control of head and foot regeneration in *hydra*.

Analytical work has confirmed and extended the conclusions of the simulations of Gierer and Meinhardt. See, for example, Granero, Porati and Zanacca (1977), Keener (1978) and Segel (1984, Chap. 8). For comprehensive surveys of the Gierer–Meinhardt ideas, see Gierer (1981a) and Meinhardt (1982). Schaller and Bodenmüller (1982) provided up-to-date information on marked progress in the chemical identification of morphogens in *hydra*. In light of the new experimental results, Kemmner (1984) formulated a revised reaction-diffusion model (with delays) for *hydra* regeneration.

As illustrated by the work of Murray (1981) and Bard (1981) on coat striping in zebras and other mammals, and of Hunding (1983) on bipolar three-dimensional patterns, lively interest continues in reaction-diffusion explanations of developmental structure. But differing explanations also are being analyzed, such as the following: (i) Edelstein and Segel (1983) provided a possible explanation for the observed concentric rings of dense growth in fungi via a model, one of whose key features is a combination of diffusion and directed *convective* flux of critical nutrient. (ii) Mitchison (1980) studied the formation of leaf vein patterns in a model (without reaction terms) for the flux-dependent diffusive flow between a line source and a line sink. This hypothesis was based on evidence found by Sachs (1969) that it is not autocatalytic inhomogeneities in the level of chemical concentration that are the primary determinants of vein pattern formation, but rather inhomogeneities in the chemical flux. (iii) Khait and Segel (1984) pointed out the possible importance of a *continuing* interplay between the response of a cell to its chemical environment and the cell's secretion-behavior. Their reaction-diffusion model contains no direct interactions between the activating and inhibiting chemicals.

Reaction-diffusion models show how a chemical pre-pattern can be established; that pre-pattern could generate observed biological structures by serving as a key for gene activation. If the structures involve shape changes, then appropriate patterns of mechanical forces must be involved. It has recently been emphasized that these forces themselves may be intimately connected with the pattern formation process (Odell et al. (1981)), Murray, Oster, and Harris (1983), Oster and Odell (1984). This work on mechano-morphogenesis is based on models for tissue that include such factors as the production by cells of traction on their environment, the tendency of cells to align along environmental anisotropies and to move up gradients of adhesiveness, and the interplay between the effects of calcium on intracellular mechanics and of cytoplasmic flow on calcium distribution.

In this section, we have tried to document the richness of the subject. We expect an accelerating pace of activity in theories of morphogenesis, owing to the accumulation,

both autonomously and led by theory, of the facts that are essential to guide further research into this fascinating subject.

4. Interaction-diffusion equations in ecology and cellular biology. A landscape (or seascape) is not homogeneous, but is in general a shifting mosaic of diverse units. The fact that part of the pattern may arise or be enhanced by ecological interactions has been suggested by several authors (for example, A. S. Watt (1947), Levin (1976), (1981), Whittaker and Levin (1977), Levin and Paine (1974), Paine and Levin (1981)), and has led to the development of a whole field, landscape ecology, now formalized in its own international society. Mathematical formalizations have played an important role in the development and codification of ideas (Levin (1979)), and are expected to be central in quantitative approaches to applied issues in landscape management (Risser, Karr and Forman (1984)).

4.1. Nonuniform stationary patterns. Segel and Jackson (1972) first suggested that the advances by Turing (1952) in the study of reaction-diffusion systems might be of significance in ecology. These authors showed that the uniform state could be unstable if the interaction of a victim (prey) of density $V(x, y, t)$ and an exploiter (predator) of density $E(x, y, t)$ were governed by

$$(4.1) \quad \begin{aligned} \frac{dV}{dt} &= V(K + \alpha V - \beta E) + D_V \nabla^2 V, \\ \frac{dE}{dt} &= E(-L + \gamma V - \delta E) + D_E \nabla^2 E. \end{aligned}$$

Here Greek letters represent positive constants, as do the diffusivities D_V and D_E . Levin (1974) considered a somewhat different system from (4.1), with the signs of δ and α reversed, and found similar results.

The justification for examining such dynamics is that attention is focused on behavior near steady state. In each case, an autocatalytic effect is introduced (through α in (4.1), through δ in Levin (1974)), motivated by ecological considerations. In (4.1) the autocatalysis may be justified by a reduction of predation efficiency as prey density increases, an effect described by Holling (1959) as one possible manifestation of the predator's functional response. In Levin (1974), justification involved social facilitation among rare predators.

Segel and Levin (1976) used a combination of successive approximation and multiple-time scale theory to develop the small amplitude nonlinear theory of (4.1); they showed that a new nonuniform steady state would be attained following destabilization of the spatially uniform state. In this paper, and in Levin and Segel (1976), it was pointed out that diffusive instabilities might explain instances of spatial irregularity in natural communities, for example the observed patchy distribution of plankton in the ocean. A very recent mathematical review of the problem of pattern formation in predator-prey systems is provided by Conway (to appear).

