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Monotone Dynamical Systems

An Introduction to the Theory
of Competitive and Cooperative
Systems

Hal L. Smith



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The author was supported in part by NSF grant #DMS 9141550.

2000 *Mathematics Subject Classification*. Primary 34C11, 34C15, 34C25, 34-XX, 34K20, 35B40, 35B50, 35K55; Secondary 44-XX, 53-XX, 58-XX.

Library of Congress Cataloging-in-Publication Data

Smith, Hal L.

Monotone dynamical systems: an introduction to the theory of competitive and cooperative systems / Hal L. Smith.

p. cm. — (Mathematical surveys and monographs, ISSN 0076-5376; v. 41)

Includes bibliographical references and index.

ISBN 0-8218-0393-X

1. Differentiable dynamical systems. 2. Monotonic functions. I. Title. II. Series: Mathematical surveys and monographs; no. 41.

QA614.8.S63 1995
515'.352—dc20

94-48032
CIP

AMS softcover ISBN 978-0-8218-4487-8

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10 9 8 7 6 5 4 3 2 1 13 12 11 10 09 08

Contents

Preface	vii
Chapter 1. Monotone Dynamical Systems	1
0. Introduction	1
1. Definitions and Preliminary Results	1
2. The Convergence Criterion	3
3. The Limit Set Dichotomy	5
4. Quasiconvergence is Generic	8
5. Remarks and Discussion	13
Chapter 2. Stability and Convergence	15
0. Introduction	15
1. Stability	15
2. The Order Interval Trichotomy	16
3. Some Global Results	18
4. Generic Convergence to Equilibrium	19
5. Unstable Equilibria and Connecting Orbits	24
6. Remarks and Discussion	28
Chapter 3. Competitive and Cooperative Differential Equations	31
0. Introduction	31
1. The Kamke Condition	32
2. Positively Invariant Sets and Monotone Solutions	34
3. Main Results	37
4. Three Dimensional Systems	40
5. Alternative Cones	48
6. The Field-Noyes Model	50
7. Remarks and Discussion	51
Chapter 4. Irreducible Cooperative Systems	55
0. Introduction	55
1. Strong Monotonicity	56
2. A Biochemical Control Circuit	58
3. Stability and the Perron-Frobenius Theorem	60
4. Competition and Migration	64
5. Smale's Construction	71
6. Remarks and Discussion	72

Chapter 5. Cooperative Systems of Delay Differential Equations	75
0. Introduction	75
1. The Quasimonotone condition	78
2. Positively Invariant Sets, Monotone Solutions, and Contracting Rectangles	81
3. Eventual Strong Monotonicity	85
4. Generic Convergence for Cooperative and Irreducible Systems	89
5. Stability of Equilibria	91
6. A Biochemical Control Circuit with Delays	93
7. Competition with Time Delays	94
8. Remarks and Discussion	98
Chapter 6. Nonquasimonotone Delay Differential Equations	101
0. Introduction	101
1. The Exponential Ordering	101
2. The Strong Order Preserving Property	107
3. Generic Convergence to Equilibrium	109
4. Stability of Equilibria	110
5. A Model of an Adult Fly Population	112
6. Remarks and Discussion	116
Chapter 7. Quasimonotone Systems of Parabolic Equations	119
0. Introduction	119
1. Parabolic Systems: The Basic Setup	120
2. Maximum Principles	123
3. Positively Invariant Sets, Comparison and Monotonicity	127
4. The Strong Order Preserving Property	132
5. Generic Convergence for Cooperative and Irreducible Systems	134
6. Stability of Equilibria	136
7. The Biochemical Control Circuit with Diffusion	139
8. Remarks and Discussion	141
Chapter 8. A Competition Model	145
0. Introduction	145
1. The Model	145
2. A Single Population	151
3. Stability of the Equilibria E_0, E_1, E_2	154
4. Coexistence	158
5. Remarks and Discussion	161
Appendix. Chain Recurrence	163
Bibliography	167
Index	173

