

MATHEMATISCHES FORSCHUNGSINSTITUT OBERWOLFACH

Tagungsbericht 24 / 1978

Mathematische Modelle in der Biologie

4.6. bis 10.6.1978

In continuation of the Oberwolfach conference on 'mathematical models in biology' in June 1975 this meeting has been arranged by K.P. Hadeler (Tübingen), W. Jäger (Heidelberg) and S. Levin (Ithaca) to give the chance to mathematicians and biologists for discussion of actual models occurring in several fields of experimental and theoretical biology as population biology, epidemics, genetics, cell biology and neurophysiology.

The mathematical methods used in constructing and analysing those models were not restricted beforehand, so it was possible to consider related problems from different points of view.

The realized programm contained some survey lectures on the biological background itself, whereas the main part of talks presented more or less detailed deterministic and stochastic models including their analysis in correlation to biological observations and experimental data.

Some contributions emphasized certain theoretical difficulties either in modelling itself or in the mathematical treatment of certain well accepted models. Moreover some aspects in the statistical evaluation of biological data were considered.

Thus, although the programm (necessarily) favoured certain subjects and problems, the spectrum of presented themes was wide enough to lead to a successful conference, which could not be held without the nice and accomodating care of the institute and its staff.

Teilnehmer

W. Alt , Heidelberg	F. Rothe, Tübingen
D.G. Aronson, Minneapolis	L.A. Segel, Rehovot (Israel)
G. Becker, Göttingen	R. Sperb, Basel
H.J. Bremermann, Berkeley	P. Tautu, Heidelberg
J.M. Cushing, Tucson (Arizona)	A. Tesei, Rom
O. Diekmann, Amsterdam	H. Thieme, Münster
K. Dietz, Tübingen	A. Wörz-Busekros, Tübingen
Th. Eisele, Heidelberg	
G. Gerisch, Basel	
U. von Hehn, Tübingen	
U. an der Heiden, Tübingen	
R. Heinrich, Berlin (DDR) - verhindert	
I. Heuch, z.Zt. Tübingen	
P. Holgate, London	
D. Mandallaz, Basel	
H. Maurer, Münster	
H. Meinhardt, Tübingen	
J.A.J. Metz, Leiden	
M. Mimura, Kobe (Japan)	
H.G. Othmer, New Brunswick	
L.A. Peletier, Leiden	
T. Poggio, Tübingen	
E.T. Poulsen, Aarhus	
A. Reissland, Bielefeld	
J. Rinzel, Bethesda	
O.E. Rössler, Tübingen	

Vortragsauszüge

W. ALT: Derivation and Analysis of a Diffusion Model
for Chemotaxis

Biological individuals are considered, whose piecewise straight locomotion (with direction θ and speed c) shows a net displacement up to the gradient of a certain chemotactic factor. The related stochastic process has the following forward equation

$$\begin{aligned} (\partial_t + c\theta \nabla_x + \partial_\tau) \sigma &= -\beta \sigma && \text{if run length } \tau > 0, \\ \sigma(\cdot, \theta, 0) &= \int_0^\infty \int_S (\beta \cdot \sigma)(\cdot, \eta, \tau) k(\cdot, \eta, \tau, \theta) d\eta d\tau. \end{aligned}$$

According to some experimental data, rather general assumptions about the stopping frequency β and the turn-angle-distribution k are made for an approximative derivation of the well-known Keller-Segel-diffusion equation and some generalizations for small mean run length τ_0 .

The coefficients in these equations are expressed in terms of characteristic properties of individual locomotion, partly depending on some specific chemoreceptor-sensor-models: especially the chemotactic sensitivity (quotient of chemotaxis coefficient and motility) is

$$\frac{\chi}{\mu} = \kappa \left(\frac{K'}{K(1+K)} - \frac{\mu_0'}{\mu_0} \right) + \frac{\lambda}{\tau_0} \kappa (2-\kappa)$$

where the first term reflects the control of run lengths by some receptor kinetics K and a start-threshold μ_0 , while the second term describes a chemotactic effect due to protruded microvilli or lamellipodia (with turning tendency $\kappa \ll 2$) sensing the chemotactic gradient directly.