Another and even more compelling body of theory regards patterns which form in spatially distributed ecological systems as a consequence of multiple stable states in the underlying dynamics (Levin (1974), (1979)). This idea seems especially important for explaining patterns in ecological systems, and has been the object of intense ecological and mathematical interest (e.g. Matano (1979)). Similarly, clinal solutions have long been of interest in population genetics (e.g. Endler (1977), Nagylaki (1978)); but interest there has focused primarily on solutions which are stabilized by underlying environmental variability.

4.2. Modified diffusion. There is an extensive mathematical literature on diffusion-reaction systems applied to ecological problems (Okubo (1980)). However, in spite of all the work that has been devoted to diffusion theory in ecology, the suitability of the most naive diffusion model for the description of animal movements requires critical scrutiny. As Skellam (1973) remarked “it is clearly much better to construct the diffusion model in relation to the realities of the grass-roots situation than to borrow some simple model, such as $\partial f/\partial t \propto \partial^2 f/\partial x^2$, from physical science or mathematical textbooks and trust in its applicability.” Skellam showed from random walk considerations that if motion is determined by varying conditions at the origin of a small step, then the approximating equation for the population density f has the form

$$(4.2) \quad \frac{\partial f}{\partial t} = \frac{\partial^2 (Df)}{\partial x^2}$$

for some function $D(x)$. If conditions at the termination of the step determine the probability of motion, the appropriate modified diffusion equation becomes

$$(4.3) \quad \frac{\partial f}{\partial t} = \frac{\partial}{\partial x} \left[D \frac{\partial f}{\partial x} - \frac{\partial D}{\partial x} f \right].$$

If D is regarded as dependent on x through a function $s(x)$ (that is if $D = D(s(x))$), then both (4.2) and (4.3) can be regarded as special cases of the taxis equation (Keller and Segel (1970))

$$(4.4) \quad \frac{\partial f}{\partial t} = \frac{\partial}{\partial x} \left[\mu \frac{\partial f}{\partial x} - \chi f \frac{\partial s}{\partial x} \right],$$

wherein $s(x)$ is the concentration of some attracting agent. Equation (4.4) has the form of a conservation law: $\partial f/\partial t = \partial J/\partial x$. The flux J has two parts, a random portion, and a tactic portion that is proportional through a sensitivity factor χ to the gradient of s . See Keller (1975), Segel (1977), (1978), and Alt (1980) for derivation of (4.4) from random walk models. Alt (1980) has also shown that more complex versions of (4.4) are appropriate in certain situations.

Kareiva (1983) recently undertook a comprehensive examination of the suitability of constant coefficient diffusion for describing the foraging movements of phytophagous insects, and found the model adequate in 8 of 12 instances. In other cases more complex models are necessitated (special cases of (4.4)). These present difficulties in parameter fitting, but substantial advances have been made recently (Banks and Kareiva (1983)), using spline methods.

4.3. Traveling population waves. If $f(x)$ is regarded as the bacterial population density and $s(x)$ as the concentration of a nutrient, then various experimental and natural situations can be modeled by (4.4) with the addition of a consumption-diffusion equation such as

$$(4.5) \quad \frac{\partial s}{\partial t} = -kf + D \left(\frac{\partial^2 s}{\partial x^2} \right).$$

Much theoretical and experimental work has been devoted to the determination of traveling wave solutions to (4.4) and (4.5) for various functions $\mu(s)$, $\chi(s)$, and $k(s)$. See G. Odell's survey in (Segel (1980, §6.7)). From the present point of view, this line of research can be regarded as having begun with the paper of Kolmogoroff, Petrovsky

and Piscounoff (1937) on traveling wave solutions to the Fisher equation for the spread of an advantageous allele

$$(4.6) \quad \frac{\partial f}{\partial t} = f(1-f) + D \left(\frac{\partial^2 f}{\partial x^2} \right),$$

and of course from the original discussion of Fisher (1937). Rigorous work on (4.6) and its generalizations can be traced via the study by Pauwelussen and Peletier (1981) of an equation that includes the effect of asymmetric migration (analogous to convection)

$$(4.7) \quad \frac{\partial f}{\partial t} = \frac{\partial^2 f}{\partial x^2} + m \frac{\partial f}{\partial x} + F(x, f).$$

Several other examples of traveling population waves are mentioned in Segel's (1984) survey of the role of taxes in ecology and cell biology. Also see the remarks below on (4.10).

4.4. Slime mold aggregation. A prototype problem for biological pattern formation is the aggregation of certain (slime mold) amoebae into more or less evenly spread collection points. A simple model for this phenomenon (Keller and Segel (1970)) regards it as an instability of the uniform state of (4.4) and

$$(4.8) \quad \frac{\partial s}{\partial t} = \sigma f - \lambda s + D \frac{\partial^2 s}{\partial x^2}.$$

Here, f denotes the density of amoebae. Equation (4.8) provides for the secretion of the attractant by the amoebae at rate σ , the destruction of the attractant by an enzyme, and the diffusion of the attractant. Post-instability behavior has been considered by Childress and Percus (1981), who showed in three dimensions that the ultimate state will be a row of delta functions. However, in one dimension, where diffusion is strong enough to overcome chemical attraction, the individual peaks will be spread out. Evidence is given that, in two dimensions, collapse to delta functions will occur only for sufficiently large values of a parameter that embodies the relative strength of chemotaxis. Additional interesting work on slime mold aggregation has been carried out by Hagan (1981), (1982) and Hagan and Cohen (1981) who discussed *inter alia* spiral waves and target patterns sometimes formed by these organisms.