Preface

There is a long history of the application of monotone methods and comparison arguments in differential equations. The early works of Müller(1926) and Kamke(1932) laid the foundation at least for ordinary differential equations. The work of Krasnoselskii(1964,1968) has been especially influential. However, not until the work of M.W.Hirsch were monotonicity methods fully integrated with dynamical systems ideas. In a remarkable series of papers entitled "Systems of differential equations that are competitive or cooperative", parts I through VI, Hirsch develops what is now often referred to as monotone dynamical systems theory. There, he shows that the generic solution of a cooperative and irreducible system of ordinary differential equations converges to the set of equilibria. Furthermore, the flow on a compact limit set of an n -dimensional cooperative or competitive system of differential equations is shown to be topologically conjugate to the flow of an $n - 1$ -dimensional system of differential equations, restricted to a compact invariant set. The Poincaré-Bendixson Theorem is established for three dimensional competitive or cooperative systems. The theory of infinite dimensional systems that preserve a partial order relation is developed in the important work Hirsch(1988b). Here one finds for instance that the generic orbit of such a system is stable and converges to the set of equilibria. Applications are made to reaction-diffusion systems.

The infinite dimensional theory of monotone systems has been heavily influenced by the work of H.Matano. The beginnings of the theory appear in Matano (1979) which focuses on semilinear diffusion equations. Matano(1984) introduces the important idea of a strongly order preserving semiflow. This condition is more flexible than strong monotonicity, used by Hirsch, because it does not require the order cone to have nonempty interior. The main result of this paper establishes the existence of monotone heteroclinic orbits and has motivated considerable research in this direction. Matano(1986) and (1987) contain outlines, without proof, of extensions of results of Hirsch using the strong order preserving property in place of strong monotonicity.

The work of Smith and Thieme(1990,1991) represents a synthesis of the approaches of Hirsch and Matano that attempts to simplify and streamline the arguments. Significant improvements in the theory are obtained with additional compactness hypotheses that are usually satisfied in the applications.

There presently exists no current account of the important results in the theory of continuous-time monotone dynamical systems and particularly, of competitive and cooperative systems of differential equations. The earlier survey Smith(1988) is now somewhat dated and, in any case, treats primarily cooperative systems. In view of the many existing and potential applications of this theory, there seems

to be a need for some overview of the topic. The present monograph is intended to serve that purpose. However, it is not intended as a comprehensive survey of the literature on monotone dynamical systems. In particular, the references do not include all the important work in this area. Nor has any attempt been made to present the most general results possible. In fact, many of the results presented here are special cases of more general ones that appear in the literature. Generality is readily sacrificed for simplicity and clarity of presentation. As the title suggests, this work is an introduction to the subject of monotone dynamics and competitive and cooperative systems. The selection of material presented here reflects a personal bias in favor of those results which are useful in applications. Some results appear here for the first time and new and simpler proofs have been found in a number of cases.

This monograph is an expanded version of a series of talks given by the author at National Tsing Hua University, Taiwan, at the invitation of Professor S.B.Hsu, during August, 1993, and supported by the National Council of Science, Republic of China. The author would like to especially thank Professor Hsu for the invitation to visit Taiwan and for his careful attention to these talks.

Many of the results presented in this monograph represent joint work with Horst R. Thieme. The author has benefited greatly from this collaboration over the years and this work would not have been possible without it. The author would also like to acknowledge the influence of his teacher and collaborator, Paul Waltman, on this work. Some of the most beautiful applications of the theory of monotone systems appear in the papers of Waltman and various collaborators. Courage to take on this project was derived from the recent collaboration of the author with Paul Waltman on a monograph titled "The Theory of the Chemostat". Finally, the author's collaborations with Robert H. Martin have greatly influenced the presentation of Chapter 7 on application of the theory to parabolic partial differential equations.

This monograph does not treat discrete dynamical systems generated by monotone mappings, an area which has flourished in recent years. Although Hirsch's work includes some results in this area, a different set of players are responsible for the major results. The book of Hess(1991) is an excellent reference for this work, as are the papers of N.Dancer and P.Hess and of P.Takac. As the reader might guess this theory is more difficult (there is no Limit Set Dichotomy) and, it seems, monotonicity does not restrict the dynamics of maps as severely as it does for flows.