D.G. ARONSON: The Asymptotic Speed of Propagation of a
General Epidemic

In 1965 D.G. Kendall modified the classical Kermack-McKendrick epidemic model to take into account spatial spread. I show the existence of a propagation threshold and an asymptotic speed of propagation in Kendall's model. The asymptotic speed agrees with the minimal wave speed found recently by Atkinson and Reuter.

G. BECKER: Tests auf "Goodness of Fit" für eine spezielle
Familie von Zählprozessen

"Goodness of Fit"-Fragen für eine spezielle Klasse von Punktprozessen (von Odd O. Aalen stammend) werden mit Hilfe einer stochastischen Zeittransformation (Lamperti, Papangelou, Rudemo, Bremaud) auf Poissonprozesse zurückgespielt und Ergebnisse analog denen der Zuverlässigkeitstheorie erhalten (Barlow et al.).

In das Modell von Aalen passen Geburts- und Todesprozesse, Migrationsprozesse und andere.

Es soll gezeigt werden, wie sich Verfahren der Zuverlässigkeitstheorie auf Modelle der Biologie übertragen lassen.

Ferner wird auf das Problem der besten Wahl von Beobachtungszeitpunkten im diskreten Modell eingegangen.

H.J. BREMERMAN: Theorie sexueller Rekombinationen von Zellen mit Anwendungen auf das Krebsproblem

Artifiziiell erzeugte Zellfusionen sind heute eine Standardmethode der somatischen Genetik. Zellfusion tritt aber auch spontan auf, ist aber weniger erforscht. Spontane Zellfusion mit nachfolgender Teilung kann zu genetischen Rekombinationen führen, die sexuellen Rekombinationen bei Einzellern wie Bakterien und Protozoen entsprechen.

Es wird eine Theorie der spontanen Zellfusion entwickelt und mit Modellen der sexuellen Rekombination im Rahmen der mathematischen Genetik verglichen. Es ergeben sich dabei Vermutungen über die Rolle von Zellfusion beim Krebs sowie eine Kritik am Verständnis sexueller Rekombinationen im Rahmen konventioneller Modelle der mathematischen Genetik.

J.M. CUSHING: Oscillations in Age Dependent Population Growth Models

It is shown, by means of a Hopf-type bifurcation theorem for Volterra integral equations, that under certain conditions nonconstant periodic solutions bifurcate from equilibrium for a nonlinear, age dependent population growth model. The model attempts to take into account gestation and/or maturation delays as well as the subsequent delays in the birth rate response to population density changes.

O. DIEKMANN: The Epidemic Model of Kermack, McKendrick
and Kendall

This lecture is concerned with the qualitative analysis of a nonlinear integral equation of mixed Volterra-Fredholm type describing the spatio-temporal development of an epidemic. Particular attention will be paid to a threshold phenomenon and the hair-trigger effect, to travelling wave solutions and to the asymptotic speed of propagation of the epidemic.

TH. EISELE: A Stochastic Model for Chemotaxis and its
Convergence to a Diffusion Process

According to the experimental data of Berg and Brown for bacterial chemotaxis a stochastic model is constructed. It involves not only the distribution of the angles at the twiddle-state and the exponential distribution of the run-length with a parameter λ , but introduces a special quantity r which is supposed to describe the main receptor-phenomenon and which reflects especially the temporal change of the concentration c of the chemotactic factor. So $\lambda = \lambda(c, r)$ depends both on c and r .

By this model, some of the experimental curves measured by Koshland (et al.) with his temporal gradient apparatus can be obtained.

Finally, if one lets the mean run-length go to zero, the convergence of this stochastic model to a diffusion process is shown in such a way that the receptor-specific quantity r and its temporal development are preserved.