4.5. Longer range effects on redistribution. In all cases that we have treated so far, the particle models that underlie the continuum transport terms have been local in character: the probability of a small step, from P to Q say, depended only on conditions at P and Q . As a first step away from this, let us consider the influence on movement by next-nearest neighboring points. This has the effect of introducing higher derivative terms into the (bracketed) expression for flux in (4.4). If the motion is isotropic, the appropriate generalization of pure diffusion is the Cahn–Hilliard equation

$$(4.9) \quad \frac{\partial f}{\partial t} = \nabla \cdot [D(f) \nabla f] - K \nabla^4 f.$$

Cohen and Murray (1981) suggested that (4.9) may be applicable to population movement, and have discussed bifurcation to nonuniform states when $D(f) = D_0 + D_2 f_2$. Novick-Cohen and Segel (1984) discussed various nonlinear results for the case where

$D(f)$ also includes a linear term, which is important in the more conventional applications of Cahn–Hilliard theory to phase changes in solutes. Falkovitz et al. (1982) provided another example of the use of the Cahn–Hilliard equation to explain structure in a problem of physical chemistry. Note the similarity between the Cahn–Hilliard equation (4.9) and Sivashinsky’s equation (3.1).

Othmer (1983) showed how higher derivative terms enter the stress-strain relationship for a material whose fibers spread mechanical influences over relatively long distances. The resulting fourth-order terms, analogous to those that appear in (4.9), play a critical role in Oster and Odell’s (1984) pattern formation theory that was mentioned at the end of §3.

Another more complex model is due to Nagai and Mimura (1983), who demonstrated the existence of asymptotic traveling solitary wave solutions for the population movement equation

$$(4.10) \quad \frac{\partial u}{\partial t} = -\frac{\partial}{\partial x} \left[\frac{\partial}{\partial x} (u^m) + \left(\int_{-\infty}^x u(\xi, t) d\xi - \int_x^{\infty} u(\xi, t) d\xi \right) \right], \quad m > 1.$$

By itself, the first part of the flux term (in square brackets) would spread bounded disturbances at a finite speed (Aronson (1980)). The second part of the flux models a situation in which the speed of an organism’s movement to the left or right depends on a balance between the relative “pressure” of all the organisms to the left and right, respectively, of the organism’s present position.

5. An ecological example of pattern in aspect. Ecologists have been interested for over 40 years (see for example Popham (1941), (1943)) in the diversity of colors or other aspects among prey species. *Apostatic selection* by predators, their tendency to concentrate their attention on relatively numerous prey (Clarke (1962)), is one conjectured mechanism for maintaining and generating diversity.

According to this scenario, a predator may form a *search image* for a frequently-encountered prey item and thereby increase its efficiency in searching. As prey densities change, the apostatic predator may switch its search image. At the level of the population, and sometimes even at the level of the individual, this in general will not be a threshold switch at a particular density; rather, the tendency to switch will be related to prey densities in a continuous fashion. Very simple organisms may require generations for mutation to replace an outdated search image. Higher organisms can switch in a very small fraction of their life span.

In this section we shall review results of Levin and Segel (1982) and Keshet and Segel (1984) for the possible effects of apostatic selection in a predator-prey interaction. Our presentation has two main purposes: to provide a concrete example of what we shall later term “pattern in aspect” and to show how familiar features of pattern generation appear in equations that seem considerably more complex than those usually treated.

For notational convenience we again shall employ the terms exploiter (e) for predator, and victim (v) for prey. Regarding the exploiters, only two dynamic features are taken into consideration. The exploiters die or abandon the particular type of victim at a rate that decreases as the density of v increases, and they switch from other prey back to v at a constant rate c . For simplicity, the switching rate from v is assumed to be given by the linear function $u + \mu v$; obviously this is meaningful only for $u < v/\mu$, but this assumption is not a critical one and is relaxed in Levin and Segel (1982). The

resulting equation is

$$(5.1) \quad \frac{\partial e}{\partial t} = c - e(\nu - \mu\nu).$$

The type or *aspect* of the victim is assumed to be describable by a single variable z . For example, z could be the frequency of the dominant victim color, or the average spot size in a patterned victim, or (Edelstein (1983)) a measure of the quality of a plant. We shall ignore boundary effects, so that z will be assumed either to be periodic or to run over the whole real line. Thus $v(z, t)$ will be the density of victims of aspect z at time t , and $e(z, t)$ will be the density of exploiters that are currently concentrating their attention on these victims.