In order to present the results in a clear way, we have tried to avoid references to the literature in the main body of each chapter. A separate section titled "Remarks and Discussion" is aimed at providing the reader with references to the literature, citations for the main results, a discussion of related results, and extensions and applications of the theory. This is where the reader will find references to more general results. A brief description of the contents of each chapter follows.

Chapter 1 develops the main tools of monotone dynamical systems theory in ordered metric spaces. These include the Convergence Criteria, the Limit Set Dichotomy and the Sequential Limit Set Trichotomy. The main result of the chapter is that, under suitable hypotheses, a generic orbit of a monotone semiflow converges to the set of equilibria.

Chapter 2 begins with results on stability and the classical order interval trichotomy. Results on global convergence and sufficient conditions for all orbits to

approach the set of equilibria are formulated. The main result of this chapter establishes sufficient conditions for the generic orbit of a monotone semiflow to converge to a single equilibrium. Here, the Krein-Rutman theorem is a principal tool. Sub-equilibrium and super-equilibrium are introduced in the final section and sufficient conditions are given for the existence of a monotone heteroclinic orbit.

Chapter 3 is essentially independent of the first two chapters, requiring only the convergence criterion (theorem 1.2) from Chapter 1. The reader who is primarily interested in ordinary differential equations can begin here. The focus is on competitive and cooperative systems of ordinary differential equations which are not necessarily irreducible. The Kamke condition is shown to imply monotonicity of the forward flow. The centerpiece of this chapter is the result that the flow on a compact limit set of an n -dimensional competitive or cooperative system is topologically equivalent to the flow of a Lipschitz $n - 1$ -dimensional system restricted to a compact invariant set. This then leads to the result that all solutions of planar competitive and cooperative systems converge to equilibrium and to the Poincaré-Bendixson theorem for three dimensional systems. An application is made to the Field-Noyes model of the Belousov Zhabotinskii reaction.

In Chapter 4, the irreducibility hypothesis is exploited for competitive and cooperative systems. It is shown to imply that the forward flow of a cooperative and irreducible system is strongly monotone. The generic convergence result of Chapter 2 is translated into the language of cooperative irreducible systems of ordinary differential equations. It is applied to two examples, a protein synthesis model in physiology and a model of two populations competing in an environment consisting of two habitats between which each population can migrate. The Perron-Frobenius theorem and its implications for the stability of steady states and periodic solutions is discussed. The important construction of Smale showing that any dynamics can be realized within the class of competitive and cooperative systems of sufficiently large dimension is described in detail.

The results of Chapter 1 and 2 are applied to quasimonotone delay differential equations in Chapter 5. The class of cooperative and irreducible delay systems is identified and the generic orbit of such a system is shown to converge to equilibrium. To each such system one can associate a cooperative and irreducible system of ordinary differential equations which has essentially the same dynamics as the system of functional differential equations. An application is given to the protein synthesis model with delays. We also show in this chapter that if a delay differential equation, which is not necessarily quasimonotone, possesses a positively invariant rectangle then one can associate to it two comparison systems of quasimonotone delay differential equations whose solutions can be compared to the original system. Therefore, quasimonotone systems arise naturally from systems of delay equations which are not quasimonotone but have a positively invariant rectangle.

In Chapter 6 the so-called exponential ordering on the space of continuous functions is introduced and shown to allow a weakening of the rather restrictive quasimonotone condition of chapter 5 for delay differential equations. The treatment follows Smith and Thieme(1991). A surprising outcome of the results of this chapter is that delay differential equations with delays which are small compared to the Lipschitz constant always generate monotone semiflows in the exponential ordering. As a result, convergence to equilibrium is generic. Application is made to a model of a fly population.

The focus of Chapter 7 is on systems of reaction diffusion equations satisfying the quasimonotone condition. It is shown that such systems define a semiflow on a subspace of the space of continuous functions on a bounded domain. A section is devoted to maximum principles, the main tool in the analysis of these systems. Monotonicity, the existence of positively invariant sets and comparison results are developed. The main result provides sufficient conditions for the generic solution to converge to equilibrium. The stability of equilibria is examined using the Krein-Rutman Theorem and an application is given to the biochemical control circuit.