G. GERISCH: Cell Interactions based on a Biochemical Oscillator

Cells of a microorganism, Dictyostelium discoideum, aggregate into a multicellular assembly in response to a chemical factor, cyclic adenosine monophosphate (cAMP). This factor is periodically synthesized and released into the extracellular space in form of pulses. Since pulses act as triggers for the synthesis and release of cAMP, the activities of all cells in an aggregation territory are coupled to each other. The molecular basis of the oscillations will be discussed.

K.P. HADELER: Fragen zur Orientierung bei Insekten

Im Anschluß an Experimente und Modellvorstellungen von Reichardt, Poggio, Varju u.a. wird ein allgemeines dynamisches Modell für die Orientierung eines Insekts nach einer Marke aus biologischen Annahmen abgeleitet. Es ergibt sich ein Differentialgleichungssystem sechster Ordnung. Unter zusätzlichen Annahmen (z.B. konstante Geschwindigkeit, Körperachse parallel zur Geschwindigkeit) erhält man einfachere Modelle, die sich mathematisch behandeln lassen.

U. AN DER HEIDEN: The Goodwin Oscillator with Delays

The Goodwin oscillator is a mathematical model for a sequence of biochemical reactions controlling the production of metabolites in a living cell by a nonlinear feedback mechanism. The times needed for transcription, translation and transport of macromolecules naturally appear in the model as delays. The resulting system of differential-difference equations

$$\dot{x}_1(t) = f(x_n(t-\tau_n)) - b_1 x_1(t),$$

$$\dot{x}_i(t) = a_{i-1} x_{i-1}(t-\tau_{i-1}) - b_i x_i(t), \quad i = 2, \dots, n,$$

is shown to exhibit three types of behaviour: unstable steady states, periodic oscillations, and irregular changes of the dependent variables. The "non-ejective fixed point theorem" of Browder is used to prove the existence of periodic solutions.

I. HEUCH: The Effect of Partial Self-Fertilization on Equilibrium Frequencies in Tristylous Plants

In tristylous species each plant may be classified as Long, Mid or Short according to the length of the style. If fertilization is only allowed between plants belonging to distinct types, then the three types must be equally frequent in an infinite population at equilibrium. But in Lythrum salicaria it appears that Long is more frequent in nature than Mid, and Mid is more common than Short. It is known that a small amount of self-fertilization is possible.

A mathematical model is set up in order to see if different degrees of self-fertilization in the three types can account for the observed deviations. It turns out that the amount of self-fertilization required is so large as to make it rather improbable that this is the real cause of the observed differences.

P. HOLGATE: Information Theory in Population Genetics

The entropy $H = -\sum x_i \log x_i$ of a subdivided biological community is a popular measure of its diversity. There is however no general theory of the way in which entropy responds to population regulating factors. I study here the changes in entropy in certain population genetic models that have been discussed by geneticists.

If we consider the entropy of the gametic frequencies in an infinite random mating population classified at two linked loci, it can be shown that it increases in time, remaining constant when the population is in equilibrium. The same is true for the gametes of a tetraploid population, at one locus. For several loci the result holds only in special cases.

In a finite population, fluctuation in gene frequency caused by stochastic effects can lead to steady loss of entropy. For the Sewall Wright model, using the diffusion approximation for a large population, the rate of decrease of expected entropy is $\frac{1}{2}(k-1)$ where k is the number of alleles. By use of an approximate formula, an allele that is absorbed can be said to 'take with it' a specified amount of entropy.

S.A. LEVIN: Adaptive Strategies in Heterogeneous
Environments

A summary of approaches to spatial heterogeneity in ecological systems is provided with emphasis upon mathematical models, pattern formation, planktonic systems, and dispersal strategies.

The problems, organisms face in adapting the fluctuating environments, are considerable and are met by averaging mechanisms on space (dispersal) or over time (perennial halst, dormancy, or diapause). Further, consideration of evolutionary strategies cannot begin blindly from optimization arguments, since it is the definition of the optimization or game theoretic problem which is the major challenge.

