

MBE:

Mathematical Biosciences and Engineering

Volume 7 • Number 1 • January 2010

ISSN 1547-1063

Vol. 7 • No. 1 • January 2010

MBE:

Mathematical Biosciences and Engineering

Volume 7 • Number 1 • January 2010

ISSN 1547-1063
Electronic ISSN 1551-0018

CONTENTS

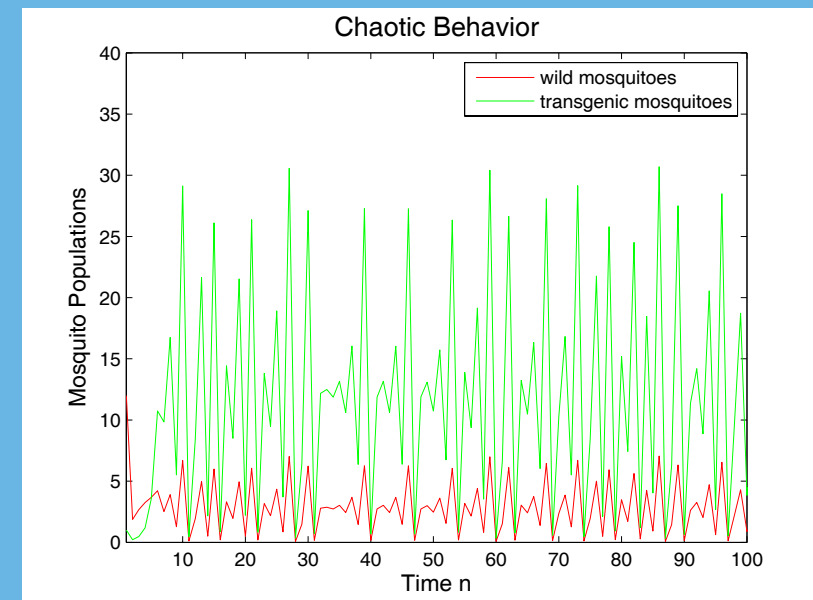
Hal L. Smith Tribute to Horst R. Thieme on the occasion of his 60th birthday	i
Adelheid L. J. Thieme Wanderings with Lady M.: A happy threesome	iv
Fred Brauer, Zhilan Feng and Carlos Castillo-Chavez Discrete epidemic models	1
Robert Stephen Cantrell, Chris Cosner and Yuan Lou Evolution of dispersal and the ideal free distribution	17
Karl Peter Hadeler Structured populations with diffusion in state space	37
Wenzhang Huang, Maoan Han and Kaiyu Liu Dynamics of an SIS reaction-diffusion epidemic model for disease transmission ...	51
Sophia R.-J. Jang Discrete host-parasitoid models with Allee effects and age structure in the host ...	67
Maria Conceição A. Leite and Yunjiao Wang Multistability, oscillations and bifurcations in feedback loops	83
Jia Li Modeling of mosquitoes with dominant or recessive Transgenes and Allee effects..	99
Xue-Zhi Li, Ji-Xuan Liu and Maia Martcheva An age-structured two-strain epidemic model with super-infection.....	123
Ya Li and Zhilan Feng Dynamics of a plant-herbivore model with toxin-induced functional response	149

(To be continued in the inside cover)

Mathematical Biosciences and Engineering

Pages 1-211

Tribute to Horst R. Thieme on the Occasion of his 60th Birthday



Guest Editors: Zhilan Feng, Hal L. Smith and Glenn F. Webb

American Institute of Mathematical Sciences • Beihang University

PREFACE:
TRIBUTE TO HORST R. THIEME
ON THE OCCASION OF HIS 60TH BIRTHDAY

It is a great pleasure to congratulate Horst on his 60th birthday and to dedicate this volume to him in honor of his many contributions to the field of mathematical biology.