The results of Chapter 7 are applied to a model of microbial competition in the chemostat with convection and diffusion in the final Chapter 8.

Some remarks on format are necessary. As the table of contents suggests, each chapter is divided into numbered sections. Results, whether they be theorems, propositions, or lemmas, are numbered consecutively within each section. For example, the third result of section 2 of Chapter 5 is labeled theorem 2.3 (or proposition 2.3 or lemma 2.3) within the text of Chapter 5. When referring to that same result in another chapter, we write theorem 5.2.3. New terms are italicized the first time they appear in the text.

The reader who is primarily interested in the applications to ordinary differential equations may read the first two sections of Chapter 1 for the basic definitions and notation and skim the main results of Chapters 1 (theorem 1.4.3) and Chapter 2 (theorem 2.4.7) before proceeding to Chapters 3 and 4.

Several colleagues read various portions of the manuscript for this monograph and provided valuable suggestions and comments. The author wishes to express his sincere thanks for their effort: C. Cosner, R.H. Martin, J.Wu, W.E. Fitzgibbon.

Finally, the author wishes to thank Linda Arneson for producing a beautiful type-set manuscript to AMS standards and Bruce Long for rendering most of the figures in the text.

Appendix. Chain Recurrence

In this appendix it is proved that a compact limit set of a flow ψ_t on a metric space X is chain recurrent. The result was originally proved by Conley (see Conley(1972) and Conley(1978)). The proof below, taken from Mischaikow et al (1994), follows one given in Robinson(1977) for mappings. As this result is needed in section 3 of Chapter 3, we use the notation from that section. We begin by recalling the definition of chain recurrence from section 3 of Chapter 3.

Let A be a nonempty invariant subset of X and $x, y \in A$. For $\epsilon > 0$, $t > 0$, an (ϵ, t) -chain from x to y in A is a sequence $\{x = x_1, x_2, \dots, x_{n+1} = y; t_1, t_2, \dots, t_n\}$ of points $x_i \in A$ and times $t_i \geq t$ such that $d(\psi_{t_i}(x_i), x_{i+1}) < \epsilon$, $i = 1, 2, \dots, n$. A point $x \in A$ is called a *chain-recurrent point* if for every $\epsilon > 0$, $t > 0$ there is an (ϵ, t) -chain from x to x in A . The set A is said to be chain recurrent if every point in A is chain-recurrent in A .

The main result of this appendix follows.

THEOREM 1. *Let L be an (omega or alpha) limit set of a (positive or negative) orbit of the flow ψ that has compact closure in X . Then L is chain recurrent.*

Our proof uses the following intuitive result.

LEMMA. *Assume that $\gamma^+(x)$ has compact closure in X and let $T > 0$ and $\gamma_T^+(x) = \{\psi_t(x) : t \geq T\}$. Given $y \in \omega(x)$ and $\epsilon > 0$, $t_0 > 0$, there exists an (ϵ, t_0) -chain*

$$\{y = y_1, y_2, \dots, y_l, y_{l+1} = y; t_1, t_2, \dots, t_l\}$$

such that $y_i \in \gamma_T^+(x)$ for $i = 2, \dots, l$, $t_i = t_0$, $1 \leq i \leq l - 1$, $t_0 \leq t_l < 2t_0$.

PROOF. Suppose that $y = \lim_{n \rightarrow \infty} \psi_{s_n}(x)$ where $s_n \rightarrow \infty$, $n \rightarrow \infty$. Choose n such that $s_n > T$ and $d(\psi_{s_n+t}(x), \psi_t(y)) < \epsilon$ for $0 \leq t \leq t_0$. Set $y_1 = y$ and $y_2 = \psi_{s_n+t_0}(x)$ and $t_1 = t_0$. Then