This problem is discussed for a number of situations, using a variation of the notion of the "evolutionary stable strategy". This leads to eigenfunction problems associated with the partial differential integral equation

$$\frac{\partial n}{\partial t} + \frac{\partial n}{\partial a} = \int_0^{\infty} \phi(a, \alpha) n(\alpha, t) d\alpha ,$$

where $n(0, t) = 0$ and $n(a, 0) = n_0(a)$,

and a related set of control problems for dispersal strategies. The solutions involve bang-bang control.

D. MANDALLAZ: Vergleich von Absterbekurven

Ein Vergleich der Absterbekurven von verschiedenen Behandlungsgruppen ist bei Tierversuchen ein schwieriges Unterfangen, da einerseits die Häufigkeit der Bindungen groß ist und andererseits die Stichproben klein sind.

Ein verteilungsfreies Verfahren von D.R. Cox wurde auf seine Gültigkeit und auf seine praktische Anwendbarkeit hin untersucht. Mit Simulationen können Schätzungen der Absterbekurven und eine Approximation der Wirksamkeit angegeben werden. Beispiele aus der biologischen Forschung illustrieren die praktische Anwendung des Verfahrens.

H. MEINHARDT: Modelle zur Strukturbildung während der Entwicklung höherer Organismen

There are indications that not every structure is determined independently, but that sets of structures (for instance, the fingers or the segments of insects) are formed under a common control. A model is proposed for space-dependent cell determination under the influence of a morphogen gradient. It provides an explanation of how groups of cells can be programmed in a particular direction and how a jump from one determination stage to the next can occur between them even though the controlling signal is of a smoothly graded morphogen concentration. Together with an earlier proposed mechanism for pattern formation, these models offer a complete system for the generation and interpretation of positional information. Experimental and theoretical results will be compared.

J.R.J. METZ: Modelling Animal Behaviour by Finite
Markov Systems

Markov chains sometimes turn out to be good descriptions of behaviour sequences of animals. The trick is the suitable dissection of the behaviour, that is to consider the appropriate time periods and to choose the right units of activity. Some heuristic methods for this purpose are described, together with some tests for Markovity. If one has arrived at a Markov chain framework all sorts of hypotheses about the structure of the behaviour can be rigorously tested within this framework. Moreover, one can estimate the transition rates, even from relatively short observation periods, as easily interpretable parameters which may be used for comparison between animals or treatments. These ideas are illustrated with examples from an ongoing research program on macaque mother infant interaction, sexual behaviour in roles and courtship in two species of fish.

Behaviour can be Markovian at different levels of resolution, e.g. if activities can be grouped into macro-activities which are such that the transitions within groups are fast compared to transitions between groups. This may also explain how a small number of Markovian activities can be compatible with the terrible complexity on a neuronal level.

M. MIMURA: On Some Reaction-Diffusion Equations with Slightly Heterogeneous Environments

We consider the following system

$$\begin{cases} 0 = d_1 u_{xx} + f(u,v) + \epsilon \tilde{f}(u,v,x) \\ 0 = d_2 v_{xx} + g(u,v) + \epsilon \tilde{g}(u,v,x) \end{cases} \text{ in } I = (0, \ell), \quad 0 < \epsilon \ll 1,$$

subject to

$$u_x(0) = u_x(\ell) = v_x(0) = v_x(\ell) = 0$$

We make several assumptions

- (1) $\exists (\bar{u}, \bar{v})$ satisfying $f(\bar{u}, \bar{v}) = 0 = g(\bar{u}, \bar{v})$
- (2) \exists invariant set $(\mathfrak{D}(\bar{u}, \bar{v}))$ in \mathbb{R}_2
- (3) (f, g) satisfy Turing's diffusion driven instability at $u = \bar{u}$ and $v = \bar{v}$
- (4) $\tilde{f}(\bar{u}, \bar{v}, x) \equiv 0$ and/or $\tilde{g}(\bar{u}, \bar{v}, x) \equiv 0$.