We are interested in the *evolution* of patterns in aspect, so that some rules for mating must be adopted. Two types of hypotheses are made, one concerned with the relative frequencies of different types of matings among victims and the second concerned with the outcome of a given mating. Mating preference, or *assortative mating*, is expressed in the assumption that a female of aspect z will choose her mate according to a normal probability distribution centered at z . Equal numbers of males and females are postulated. The outcome of a mating between partners of aspects z_1 and z_2 is assumed to be normally distributed about the mean parental type $(z_1 + z_2)/2$. (This may be relaxed (Levin and Segel (1982)) to account for the incomplete *heritability* of the trait.) Justification for these assumptions and their relation to various discrete models are discussed by Levin and Segel (1982) in the special case that a female's reproduction rate is a constant r , independent of phenotype. These authors show that the appropriate governing equation (based on extensions of conventional models of quantitative inheritance) is

$$(5.2) \quad \frac{\partial v}{\partial t}(z, t) = -kv(z, t)e(z, t) + r \int \int v(\eta, t)v(\xi, t) \frac{\alpha(\eta - \xi)}{W(\eta, t)} \phi\left(\frac{\eta + \xi}{2} - z\right) d\eta d\xi.$$

Here integrals run from $-\infty$ to ∞ ; k and r are positive constants, and

$$(5.3) \quad W(\eta, t) = \int \alpha(\eta - \xi)v(\xi, t) d\xi.$$

The assortativity and progeny-distribution distributions α and ϕ are given explicitly by

$$(5.4a) \quad \alpha(z) = (2\pi\sigma_\alpha^2)^{-1/2} \exp\left(-\frac{z^2}{2\sigma_\alpha^2}\right),$$

$$(5.4b) \quad \phi(z) = (2\pi\sigma_\phi^2)^{-1/2} \exp\left(-\frac{z^2}{2\sigma_\phi^2}\right).$$

In (5.2), the term $-kve$ represents a mass-action assumption for the consumption of victims by exploiters. Note that in this very simple model the exploiter generation time is long and the victim population is assumed to constitute only a negligible portion of the exploiter diet, so that no measurable immediate benefit accrues to the exploiters from the consumption of victims.

Much information concerning the mathematical problem posed by (5.1) and (5.2) can be obtained by a quite conventional analysis. We first determine that there are two

steady, homogeneous (in z) states, one in which the victims are extinct, and a nontrivial one

$$(5.5) \quad \bar{v} = r\mu^{-1}(S - P), \quad \bar{e} = rk^{-1}, \quad S > P.$$

Here S and P are dimensionless parameters that represent, respectively, measures of switching and predation:

$$(5.6) \quad S = \frac{v}{r}, \quad P = \frac{ck}{r^2}.$$

The next step is to make a linear stability analysis of the solution (5.5). This proceeds easily, because of the assumption that the kernels are gaussian. We write

$$(5.7) \quad v(z, t) = \bar{v} + \hat{v}(z, t), \quad e(z, t) = \bar{e} + \hat{e}(z, t).$$

Linearizing the equations for \hat{v} and \hat{e} , and considering solutions of the form

$$\hat{v}(z, t) = v^*(t)\exp(iqz), \quad \hat{e}(z, t) = e^*(t)\exp(iqz),$$

we obtain the following system of ordinary differential equations for $v^*(t)$ and $e^*(t)$:

$$(5.8) \quad \frac{dv^*}{dt} = -(k\bar{v})e^* + (L - 1)rv^*, \quad \frac{de^*}{dt} = -(\nu - \mu\bar{v})e^* + (\mu\bar{e})v^*.$$

Here

$$(5.9) \quad L = \tilde{\alpha}\left(\frac{q}{2}\right)[2 - \tilde{\alpha}(q)]\tilde{\phi}(q),$$

where the tilde denotes a Fourier transform. Alternatively

$$(5.10) \quad L = (2 - \tilde{\alpha})\tilde{\alpha}^{\beta+1/4} \quad \text{where } \beta \equiv \sigma_\phi^2/\sigma_\alpha^2.$$

In particular it is the case (Levin and Segel (1982)) that if

$$L_{\text{cr}} \equiv \min(P + 1, S/P) < 1.27,$$

then when $\beta < \beta_{\text{cr}}$ there is a band of wavenumbers q corresponding to growing disturbances, where β_{cr} is given implicitly by

$$(5.11) \quad \left[\frac{2}{\beta_{\text{cr}} + 5/4} \right]^{\beta_{\text{cr}} + 5/4} \left(\beta_{\text{cr}} + \frac{1}{4} \right)^{\beta_{\text{cr}} + 1/4} = L_{\text{cr}}.$$

The preceding linear analysis was used by Keshet and Segel (1984) to guide the selection of parameters for a numerical analysis of the full nonlinear system (5.1), (5.2), just beyond the bifurcation, assuming periodic boundary conditions. Fig. 1 shows the results of one major calculation with a parameter set for which linear theory predicts monotonic instability (based on a real destabilizing eigenvalue) of the coexistence state (5.5). Here the solution settles down to a new periodic nonuniform steady state where spikes of concentrated victims and exploiters are separated by segments of aspect that are devoid of victims. This “row of spikes” pattern is reminiscent of findings in rather different contexts, as in the paper by Mimura, Nishiura and Yamaguti (1979). The same sort of pattern was also found by Hopf and Hopf (1984) in an ecological study that is closely related to the work being described here.