$$d(\psi_{t_1}(y_1), y_2) = d(\psi_{t_0}(y), \psi_{s_n+t_0}(x)) < \epsilon.$$

Choose m such that $s_m > s_n + 2t_0$ and $d(\psi_{s_m}(x), y) < \epsilon$. Let $k \geq 1$ be such that $s_m - s_n - t_0 = kt_0 + r$ for some r , $0 \leq r < t_0$. Let $y_3 = \psi_{s_n+2t_0}(x)$, $y_4 = \psi_{s_n+3t_0}(x)$, \dots , $y_{k+1} = \psi_{s_n+kt_0}(x)$, $y_{k+2} = y$, and $t_i = t_0$, $1 \leq i \leq k$, $t_{k+1} = t_0 + r$. Then $d(\psi_{t_i}(y_i), y_{i+1}) = 0$, $i = 2, \dots, k$ and $d(\psi_{t_{k+1}}(y_{k+1}), y_{k+2}) = d(\psi_{s_m}(x), y) < \epsilon$. □

PROOF OF THEOREM 1. We begin by treating the case that $L = \omega(x)$ where $\gamma^+(x)$ has compact closure in X . The other case can be reduced to this one by time reversal, as will be shown in the last paragraph of the proof.

Let $y \in \omega(x)$ and $\epsilon > 0$, $t_0 > 0$. By the Lemma, for each $n = 1, 2, \dots$, there exists a $(\frac{1}{n}, t_0)$ -chain belonging to $\gamma_n^+(x)$ having the properties described in the Lemma with $T = n$. Let y_i^n , $1 \leq i \leq l_n + 1$, be the points of the $(\frac{1}{n}, t_0)$ -chain, t_i^n be the times, $1 \leq i \leq l_n$, ($t_i^n = t_0$, $1 \leq i \leq l_n - 1$, $t_0 \leq t_{l_n}^n < 2t_0$) and set $C^n = \{y_i^n : 1 \leq i \leq l_n\}$.

Since $C^n \subset \overline{\gamma^+(x)}$ and $\overline{\gamma^+(x)}$ is compact in X , by passing to a subsequence, if necessary, we can assume that $C^n \rightarrow C$ as $n \rightarrow \infty$ in the Hausdorff metric on the space of closed subsets of $\overline{\gamma^+(x)}$, where C is a nonempty compact subset of $\overline{\gamma^+(x)}$. In fact, as $y \in C^n \subset \overline{\gamma_n^+(x)}$ it follows that $y \in C \subset \omega(x)$.

Choose δ , $0 < \delta < \epsilon/3$, such that whenever $z_1, z_2 \in \overline{\gamma^+(x)}$ and $d(z_1, z_2) < \delta$ then $d(\psi_t(z_1), \psi_t(z_2)) < \epsilon/3$ for $0 \leq t \leq 2t_0$. Fix n such that $1/n < \epsilon/3$ and $D(C^n, C) < \delta$, where D denotes the Hausdorff metric. Drop the superscript n on y_i^n and t_i^n . Then we have

$$d(\psi_{t_1}(y_1), y_2) = d(\psi_{t_0}(y), y_2) < \frac{1}{n} < \frac{\epsilon}{3}.$$

Set $z_1 = y$ and choose $z_2 \in C$ such that $d(z_2, y_2) < \delta < \epsilon/3$. Then

$$\begin{aligned} d(\psi_{t_1}(z_1), z_2) &= d(\psi_{t_0}(y), z_2) \\ &\leq d(\psi_{t_0}(y), y_2) + d(y_2, z_2) \\ &< 2\epsilon/3. \end{aligned}$$

Since $d(z_2, y_2) < \delta$, it follows that

$$d(\psi_{t_2}(z_2), \psi_{t_2}(y_2)) < \epsilon/3.$$

Choose $z_3 \in C$ such that $d(z_3, y_3) < \delta < \epsilon/3$. Then

$$\begin{aligned} d(\psi_{t_2}(z_2), z_3) &\leq d(\psi_{t_2}(z_2), \psi_{t_2}(y_2)) \\ &\quad + d(\psi_{t_2}(y_2), y_3) \\ &\quad + d(y_3, z_3) \\ &< \frac{\epsilon}{3} + \frac{1}{n} + \delta < \epsilon. \end{aligned}$$

