# Dynamics of structured populations

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## 1 Overview of the Field

### 1.1 Overview

In order to accurately describe and fully understand the dynamics of populations, one needs to consider the different stages and functions of individuals as well as their spatial distribution. It is particularly challenging to model and analyze the interplay between stage structure and movement ability. The resulting mathematical equations are in the form of systems of (partial) differential equations, functional differential equations, integro-differential equations, difference equations or integral equations.

This 5-day workshop provided a unique opportunity to bring together specialists from different fields to discuss recent progress in the qualitative analysis of structured population models, with regards to pattern formation, front propagation, and bifurcation phenomena. Special attention was given to the applications in spread and control of epidemic diseases, invasion and persistence in ecological systems as well as in biomedical and cancer modeling.

### 1.2 Objectives

A standard method in the mathematical modeling of populations and their interactions is to model the populations as whole entities and derive equations for all relevant classes. This method typically leads to systems of ordinary or partial differential equations. While their exploration continues, the qualitative behavior of these models and their relevance to biological applications is fairly well understood. Ongoing biological research provides us with more detailed insight into the structure of populations and the individual behavior of its members. To include these biological details into more refined models is a chance and a challenge.

For example, the larval stages in mosquitoes can be included into a new model for West-Nile Virus, the social order in wolf packs can be included into models for home-range formation, or the cell reproduction cycle can be included into tumor growth and treatment models. Typical structure variables are age, size, stage, function, spatial location, genotype, or phenotype. A combination of one or more of these structure variables into a model leads to systems of reaction-diffusion equations, integro-difference and integro- differential equations, integral equations, matrix models, hyperbolic and parabolic partial differential equations, and stochastic processes. The methods for analyzing these structured population models are based on linear algebra, dynamical system theory, and the theory of ordinary and partial differential equations.

During this workshop we focused on three main topics of structured population modeling:

1. Theory of structured populations
2. Spatial models
3. Epidemiology and diseases

## 1.3 Theory of structured populations

Population structures result from the simple fact that individuals are different with respect to age, stage, size, gender, and location. Structure can also be generated by the involvement of many species like host, vector and parasite in an epidemic model or of multiple parasite strains. Structured population models are a suitable intermediate between abundance models and agent-based models. The conference presented an update on the development of an encompassing theory which occurred during the last 25 years. This theory is based on linear and nonlinear functional analysis, notably the theory of dual operator semigroups and their nonlinear perturbation. It allows a relatively easy study of stationary population states, their stability, and the bifurcation of other stationary states or periodic solutions. The bifurcation is intimately linked to mathematical or biological threshold parameters like the spectral bound (or radius in discrete time) of the linearized system or a basic reproduction number. Different reproduction numbers seem to be possible depending on the biological emphasis though they share the same threshold characteristics. Fortunately convenient graph-theoretic methods are available to calculate the reproduction numbers if there are finitely many distinct individual stages.

The use of the general theory was illustrated in discussing evolutionary trends in endophyte metapopulation models. Structured population models have the advantage to make important population dynamic parameters explicit, and the sensitivity of the model dynamics to these parameters becomes an important and sometimes daunting task. In stage-structured models the sensitivity analysis can be performed through novel approaches based on matrix calculus.

## 1.4 Spatial models

Since the 1970's, the classical models for spatial spread of populations in the form of reaction-diffusion equations have been studied widely and applied successfully to many different questions in biology. However, their applicability to certain biological systems is limited and new approaches are needed. Alternative models in the form of hyperbolic transport equations or parabolic/hyperbolic Fokker-Planck equations structure the population into velocity classes and describe how individuals change velocity. These models have received much attention, and their relationship to the classical reaction-diffusion models is fairly well understood through scaling and moment closure methods.

Another recent development in modeling spatial spread of populations is to incorporate different compartments for different modes of movement or even a compartment for non-moving individuals. These models capture biologically diverse phenomena such as seeds being transported by wind and by birds, animals and cells stopping their movement to reproduce, and proteins in the cell nucleus undergoing binding-unbinding events with immobile cell structures. Mathematically speaking, these structured models come in the form of integro-differential or integro-difference equations (with mixed dispersal kernels), integral equations, and as systems of coupled partial and ordinary differential equations. It is known that dividing the population into compartments with different movement characteristics can significantly alter the models predictions, e.g., regarding invasion speeds and stability.

While there is an overwhelmingly rich qualitative mathematical theory available for reaction-diffusion equations, a similarly complete theory for these alternative structured models is only just emerging. One focus of this workshop was on novel developments of the qualitative theory of spatially structured population models. Advances in this area help in the choice of the most appropriate model for different applications in biology, such as the dynamics of the immune system, the epidemic spread of an infectious disease, and the invasion of microbes.

### 1.5 Epidemiology and diseases

The transmission characteristics of newly emerging diseases, such as SARS, West Nile Virus, and AIDS, are quite different from the local periodic outbreaks of “classical” infectious diseases, such as childhood diseases, and new models and methods are discussed to describe and analyze these outbreaks. Spatial heterogeneity is an important factor to consider in the spread of many diseases, e.g., influenza. Models for realistic vaccination schedules usually require the inclusion of the population age structure, in particular if antiviral doses are limited. Infection-age is a crucial structural variable in models for the emergence and spread of antibiotic-resistant bacteria, be it in the treatment of tuberculosis or the prevention of hospital-acquired infections.