Under the above conditions we prove the existence of solutions $(u(x), v(x))$ for any $(d_1, d_2) \in \mathbb{R}_2^+$. Moreover, under the condition (3) we get to know spatial patterns of the solutions. A typical example is Gierer-Meinhardt model occurring in biology.

H.G. OTHMER: Pattern Formation in Reaction-Diffusion Equations

Numerous examples are known of reacting systems that show various kinds of spatio-temporal patterns. We report some results on how the structure of a general reaction network is reflected in the dynamics, both in spatially-uniform and nonuniform systems. Necessary and sufficient conditions for the absence of stationary instabilities with arbitrary diffusion rates are given. A class of stable kinetic mechanisms that can lead to oscillatory instabilities in the presence of diffusion is analyzed.



L.A. PELETIER: Clines

In Fisher's model for the propagation of genetic material, one is led to the study of the nonlinear diffusion equation

$$u_t = u_{xx} + \lambda f(x,u) \quad x \in \Omega, t > 0. \quad (*)$$

In this equation the diffusion term reflects migration, and the nonlinear source term selection. Equation (*) is used to explain the occurrence of stationary gradients in the genetic composition of the population. Such gradients are sometimes called clines. In this talk we shall discuss the existence and stability of clines for different types of functions f .

T. POGGIO: A New Approach to Synaptic Interactions

(This work was done with V. Torre)

In passive dendritic structures the change in membrane potential at any point is a linear functional of current inputs at arbitrary locations, i.e. $\Delta V_i = \sum_j K_{ij} * I_j$, where K_{ij} are the Green functions associated with the parabolic cable equation and can always be found for arbitrary dendritic structures. At the synapses, however, $I_j = g_j (E_j - V_j)$ where g_j are conductance changes to specific ions (with an equilibrium potential E_j) and represent the real "inputs". As a consequence V_i is a nonlinear functional of the inputs g_j . It is proved that (i) \underline{V} is an analytic functional of \underline{g} (for all bounded $\underline{g} \in C([0, T]^n)$) and (ii) \underline{V} is given explicitly by a Volterra-like series in the inputs \underline{g} (for 1 input $V = h_0 + h_1 * g + h_2 ** g + \dots$)

where all kernels are obtained in a simple way from the Green function associated with the linear cable equation. All terms of the representation can be written in terms of elementary graphs. Interactions between synaptic signals in arbitrary dendritic structures can be studied in this framework. It is conjectured that nervous systems may selectively exploit these nonlinear interactions for performing simple, nontrivial computations.

E.T. POULSEN: A Population Model with Selection and Population Regulation

We study properties of the following model: Consider three genotypes $(G_1, G_2, G_3) = (AA, AB, BB)$, assume distinct generations and consider a panmictic population. The genotypes are assumed to have different fertilities b_1, b_2, b_3 , and the zygotes are assumed to have different viabilities p_1, p_2, p_3 . Furthermore, during the growing-up phase, the genotype-numbers u_1, u_2, u_3 are assumed to decrease according to the differential equations

$$\dot{u}_i = -(d_i + \sum_j c_{ij} u_j) u_i .$$

In the absence of variation this model produces discrete logistic growth. With genetic variation it gives models with either "soft" or "hard" selection as well as intermediate cases (depending upon the choice of the dynamic parameters).

We have found examples with 3 polymorphic equilibria and models with a stable limit cycle surrounding an unstable equilibrium (a "lemming cycle").