Furthermore, $d(z_3, y_3) < \delta$ implies

$$d(\psi_{t_3}(z_3), \psi_{t_3}(y_3)) < \epsilon/3,$$

so we choose $z_4 \in C$ such that $d(z_4, y_4) < \delta < \epsilon/3$. As above, $d(\psi_{t_3}(z_3), z_4) < \epsilon$. Clearly, we may continue in this way, finding $z_i \in C$ with $d(z_i, y_i) < \delta$, $i = 1, 2, \dots, l = l_n$ and t_i , $i = 1, 2, \dots, l - 1$, such that $d(\psi_{t_i}(z_i), z_{i+1}) < \epsilon$ for $i = 1, 2, \dots, l - 1$. Since $d(z_l, y_l) < \delta$, we may conclude $d(\psi_{t_l}(z_l), \psi_{t_l}(y_l)) < \epsilon/3$. Set $z_{l+1} = y$ and observe that

$$\begin{aligned} d(\psi_{t_l}(z_l), z_{l+1}) &\leq d(\psi_{t_l}(z_l), \psi_{t_l}(y_l)) \\ &\quad + d(\psi_{t_l}(y_l), y) \\ &< \frac{\epsilon}{3} + \frac{1}{n} < \frac{2}{3}\epsilon. \end{aligned}$$

We have constructed an (ϵ, t_0) -chain in $C \subset \omega(x)$ joining the point y to itself. Since $y \in \omega(x)$, $\epsilon > 0$, $t_0 > 0$ were arbitrary, it follows that $\omega(x)$ is chain recurrent.

The following ideas show that the case that $L = \alpha(x)$ can be reduced to the former case. First note that if $L = \alpha(x)$ for the flow ψ_t then $L = \omega(x)$ for the flow $\phi_t \equiv \psi_{-t}$ and therefore L is chain recurrent for the flow ϕ_t by the proof given above. We must show that L is chain recurrent for ψ_t . Fix $y \in L$, $\epsilon > 0$ and $t > 0$. We will show that there is an (ϵ, t) -chain from y to y . Since L is compact, we can choose $\delta > 0$ such that $\delta < \epsilon$ and whenever $x_1, x_2 \in L$ and $d(x_1, x_2) < \delta$ then $d(\psi_t(x_1), \psi_t(x_2)) < \epsilon$. Now, since y is a chain recurrent point for ϕ_t , there exists a $(\delta, 2t)$ -chain $\{y = x_1, x_2, \dots, x_{n+1} = y; t_1, t_2, \dots, t_n\}$ of points $x_i \in L$ and times $t_i \geq 2t$ such that $d(\psi_{-t_i}(x_i), x_{i+1}) < \delta$, $i = 1, 2, \dots, n$. Let $y_2 = \psi_{-t_n+t}(x_n)$, $y_i = \psi_{-t_{n+2-i}}(x_{n+2-i})$ for $i = 3, 4, \dots, n+1$, $y_1 = y_{n+2} = y$, $s_1 = t$, $s_2 = t_n - t$, $s_i = t_{n+2-i}$ for $3 \leq i \leq n+1$. Then, $s_i \geq t$ for $1 \leq i \leq n+1$ and $d(\psi_{s_1}(y_1), y_2) = d(\psi_t(y), \psi_t(\psi_{-t_n}(x_n))) < \epsilon$ because $d(y, \psi_{-t_n}(x_n)) < \delta$. Also, $d(\psi_{s_2}(y_2), y_3) = d(x_n, \psi_{-t_{n-1}}(x_{n-1})) < \delta < \epsilon$. For $3 \leq i \leq n$, $d(\psi_{s_i}(y_i), y_{i+1}) = d(x_{n+2-i}, \psi_{-t_{n-i+1}}(x_{n-i+1})) < \delta < \epsilon$. Finally, $d(\psi_{s_{n+1}}(y_{n+1}), y_{n+2}) = d(x_1, y) = 0$. Thus, $\{y_1, y_2, \dots, y_{n+2}; s_1, s_2, \dots, s_{n+1}\}$ is an (ϵ, t) -chain from y to y for the flow ψ . It follows that y is a chain recurrent point for the flow ψ . \square

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Subject Index

A

absorption principle, 8
algebraic multiplicity one, 20, 60, 92, 137
alpha limit set, 32
approximate from below (above), 8
asymptotically stable from above, from below, 15
asymptotically stable point, 15
attracting periodic orbit, 4