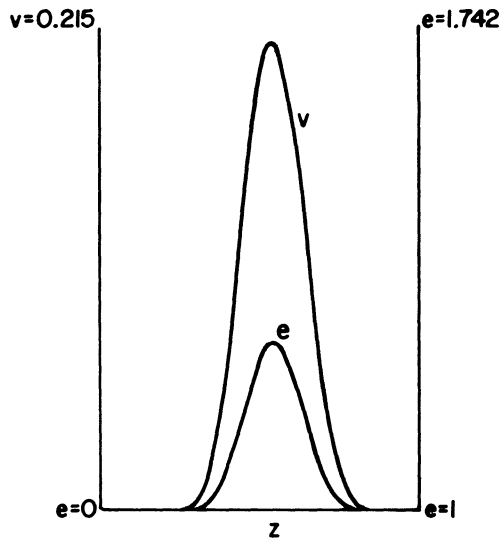


FIG. 1. Inhomogeneous steady state obtained by numerical analysis of (5.1) and (5.2) subject to periodic boundary conditions. For details, consult Keshet and Segel (1984), from which this figure was reproduced.

The result of Fig. 1 allows us to sketch the following possible coevolutionary scenario for the emergence of diversity. Selection favors some predators whose labile search images improve their ability to locate prey. As a consequence, mutations or random combinations affecting prey aspect induce selective regimes which favor certain types, and gradually the prey aspect distribution shifts. Our mathematical analysis shows the possible instability of the state of maximum diversity, in which all types are equally represented in the population. Thus, if predator pressure increases sufficiently, diversity may decrease as the population breaks up into “clumps” of organisms that bear similar aspects. Of course, the direction of evolution may instead be from a few specialized types towards higher diversity. In this case, the instability of the maximum diversity situation provides evidence that there are limits to how far diversification will proceed, and may provide some indication of the distributional patterns to be expected.

The “distance” between clumps is approximated by the critical wavelength of linear stability theory, where (Levin and Segel (1982))

$$(5.12) \quad \frac{\lambda_{cr}}{\sigma_{\alpha}} = \frac{\pi\sqrt{2}}{[\ln(1/2 + 2/(4\beta_{cr} + 1))]^{1/2}}.$$

The minimum value of this ratio (when $\beta_{cr} = 0$) is 4.64, so that the overwhelming majority of matings are between members of the same clump. The clumping thus produces the reproductive isolation that is a prerequisite of *sympatric speciation*—speciation without the necessity of physical separation. There is also relevance to the issue of *species packing* since, for a given range of aspect, the critical wavelength (5.12) of linear theory sets bounds on the number of coexisting species.

Various questions remain open. Of these we mention only the relaxation of the assumption that the aspect variable ranges from $-\infty$ to ∞ . Imposition of periodicity obviously is called for when dealing with such characteristics as emergence times in insects or flowering times of plants, but also might be appropriate for example when aspect is hue (at least for humans, hue is organized on a color wheel), or spot size

(under some circumstances if spots become very large, then the background appears as small spots). Moreover, boundary effects are not expected to be too important if the size of the aspect domain is large compared to the instability wavelength; but there are certainly instances where boundary effects could play a crucial role. In situations where aspect may be regarded as semi-infinite, the linear stability analysis requires the use of Wiener–Hopf techniques. The problem becomes harder still when z is confined to a bounded interval. The proper formulation is not obvious in either case.

6. Other examples of ecological structure under generalized redistribution. In the previous section we reported on a particular ecological interaction that gave rise to a nonlocal redistribution operator, but that nonetheless exhibited post-bifurcation behavior typical of reaction-diffusion equations and other instances where redistribution is local. To dispel suspicion that our findings are dependent on the particular example studied, we now present several other (mostly new) ecological applications of nonlocal redistribution. The first example will be worked out in a little detail, to drive home the point that the stability calculations for redistribution operators with gaussian kernels are not appreciably more difficult than for diffusive redistribution; the others will be presented briefly, as a sampling from a catalogue. The methods are straightforward, and identical among examples.

6.1. Distributed Allee effect and resource limitation. Our first example treats a situation where familiar concepts such as localized reproduction and resource limitation are generalized to take on a distributed character. Here $N(z, t)$ will denote the density at time t of a species whose activities are centered at point z . Random motion about the center of activity will be modeled by a diffusion term. At low densities the reproduction rate of the organism will be given by a constant r . The greater ease of finding mates when the population density increases will be represented by an autocatalytic or *Allee* term proportional to the constant a . In addition, higher population levels will cause a depletion of resources, which in turn brings about a decrease in the per capita birth rate—denoted here by a term proportional to b . These considerations yield the equation

$$(6.1) \quad \frac{\partial N(z, t)}{\partial t} = rN(z, t) \left[1 + a \int \alpha(z - \xi) N(\xi, t) d\xi - b \int \beta(z - \xi) N(\xi, t) d\xi \right] + D \frac{\partial^2 N(z, t)}{\partial z^2}.$$

As before, integrals will run from $-\infty$ to ∞ . Also here and throughout this section we shall employ Greek letters to represent gaussian functions of the “distance” between two values of a variable. Thus, α again satisfies (5.4), while β satisfies the corresponding equation

$$(6.2) \quad \beta(z) = (2\pi\sigma_\beta)^{-1/2} \exp(-z^2/2\sigma_\beta^2).$$

Note that σ_α and σ_β in general are different, representing different characteristic excursions from “home base” in searching for a mate and foraging.