J. RINZEL: On Repetitive Activity in Nerve

A typical experimental stimulus-response curve for a single nerve fiber illustrates steady temporal frequency ω versus steady current strength I and often exhibits two threshold values of I below and above which the nerve does not fire repetitively. The experimental picture will be compared with bifurcation diagrams, ω and solution amplitude versus I , for periodic solutions to the Hodgkin-Huxley and FitzHugh-Nagumo equations. Results for both the case of a uniform stimulus (space-clamped nerve) and of a point source will be described, their qualitative differences contrasted, and experimental implications outlined. Critical values of I correspond to Hopf bifurcation of spatially uniform and non-uniform time periodic solutions respectively; examples of both sub- and super-critical bifurcation are found. For the point source case with adequate I , the numerical solution, far from the point source, is a periodic spike train with ω dependent on I . These wave trains belong to the family of periodic traveling wave solutions which we have determined, along with their dispersion relation, independently as particular solutions to the nonlinear parabolic partial differential equations.

O.E. RÖSSLER: Simple 3-Variable Chaos

In continuous systems, "chaos" is defined by the presence, in a cross-section through trajectorial flow in state space, of an invariant set of measure zero which is locally a product of Cantor set and a one-dimensional arc. A folded-over (walking-stick shaped) cross-section is the simplest possibility to obtain an attracting such set. Several simple "double looped" autonomous 3-variable systems possess a chaotic attractor. However, certain single-looped control systems (with a smooth, non-monotone feedback term) are also appropriate. A third class is 3-variable mass action systems; for example, a combination of a Lotka-Volterra oscillator and a Gause switch. A fourth class is those autonomous 3-variable systems which are equivalent to a periodically forced 2-variable system. Several cases can here be distinguished, for example: chaos in a periodically forced EVP monoflop.

F. ROTHE: Global Existence Results for a Simple Model of Pattern Formation

For the concentrations u and v of two chemical substances, a simple reaction-diffusion system $u_t = \mu \Delta u + f(u) - v$, $\epsilon v_t = \Delta v + u - v$ resembling to FitzHugh-Nagumo model is considered in a bounded domain Ω . For $\mu \ll 1$, the stationary homogeneous state is unstable if $\lambda = f'(0)$ is appropriate chosen between λ_1 and 1 , but stable for the pure reaction system. This leads to formation of inhomogeneous spatial patterns. They are stationary points of the functional

$$\mathcal{L}(u) = \int_{\Omega} \left(\frac{1}{2} \mu |\nabla u|^2 + \frac{1}{2} u(1-\Delta)^{-1} u - F(u) \right) dx \text{ on the space } \Pi^1(\Omega)$$

(where $F(u) = \int_0^u f(u') du'$) . Hence existence can be proved by minimaxing this functional over sets with fixed topological genus.

L.A. SEGEL: On Some Biological Applications of Perturbation Theory

The concept of scaling and some applications of regular and singular perturbation theory in biology will be surveyed. The survey will include an up-to-date status report on standing gradient (osmotically driven) flow plus a usual and slightly unusual use of the pseudo steady-state hypothesis in biochemistry.

R. SPERB: Über ein mathematisches Modell zur Beschreibung der Aggregation von Amöben

Das Modell, das hier vorgestellt wird, ist eine Erweiterung eines Modells von Keller & Segel (J. Theor. Biol. 26). Der Start der Aggregation wird hierbei erklärt als Instabilität der stationären Lösung eines zugehörigen parabolischen Systems. Im Gegensatz zu Keller und Segel hängt in unserem Falle die Instabilität aber nur von der Kinetik eines zugehörigen Produktionsprozesses ab, und nicht von der Gestalt des Grundgebietes oder von Diffusionskonstanten. Im weiteren erklärt das Modell das von Gerisch und anderen beobachtete oszillatorische Verhalten der Cyclic AMP Konzentration.