B

basin of attraction, 19
Belousov-Zhabotinski reaction, 50
Biochemical control circuit, 58, 93, 139
Borel measure, 79, 86, 105
Brouwer Fixed Point Theorem, 45, 96

C

chain recurrent set, 40, 163
conditionally completely continuous operator, 9
completely continuous operator, 9
Colimiting principle, 6
compact operator, 19, 121
competitive system, 31, 34, 48
concave operator, 153
contracting rectangle, 84, 97
Convergence criterion, 3
convergent point, 2
cooperative system of ODEs, 31, 34, 48
cooperative system of FDEs, 88
cooperative system of PDEs, 129
cooperative and irreducible system of ODEs, 56
cooperative and irreducible system of FDEs, 88
cooperative and irreducible system of PDEs, 133

D

dissipative system, 59

E

equilibrium point, 2
eventually strongly monotone semiflow, 3, 85, 89
essential infimum, 107
exponential ordering, 102

F

falling interval, 37
Field-Noyes model, 50
fixed point index, 17
Floquet multiplier, 64
flow, 32
full orbit of Φ , 26, 62

H

Hausdorff metric, 16, 164
hyperbolic point, 43

I

invariant set, 2
Intersection principle, 6
irreducible matrix, 43, 56

K

Kamke condition, 32
Krein-Rutman Theorem, 19, 20, 93

L

Limit set dichotomy, 5, 8, 21
Limit set separation principle, 8
Lipschitz vector field, 38
Lotka-Volterra system, 35, 58, 64, 69, 94

M

maximum principle, 123
mild solution, 122
monotone semiflow, 2

N

Nagumo condition, 127
negative orbit, 32

N

Nonordering of limit sets, 5
 normal cone, 15

O

orbit, 2
 order convex, 18
 order interval, 15
 Order interval trichotomy, 17
 order stable equilibrium, 73
 omega limit set, 2, 26

P

p-convex, 33
 p_m -convex, 48
 partial order relation, 1, 48
 Perron-Frobenius Theorem, 43, 60
 Poincaré-Bendixson Theorem, 40,41
 point spectrum, 92
 positive cone, 1, 48
 positively invariant set, 2, 34, 81
 positive orbit, 32
 positive semigroup, 99
 principal eigenvalue, 137
 principal eigenvector, 137

Q

quasiconvergent point, 2
 quasipositive matrix, 60
 quasimonotone condition, 78, 129

R

rising interval, 37

S

semiflow, 2
 semigroup, 121
 Sequential limit set trichotomy, 9
 sign-stable matrix, 49
 sign-symmetric matrix, 49
 Smale's construction, 69
 spectral radius, 20, 60
 stability modulus, 60, 91, 110
 stable point, 15
 stable manifold, 43
 strictly monotone semiflow, 24
 Strong parabolic maximum principle, 124
 strongly monotone semiflow, 3
 strongly order preserving semiflow, 2
 strongly positive operator, 19
 sub-equilibrium (strict), 24, 35
 super-equilibrium (strict), 24, 35
 sub-(super-)solution, 130

T

topologically equivalent vector fields, 38
 totally ordered set, 12
 type K vector field, 32

U

uniformly elliptic differential operator, 121
 uniformly parabolic differential operator, 123
 unrelated points, 34

V

vector field, 32

W

w-norm, 21

This book presents comprehensive treatment of a rapidly developing area with many potential applications: the theory of monotone dynamical systems and the theory of competitive and cooperative differential equations. The primary aim is to provide potential users of the theory with techniques, results, and ideas useful in applications, while at the same time providing rigorous proofs. Among the topics discussed in the book are continuous-time monotone dynamical systems, and quasimonotone and nonquasimonotone delay differential equations. The book closes with a discussion of applications to quasimonotone systems of reaction-diffusion type. Throughout the book, applications of the theory to many mathematical models arising in biology are discussed.

Requiring a background in dynamical systems at the level of a first graduate course, this book is useful to graduate students and researchers working in the theory of dynamical systems and its applications.

ISBN 978-0-8218-4487-8



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