Horst Thieme has been, over a period of thirty years, one of the most productive scientists in Mathematical Biology, with numerous works on subjects centered on population biology and transmission and control of infectious disease. He has provided a number of rigorous mathematical tools for the study of structured populations, the problem of biological invasion, and the limiting behavior of epidemic and other population models. Horst Thieme's work can be characterized by deep insight into the underlying structure of biological phenomena and mechanisms, great skills in entering these insights into feasible models, and by rigorous mathematics validating or sometimes rejecting modeling approaches.

Horst's earliest contributions, beginning in the late 1970s, centered on Volterra integral equations. These works focused on asymptotic estimates of solutions and, in their application to epidemiology, to the asymptotic speed of spread of an epidemic. These works continue to be cited to this day. He continued this work in the early 1980s, studying renewal theorems for Volterra integral equations in full generality. This is basic work that lies at the foundation of the very general renewal approach to populations structured by age or size and connects this theory to the semigroup approach.

In 1984, a first paper with Odo Diekmann and Henk Heijmans appeared, and this team of population modelers, later joined by Mats Gyllenberg, Philippe Clément, Hans Metz, and others, continued their collaboration until now, with Horst Thieme as a coauthor for at least fifteen years.

Horst's joint paper with H. Bremermann, "A competitive exclusion principle for pathogen virulence," was among the first to rigorously establish the principle that in the absence of multiple infections and the presence of complete cross-immunity, only the parasite strain with the maximal basic replacement ratio survives. It has spawned considerable recent research focusing on relaxing the assumptions such that multi-strain coexistence can occur. A recent Thieme book chapter extends the earlier work on competitive exclusion but also shows that a strain that would become extinct on its own can coexist with a more virulent one if it protects the host against the more virulent strain.

In the 1990s Thieme took on the problem of persistence. His paper on weak persistence (1993) is now a classic in that field. Its main theme is that the strong compactness assumptions on the dynamics typically assumed in order to obtain (uniform) persistence can be substantially relaxed and this allows the theory to be much more broadly used. The paper also contains applications of persistence theory to some well-known models in epidemiology, providing conditions for both host

persistence and disease persistence (endemicity). Following this work, persistence theory began to become a critical tool in the analysis of epidemic models. His subsequent work on persistence extended the theory to non-autonomous dynamical systems.

One of Thieme's most cited works provides mathematically rigorous support for the commonly exploited simplifications that we all use in analyzing problems arising in biomathematics. If one or more components of a dynamical system converge, it is natural to study the reduced system obtained by "freezing" these components at their limiting values. The hope is that limit sets would be the same for the original and reduced systems. This turns out to be false but Thieme shows that key aspects of the Poincaré-Bendixson theory can be applied to the original system if the reduced system is two-dimensional.

Horst's highly cited 2003 monograph "Mathematics in Population Biology" has become a classic reference book on population modeling and mathematical epidemiology but also for the many analytical tools lucidly described there.

Many researchers in mathematical biology may not be aware of Horst's extensive research in non-standard ways of generating dynamical systems in infinite dimensional spaces (integrated semi-groups generated by non-densely defined operators). This work has many applications in mathematical biology and will continue to be useful in the future.

Paul Waltman introduced me to Horst in Bonn in 1978 at the conference "Functional differential equations and approximation of fixed points." I got to know him better in 1986 when he invited me to visit the Center for Stochastic Mathematical Models in the Natural Sciences at the University of Heidelberg where he was doing postdoctoral research. While there, I very much enjoyed the hospitality of Horst and Adelheid and daughters Ruth and Clara. Although my stay was for only a few weeks, I left feeling like part of the family. As a result of the visit, I was greatly impressed with Horst's analytical powers and his research in mathematical biology. The Thieme family left Germany when Horst took a visiting research professorship at Harvey Mudd College in 1987 and the possibility of attracting him to Arizona State University did not take long to germinate in my mind. The ASU research group in mathematical biology began in 1988 with the hiring of Horst, Yang Kuang, and Steve Baer. It has since flourished, due in no small part to Horst's rising stature in the field. My research collaborations with Horst, which began shortly after he arrived at ASU, have produced my most satisfying work. These collaborations focused on monotone dynamical systems and their applications to delay differential equations and to asymptotically autonomous dynamical systems. We continue our collaboration on a forthcoming monograph "Dynamical Systems and Population Persistence."