Since $\int \alpha(z) dz = \int \beta(z) dz = 1$, equation (6.1) has the uniform steady state solution \bar{N} , where

$$(6.3) \quad \bar{N} = (b - a)^{-1}.$$

We shall assume that $b > a$, so that this solution is feasible. To prove the stability of (6.3) we introduce the perturbation variable \hat{N} by

$$(6.4) \quad \hat{N}(z, t) = N(z, t) - \bar{N}.$$

Discarding all except linear terms in $\hat{N}(z, t)$, we consider solutions of the form

$$(6.5) \quad \hat{N}(z, t) = N^*(t) \exp(iqz).$$

(We assume that all appropriate solutions of the linearized system can be constructed by Fourier superposition.) Upon substituting (6.5) into the linearized equation for N , we obtain

$$(6.6) \quad \frac{dN^*}{dt} = r [a\tilde{\alpha} - b\tilde{\beta} - Dq^2] N^*.$$

Tildes denote Fourier transforms, so that for example

$$(6.7) \quad \tilde{\alpha} = \exp\left[\left(-\frac{1}{2}\right)\sigma_\alpha^2 q^2\right].$$

If we introduce $k = (\frac{1}{2})\sigma_\alpha^2 q^2$ and the dimensionless parameters

$$(6.8) \quad \theta \equiv \frac{\sigma_\beta^2}{\sigma_\alpha^2}, \quad B = \frac{b}{a}, \quad \bar{D} = \frac{2D}{a\sigma_\alpha^2},$$

then we see that N^* increases exponentially for k 's such that

$$(6.9a, b) \quad f(k) > \bar{D}k \quad \text{where } f(k) \equiv e^{-k} - Be^{-\theta k}.$$

Thus (6.9) specifies the conditions for instability of the uniform state. If $\theta < 1$, f is always negative (since $B > 1$ by assumption) and the uniform state is stable. If $\theta > 1$, $f(k)$ crosses the k -axis exactly once, so that the curves $y = f(k)$ and the line $y = \bar{D}k$ have the shapes depicted in Fig. 2. It is clear that for fixed B and θ , for example, inequality (6.9) will be satisfied for a range of k if \bar{D} is sufficiently small. If \bar{D} is decreased from a large value, say by an increase in the cooperativity range σ_α , then instability of the uniform state will set in at the value \bar{D}_c and the wavenumber k_c that define the point of tangency of $f(k)$ and $\bar{D}k$. Thus

$$(6.10) \quad f(k_c) = \bar{D}k_c, \quad \left. \frac{df(k)}{dk} \right|_{k=k_c} = \bar{D}.$$

See Fig. 2.

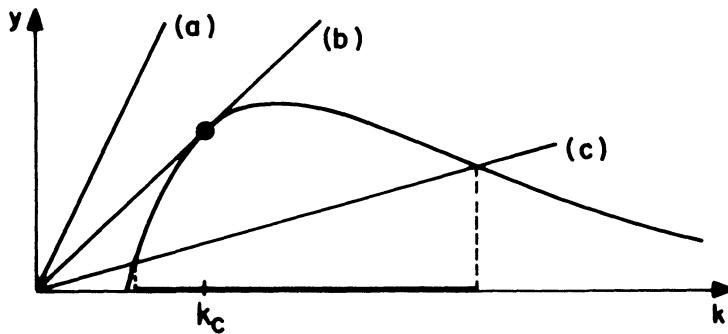


FIG. 2. Graph of $y = f(k)$ (6.9b) and $y = Dk$ for (a) large, (b) critical, and (c) small values of D . In case (c), inequality (6.9a) is satisfied for a range of wavenumbers q given by $q = \sigma_\alpha^{-1}(2k)^{1/2}$, where k lies in the heavily shaded portion of the k -axis.

To be more explicit, let us make the additional assumptions that B and θ are close to unity and (as is then required for (6.10) to have a solution) that \bar{D} is small. Then if ε , h , and d are defined by

$$(6.11) \quad \theta = 1 + \varepsilon, \quad B = 1 + \varepsilon h, \quad \bar{D} = \varepsilon d, \quad \text{where } \varepsilon \ll 1,$$

we obtain after a little calculation that to first approximation (6.10) implies

$$(6.12) \quad h - k = dke^k, \quad 1 + h - k = de^k.$$

Elimination of h yields $(1 - k)^{-1} = de^k$, which shows that $k < 1$, since $d > 0$.

Elimination of d in (6.12) yields a quadratic with a single solution less than unity. Consequently, explicit formulas for k_c and D_c can be found, namely

$$(6.13) \quad k_c = 1 + \frac{1}{2}h - \left[1 + \frac{1}{4}h^2\right]^{1/2}, \quad \text{so that } \bar{D}_c = \varepsilon(1 + h - k_c)\exp(-k_c).$$

Thus a randomly dispersing population with a sufficiently strong distributed Allee effect cannot maintain a uniform spatial distribution. We expect that a new nonuniform steady distribution will result, although we have not carried out any nonlinear calculations for this example. We stress that the present examples show that pattern can arise on a single trophic level (i.e., in a single equation). This is in contrast to more traditional reaction-diffusion models for pattern formation, which require the interaction between two species.