A. TESEI: On a System of Reaction - Diffusion Equations

We study the asymptotical behaviour as $t \rightarrow \infty$ of positive solutions of the following system:

$$(\S) \left\{ \begin{array}{l} \partial_t u = \Delta u + \lambda u - uv \\ \partial_t v = u - pv \\ u = 0 \\ u = u_0, v = v_0 \end{array} \right. \begin{array}{l} \text{in } \Omega \times (0, \infty) \\ \text{on } \partial\Omega \times (0, \infty) \\ \text{in } \Omega \times \{0\} \end{array}$$

where $\Omega \subset \mathbb{R}^3$ is open bounded, $\lambda \in \mathbb{R}$, $p > 0$; u_0, v_0 are given nonnegative functions. It is shown that for $\lambda > \lambda_0$, $p > 0$ (λ_0 denoting the principal eigenvalue of the Laplacian with homogeneous Dirichlet boundary conditions) a unique strictly positive equilibrium solution of (§) exists, which is asymptotically stable in the space $L^2(\Omega) \oplus C^0(\bar{\Omega})$. Attractivity and stability results are also proved in the case $p = 0$ by monotone methods.

H. THIEME: Density-Dependent Regulation of Spatially Distributed Populations and their Asymptotic Speed of Propagation

Let the development of a spatially distributed population be described by the nonlinear integral equation

$$u(t, x) = u_0(t, x) + \int_0^t \int_{\mathbb{R}^N} g(u(t-s, x+y)) \cdot k(s, |y|) ds dy .$$

u denotes the density of the reproductive individuals, k describes their migration, $g(u)$ gives the number of offspring which has been produced by u individuals and

has survived still the reproductive stage. Let g be a reproduction curve, i.e. $g(u) = 0$, $g(u) > 0$ for $u > 0$, $\frac{g(u)}{u}$ strictly decreases on $[0, \infty)$, g Lipschitz continuous.

Let $u_0(t, x) \rightarrow 0$ for $t \rightarrow \infty$ uniformly on \mathbb{R}^N ,

$$k^* := \int_0^\infty \int_{\mathbb{R}^N} k(s, |y|) ds dy < \infty.$$

Theorem a) If $k^* \cdot g'(0) < 1$, then $u(t, x) \rightarrow 0$ for $t \rightarrow \infty$ uniformly on \mathbb{R}^N .

b) If $k^* \cdot g'(0) > 1$, then there is some $c^* > 0$ with the following properties:

(i) If $c > c^*$, then $u(t, x) \rightarrow 0$ for $t \rightarrow \infty$, $|x| \geq ct$.

(ii) If $0 < c < c^*$, then $\liminf_{t \rightarrow \infty} u(t, x) > 0$, $|x| < ct$.

If $u \cdot g(u)$ strictly increases on $[0, \infty)$, then

$u(t, x) \rightarrow U$ for $t \rightarrow \infty$, $|x| \leq ct$, where U is the positive real number with $k^* \cdot g(U) = U$. If $g(u) = ue^{-u^\alpha}$, $\alpha > 0$, then, for $1 < k^* \leq e^{2/\alpha}$, $u(t, x) \rightarrow \sqrt[\alpha]{\ln k^*}$ for $t \rightarrow \infty$, $|x| \leq ct$.

A. WÖRZ-EUSEKROS: Global Stability in Ecological Models with Delay

A population of p interacting species which is spatial homogeneous is considered. It is assumed that the densities x_i satisfy a system of integro-differential equations of the following type

$$\dot{x}_i(t) = x_i(t) \left(\beta_i + \sum_{j=1}^p \alpha_{ij} x_j(t) + \sum_{j=1}^p \gamma_{ij} \int_{-\infty}^t F_{ij}(t-\tau) x_j(\tau) d\tau \right), i=1, \dots, p.$$

where the integral kernels F_{ij} are nonnegative, continuous \mathcal{L}^1 -functions normalized by $\int_{-\infty}^0 F_{ij}(\tau) d\tau = 1$, $i, j = 1, \dots, p$.

In the case that the integral kernels satisfy linear differential

equations with constant coefficients a sufficient condition for the global stability in \mathbb{R}_+^D of a positive equilibrium state is derived. The result is applied to a predator prey system where the numerical response of the predators contains a continuous time delay.

W. Alt (Heidelberg)

A. Wörz-Busekros (Tübingen)

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