Many of the contributions to this volume come from participants in the very successful conference on Differential Equations and Applications in Ecology and Epidemiology, organized by Zhilan Feng and Tim Lant, held at Purdue University in December 2008 in honor of Horst's Birthday. Aside from many exciting research reports typical of such a conference, the meeting was distinguished by a wonderful banquet after which many of Horst's former students, colleagues, and mentors provided personal reflections on their experiences with Horst. Without a doubt, the most memorable of these, even beating out Horst's rendition of "The Song of John Matrix," was the masterful power point presentation "Wanderings With Lady M." given by Adelheid Thieme, which appears first in this volume.



Mathematical Biology Conference
December 8-10, 2008
 (Left to Right)
 First Row: Fred Brauer, Zhilan Feng, Rongsong Liu, Maria Leite, Adelheid Thieme, Horst Thieme, Lih-Ing Wu Roeger, Maia Martcheva
 Second Row: Fabid Milner, Yiding Yang, Thanate Dhirasakdanon, Willi Jaeger
 Third Row: Jia Li, Linda Allen, Xiaohong Wang, Libin Rong, Dashun Xu, Shingo Iwami
 Fourth Row: Yuan Lou, Sophia Jang, Azmy Ackleh, Grisele Torres-Garcia, Takatumi Suzuki, Zhipeng Qiu
 Fifth Row: Ruijun Zhao, Glenn Webb, Xiaoqiang Zhao, Hal Smith
 Sixth Row: Daniel Maxin, Wenzhang Huang, Laurentui Segal, Pauli Saicenu, K.P. Hadeler
 Seventh Row: David Gerberry, A.J. Metz, Mats Gyllenberg, Odo Diekmann

FIGURE 1. Conference participants.

Guest Editor:
 HAL L. SMITH

WANDERINGS WITH LADY M.: A HAPPY THREESOME

Adelheid L. J. Thieme

Department of English
Arizona State University
Box 870302
Tempe, AZ 85287-0302, USA



I met Horst at the University of Münster, Germany, in July 1972. While I was at the university, one of my goals was to find a husband. I wanted my husband to be Catholic, so I decided to join a bible study group, where I thought I would find many suitable “candidates.” Unfortunately though, I was wrong. There were only two Catholics. One of them was definitely not an option, and then there was ... Horst. He was a challenge, and I guess all participants of this conference know what I mean. But some people just grow on you, which happened in Horst’s case.

As our relationship was getting more serious, he said to me one day: “I need to tell you something. I am already engaged, and no matter what is going to happen between the two of us, I’m not going to give up my fiancée. If you manage to get along well with her, the three of us can have a good life together. I would like you to give the three of us a chance.”

I agreed to meet her. It was at his doctoral graduation ceremony, in April of 1976, that I first made her acquaintance. Her name was Mathematica (in German, Horst always called her “Meine Verlobte, die Mathematik”), and her appearance was somewhat unusual. She wore a white dress imprinted with black integral signs, and instead of a purse she carried a notepad and a pencil. She was very business-like. When she looked at you, you could tell that she had a sharp, analytical mind. She introduced herself to me as “Mathematica” and told me, “You may call me Lady M. for short.” We did not talk a lot. “I hear you are considering the position of the wife,” she said. “Do you know about Horst and me?” I told her that I was informed.

“So, what did you think of her?” Horst asked me after our first meeting. “She looked rather stern and demanding. And I wouldn’t be surprised if she were quite a taskmaster,”

I said. “That is true,” Horst replied, “but I know how to keep her in check. Would you agree to becoming a member of our threesome?”