6.2 Assortative mating with density-dependent death rate. Another model that demonstrates how structure can arise on a single trophic level is the following, where assortative mating is combined with a death rate that increases with population density:

$$(6.14) \quad \frac{\partial V(z, t)}{\partial t} = -\frac{V(z, t)}{\nu - \mu V(z, t)} + r \int \int V(\eta, t) V(\xi, t) \frac{\alpha(\eta, \xi)}{W(\eta, t)} \phi(\eta, \xi, z) d\eta d\xi.$$

The death term is written in a slightly unconventional way; but what we have done merely is to substitute into (5.2) the steady state solution of (5.1), setting $k_c = 1$ without loss of generality. This of course means that the nonhomogeneous steady solution for V in Fig. 1 is also applicable in the present case.

6.3. Distributed predator-prey interaction. Consider the following equations with distributed (Lotka-Volterra type) interactions between exploiters and victims:

$$\begin{aligned} \frac{\partial E(z, t)}{\partial t} &= rE(z, t) \left[1 - a \int \alpha(z, \xi) E(\xi, t) d\xi \right] \\ &\quad + bV(z, t) \int \beta(z, \xi) E(\xi, t) d\xi + D_1 \frac{\partial^2 E(z, t)}{\partial z^2}, \\ \frac{\partial V(z, t)}{\partial t} &= sV(z, t) \left[1 - c \int \gamma(z, \xi) V(\xi, t) d\xi \right] \\ &\quad - gV(z, t) \int \beta(z, \xi) E(\xi, t) d\xi + D_2 \frac{\partial^2 V(z, t)}{\partial z^2}. \end{aligned}$$

In contrast with the nondistributed case, analysis shows that the uniform state can become monotonically unstable even though no autocatalysis (such as an Allee effect) has been postulated. Again, in contradistinction to the nondistributed case even with an

Allee effect, with the present model there are conditions that will lead to an oscillatory instability of the uniform state, and hence potentially to a temporarily periodic final state.

6.4. Switching. For a final ecological model, let us consider the effect of switching. Imagine a population whose density, when homogeneous, is governed by the standard logistic equation

$$(6.15) \quad \frac{dn(t)}{dt} = rn(t)[1 - K^{-1}n(t)].$$

Suppose now that the population density may depend on the space or aspect variable z . Assume that organisms abandon their present "location" at a rate S that depends on the population density within a range of magnitude σ_θ , and that such organisms are normally redistributed, with standard deviation σ_ψ , about the location just abandoned. The governing equation is

$$(6.16) \quad \frac{\partial n(z, t)}{\partial t} = rn(z, t)[1 - n(z, t)/K] - S[N(z, t)]n(z, t) + \int \psi(z - \xi)S[N(\xi, t)]n(\xi, t)d\xi,$$

where

$$(6.17) \quad N(z, t) = \int \theta(z - \eta)n(\eta, t)d\eta,$$

and where ψ and θ are gaussian with standard deviations σ_ψ and σ_θ respectively. Note that if N is independent of z then (6.16) reduces to (6.15).

We present no details of the analysis, but just report that calculations very similar to those used to analyze (6.1) show that the uniform steady state can become unstable if $S' < 0$, i.e., if switching is more likely at low population densities. Levin and Segel (1982) have presented further examples in which the simple switching assumptions of (5.1) are replaced by more elaborate assumptions of the type used in (6.17).

7. Patterns from long range-interactions in epidemiology and neurophysiology. In §6 we examined the consequences of assuming that certain ecological interactions take a distributed form. Interactions of this type have been postulated for some time in epidemiology. In 1965, for example, D. G. Kendall considered susceptible and infectious individuals whose densities S and I depend on a single spatial variable x and the time t . The infectivity rate for susceptibles centered at a particular point x was taken to be proportional to a weighted combination of the infectives in the neighborhood of x . Assuming removal (by death or recovery) at fractional rate ρ , one obtains the equations

$$(7.1) \quad \frac{\partial S(x, t)}{\partial t} = -kS(x, t) \int_{-\infty}^{\infty} I(x - y, t)\alpha(y)dy = -\frac{\partial I(x, t)}{\partial t} - \rho I(x, t),$$

where

$$k > 0, \quad \rho > 0, \quad \alpha(y) > 0, \quad \int_{-\infty}^{\infty} \alpha(y)dy = 1.$$

Aronson (1977) proved that under suitable conditions on α and the initial state, there is a unique asymptotic travelling wave solution to (7.1) if the initial density of susceptibles

is high enough and/or if the removal rate is low enough. In analogy with the case for the Fisher equation (4.6), the actual asymptotic speed of the spreading epidemic is the smallest of a continuum of speeds to which correspond a nondeforming travelling wave solution.

Neurophysiology provides another example in which distributed interactions are important. In brain tissue, it is reasonable to suppose that the influence of one neuron on another depends on a (synaptic) weighting function w multiplied by a probability that depends only on the distance between the neurons. Following this approach, Ermentrout and Cowan (1979) searched for patterned solutions in an interaction between populations of neurons governed by

$$(7.2a) \quad E(x, y, t) = S_e \left[\int_{-\infty}^t h_e(t-r) W_E(x, y, \tau) d\tau \right],$$

$$(7.2b) \quad I(x, y, t) = S_i \left[\int_{-\infty}^t h_i(t-\tau) W_I(x, y, \tau) d\tau \right].$$

Here $E(x, y, t)$ and $I(x, y, t)$ denote the firing rates of excitatory and inhibitory neurons at point (x, y) and time t . S_e and S_i are output functions for the two cell types, while h_e and h_i are temporal response functions incorporating such factors as delays, rise times, and decay rates. The functions W_E and W_I represent weighted distributed inputs:

$$\begin{aligned} W_E &= \alpha_{ee} W_{ee}(E) - \alpha_{ie} W_{ie}(I), \\ W_I &= \alpha_{ei} W_{ei}(E) - \alpha_{ii} W_{ii}(I). \end{aligned}$$

Here

$$W_{\xi\eta}[f(x, y, \tau)] = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} w_{\xi\eta}[(x-x')^2 + (y-y')^2] f(x', y', \tau) dx' dy',$$

where ξ and η can represent either e or i . The α 's are positive constants. Applying the ideas of Sattinger (1979) in a nonlinear stability analysis, Ermentrout and Cowan (1979) discussed the patterns that can emerge from (7.2). When the mapping between the visual field and the cortex is applied, these patterns are strongly reminiscent of visual hallucinations that are sometimes associated with migraine, drug effects, epilepsy, and other conditions.

Additional research in this general area of patterning in neurophysiology can be found in the conference proceedings edited by Amari and Arbib (1982) and by Basar et al. (1983).

8. Summary and discussion. We began our survey with a brief mention of efforts to understand the shifting colors produced by the Belousov–Zhabotinskii reaction. The attractiveness of this model system was apparent from the fact that it exemplifies such recurring themes of pattern formation as solitary and rotating waves, and spiral and target patterns. Examples from flame theory, reactions involving membrane-bound enzymes, metallurgy, and electrochemistry, were mentioned as illustrations of the extension of purely chemical models to biochemical and physical-chemical contexts.

In an examination of theories for the generation of pattern in developmental biology, we pointed out that there is a great deal of work still being done along the lines of Turing–Gierer–Meinhardt reaction-diffusion theory. In addition, there are generalizations and deviations of various kinds. Reaction is strongly simplified, or eliminated entirely, for example, in theories that rely on flux-dependent diffusion. Communication

by diffusion is supplemented by direct convection, or even replaced entirely by mechanical interaction.

Illustration was given of the fact that reaction-diffusion equations are but the simplest descriptions for population interaction and redistribution in ecology and cellular biology. Familiar structures such as traveling waves and aggregations appear in models that are enriched by effects of taxis and longer-range sensing or mechanical interaction.

We next considered in some detail a model that featured a nonlinear integro-differential equation. The integral terms arose because of the nonlocal nature of the mating between organisms of different aspects. We showed that it is surprisingly easy to perform a linear stability analysis of possible uniform solutions, both for the original model and also for several other examples of nonlocal interaction and redistribution operators. We pointed out that such operators can occur quite commonly in various ecological and evolutionary contexts. Indeed, in a paper that treats other examples of distributed equations, Rocklin and Oster (1976) correctly emphasized the importance of such models by stressing that "To regard a population as a collection of identical individuals is to overlook the central fact of evolutionary theory: natural selection acts on phenotypic variability amongst the individuals."

Integral operators were also shown to be of importance in epidemiology and neurophysiology. This demonstration constituted a last piece of evidence for one of our principal conclusions: the familiar equations of diffusion and reaction can easily be generalized to include the effects of nonlocal interaction—both by the inclusion of higher derivative terms and of integral terms. Many of the major structural features of the original solutions are retained, but with important modifications that reflect the increasing realism of the models.

We emphasized that "aspect" variables often can be used with profit to supplement spatial variables in describing the world around us. We mention such examples of aspect as hue, color, and spot size in butterflies, emergence times of insects, flowering times of plants, or chemical cues or "quality" in a plant. Other examples range from the age, size, or maturity of cells (see Rubinow's §6.6 in Segel (1980), and also Diekmann et al. (1983)), to the flavor of toothpaste (Keshet and Segel (1984)) and other more profound measures of economic and social advantage (Gierer (1981b)).

Spatial structures as made evident, for example, in the Taylor and Bénard fluid flow problems, have for decades been the objects of intensive study—both for their own sake and as prototypes for the emergence of spatial structure in other flows. Recently "dissipative structures" governed by reaction-diffusion equations and their generalizations have come into the limelight. It is often argued that the conditions for such structures are rather special, too restrictive to be of general interest. We have provided evidence to the contrary by showing that symmetry-breaking occurs in a wide range of systems that possess suitable combinations of activation and inhibition. In particular, we believe that such phenomena are of general importance in understanding the evolution and development of diversity in ecological systems.

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