“It’s a deal,” I said. The deal was closed July 2, 1976, when we got married in St. John the Baptist’s Catholic Church in my home village, Gimfte. Willi Jaeger kindly agreed to be the best man at our wedding.



Life as a threesome was easy at first. Horst would spend his days with Lady M. in the math department at the university, and I would teach at a college-prep school. He would spend the evenings and the weekends with me. Only occasionally, while we were sitting at the dinner table, would he look at me absent-mindedly, as though he were in a different world. “Never mind, I was just talking to her,” he would say apologetically. Sometimes, in the morning, he would wake up all groggy, go to his study right away and scribble some notes on a notepad. Then he would sigh and say, “I had such a great idea during the night, and I thought the proof would work, but she just proved me wrong.”

In 1979, Lady M. got restless for the first time. She suggested she and Horst would go to Heidelberg, where he could work with the group around Willi Jäger and get involved in intriguing research at the center for Stochastic Mathematical Models in the Natural Sciences. She knew that, due to professional obligations, I would have to stay behind in Münster, but she used all her persuasive power. “You want him to realize his dreams, don’t you? After all, you are his wife,” she said. She knew me well enough, and I gave my consent to Horst and her moving to Heidelberg alone.



Horst and I became excellent customers of the Deutsche Bundesbahn, traveling between Münster and Heidelberg every weekend. We were looking forward to the weekends and enjoyed our second honeymoon with romantic dinners at cozy restaurants, long walks along the river Neckar, hikes up the Heiligenberg in Heidelberg, and visits to the surrounding castles. In 1980, when I obtained a teaching position at the

During the twelve months that we lived apart,



Gymnasium Walldorf near Heidelberg, we resumed the life we had known in Münster. When Ruth, our older daughter (who is now 26) entered our life, Horst would leave Lady M. and the office in the late afternoon and devote the rest of his time to his family. The nights with a baby were stressful, so Lady M. stepped in and arranged for Horst to attend mathematical conferences. He would return refreshed, since he had been able to get a full night's sleep for several days. This was not totally unselfish on her part. She realized that he would only spend productive days with her if she made sure that he would be well rested.

In 1983, she bestowed a special honor on him. To recognize him for his achievements after his “habilitation”, she placed a special high head on his head. At the end of his habilitation talk on chaos, he thanked her with the following alliterative poem:

Chaos

Tierisch tosen Turbulenzen,
Trajektorien treiben's toll,
Tori taumeln trunk'ne Tänze,
Im Attraktor turmt der Troll.

See the English version below:

Torrents thunder turbulences,
Trajectories take their toll,
Tori tumble turbid dances,
The attractor traps a troll.



In 1984,

Lady M. became restless again. She had found a position for Horst as a research visitor at the Center for Mathematics and Computer Sciences in Amsterdam, where one of her other minions, Odo Diekmann, was working. At that time, I was not employed because I was taking care of Ruth, who was two years old, and her baby sister, Clara, who was born in March 1985. For me, the stay in Amsterdam that Lady M. had organized was a welcome diversion. After Horst had tended to his duties with Lady M., we would explore the city by bike, walk along the grachten, and drive to the beach at Zaandvort.

After our stay in Amsterdam, Lady M. redirected Horst to Heidelberg as a Heisenberg scholar at the research center Stochastic Mathematical Models in the

Natural Sciences. Then, in 1987, Lady M. had new plans. This time, she had Horst stay as a visiting professor at Harvey Mudd College in Claremont, California. He collaborated with the late Stavros Busenberg, the late Ken Cooke, and some other researchers whom she had ensnared. During the week, Lady M. occupied Horst's time, but at the weekends we would, as a family, stroll through the beautiful Rancho Santa Ana Botanic Garden, ride an elephant at the Los Angeles Zoo, or explore Laguna Beach.

Life was good until March of 1988, when Lady M. and I got into a serious fight. I had been hoping to return to Germany for good, but Lady M. urged Horst to accept a position at Arizona State University. I vividly remember the duel that we fought in the backyard of the house we had rented on Baughman Avenue in Claremont.



“Do you really expect me to move away from Germany, from all my family and friends, and on top of that to a place where I need to speak English all the time?” I asked.

“Yes,” she said. (She was never much of a talker.)

“Do you know that I want to resume my teaching job in Germany?”

“Yes,” she said, “but there will also be teaching opportunities in Tempe. Accepting that position at ASU will be very good for

Horst, and for you, too. I will take care of your whole family, and I will give you much more than you can imagine at this time. I promise.”



We packed all our belongings in Germany in a container, took 8 suitcases with items that we would need while our furniture was on the ocean, and started a new life in Tempe, Arizona. The people from the moving company had no idea how to assemble German furniture. Hal Smith was kind enough to help Horst tackle this difficult task.

Lady M. introduced Horst to the wide circle of her admirers, and she stimulated his creativity and productivity. I began a slow but steady ascent to building a satisfying professional career, and she also took good care of our daughters.

Every now and then, especially in the last years, she arranged for gatherings of her followers in remote places, and she also included me. We visited some wonderful



places like the Flower Garden in Hamamatsu, Japan; Buddhist temples in Kyoto; the Museum of Terra Cotta Warriors in Xi'an; a park commemorating the glorious days of the Tang dynasty, a museum where Horst conversed with the spirit of Confucius; a park displaying sculptures from 133 countries in Changchun; and the Great Wall of China.



We also explored Poitiers, France, together with Stefan Van Gils, Mats Gyllenberg and Odo Diekmann.

In the summer of 2008, we took a trip to Luminy, France, where we enjoyed the wonderful scenery of the “calanques” together with Karl and Helgard Haderl.

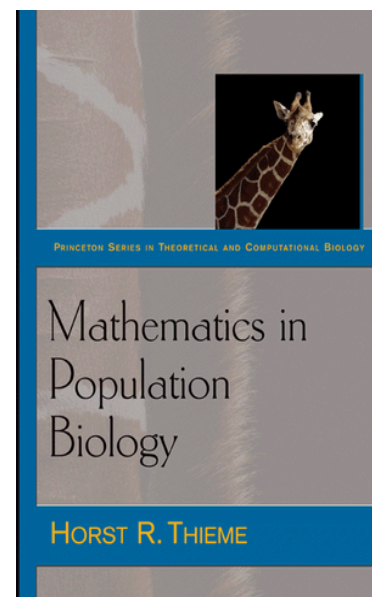


It was also a pleasure to explore Le Havre with Maia Martcheva and her husband.



In the course of the 20 years that he has spent teaching at Arizona State University, Horst has collaborated extensively with other mathematicians. This collaboration has led to a publication list of more than one hundred entries. He particularly enjoyed working with his students and introducing them to Lady M. I know that, in his scholarly work, he is committed to excellence. When it comes to his students, he is extremely supportive, not only of their research but also in anything that pertains to their personal well-being.

Horst invested a lot of time and energy in his first book, *Mathematics in Population Biology*. When it was nearing completion, Lady M. gave me a special assignment. “I want this book to be perfect”, she said.



“You don’t know anything about mathematics, which is unfortunate but cannot be helped. However, you know something about spelling and punctuation. So your task will be to proofread the mechanics of the text, and in return I will make sure that Horst dedicates his first book to you.”

On the whole, Lady M. has kept her promise of taking care of us all. I am glad that I agreed to our pact, and Horst, Lady M. and I have formed a happy threesome for 36 years. Our daughters also appreciate Horst for his generosity, his support, and his fairness.

This week, December 8-10, 2008, Lady M. is holding a conference in honor of Horst’s 60th birthday. She recruited Zhilan Feng and Tim Lant, who count among her faithful followers, to organize this meeting. I would like to personally thank Zhilan and all the participants of this conference for making this week so special for Horst, the love of my life.