When no vaccine is available (e.g., SARS) control by isolation and/or quarantine can be built into a model. In particular, in light of the threats of terrorism, there is an increased need to understand and to model spatial spread of epidemics as well as optimal vaccination strategies and control. Among other things, this modeling requires a blending of different mathematical techniques and the embedding of these epidemic models into a more general class of structured population models, as they have been discussed at our workshop.

Mathematical modeling in medicine has become a major focus of research and has contributed new insights into medical processes on the individual, cellular and intra-cellular level. The techniques and analytical methods, originally developed in the context of population dynamics, are now being extended to medical applications. For example, transport equations play a role for the conduction of nervous impulses, hyperbolic models are used to model movement of leucocytes, and reaction-diffusion equations are used to model embryonal development, wound healing, and angiogenesis in cancer. The relevant population structures include the cell reproduction cycle, the circadian rhythm, the age of an organ or tissue and the stages in cell development (for example six stages are involved in the modeling of stem cell differentiation into blood cells). Again, ordinary and partial differential equations and integro-differential equations are the major tools for biomedical modeling. Questions of interest include pattern formation (in development), persistence (in cancer) and control (in diseases and in the immune system). During this workshop we emphasized the extension of the existing mathematical modeling methods to biomedical applications. We focused on new questions and therapies that make use of structured population modeling, for example taking account of the cell reproduction cycle in chemotherapy treatment planning. Furthermore, we discussed modeling and implications of resistant bacterial strains.

## 2 Presentations of Recent Developments

Some participants were selected to give either 20 or 40 minute talks, which were grouped into sessions according to the three overarching themes of the workshop. One outstanding full-hour lecture was given by Karl Hadeler on past, present and future research on transport equations and quiescent states. The workshop allowed younger researchers and postdocs to present their results and experienced researchers to present an overview of their work. All the presentations were of very high quality and stimulated interesting discussions, some leading to new collaborations. Speakers and abstracts of contributed talks are listed below in alphabetical order:

**Lora Billings**
**ADE in multi-strain disease models**
As we increase our resources to fight disease, pathogens become more resilient in their means to survive. One example is antibody-dependent enhancement (ADE), a phenomenon in which viral replication is increased rather than decreased by immune sera. We study the complex dynamics induced by ADE in multi-strain disease models and investigate the effects of vaccine campaigns. In particular, we study the consequences of using single-strain vaccines, which would increase the virulence in other infections.

**Thanate Dhirasakdanon**
**A sharp threshold for disease persistence in host metapopulations**
A sharp threshold is established that separates disease persistence from the extinction of small disease outbreaks in an SEIRS type metapopulation model where the travel rates between patches can depend on disease prevalence. The threshold is formulated in terms of a basic replacement ratio (disease reproduction number), $R_0$, and, equivalently, in terms of the spectral bound of a transmission and travel matrix. Since frequency-

dependent (standard) incidence is assumed, the threshold results do not require knowledge of asymptotic behavior of disease-free dynamics. As a trade-off, for $R_0 > 1$, only uniform weak disease persistence is shown in general, while uniform strong persistence is proved for the special case of constant recruitment of susceptibles into the patch populations. For $R_0 < 1$, Lyapunov's direct stability method shows that small disease outbreaks do not spread much and eventually die out. (joint work with H.R. Thieme and P. van den Driessche)

**Hal Caswell**

**Some new sensitivity analyses of matrix population models**

Sensitivity analysis of growth rates in linear structured population models is well-developed and frequently used. Sensitivity analysis of other demographic properties, and of nonlinear models, is not as well understood. I will present some new approaches, based on matrix calculus, that make the analyses easy. With examples, of course.

**Odo Diekmann**

**How to miss a key point for 25 years, but see it at last?**

The real contents of the lecture would be: how to represent the state of a structured population? Answer : by way of the history of the population birth rate and the history of the environmental interaction variables (even though logic suggests to use a distribution over the state space of individuals). Motivation: with this choice of p-state space the sun-star theory of delay equations applies (and so a wealth of results comes for free).

**Kevin Flores**

**Modeling the Progression of Malignancy in Cancer**

There is strong biological evidence for the selection of cells with malignant phenotypes in the progression of many cancers. Selection of a phenotype is associated with particular molecular or genetic abnormality and an extracellular environment that makes such an alteration favorable. In this talk we propose 2 structured models of such a scenario in 2 structurally distinct cancers. We first describe the simplest example of this mechanism of selection in a model of Chronic Myelogenous Leukemia, where the selection is artificially imposed by the drug Gleevec and the selection is for resistant phenotypes. We then describe a model of Colon Cancer progression, where cell differentiation and cycle time are taken into account using distinct differentiation classes and cycle-age structure, respectively; we will hypothesize that this model can be used to describe the selection for p53 gene mutants under competition for oxygen and show how it can be used to model cell cycle specific chemotherapy.

**Cindy Greenwood**

**Stochastic effects in SIR modeling**

A number of stochastic effects in the SIR epidemic model are important even when populations are large, e.g. bimodality of epidemic size distributions, stochastically sustained oscillations in numbers of infective individuals. I have recently written a book chapter on this.

**Mats Gyllenberg**

**Ecology and evolution of symbiosis in structured metapopulations**

We present a model for symbionts in plant host metapopulation. Symbionts are assumed to form systemic infection throughout the host and pass into the host seeds, but also to reproduce and infect new plants by spores. Thus, we study a metapopulation of qualitatively identical patches coupled through seeds and spores dispersal. Symbionts that are only vertically inherited cannot persist in such a uniform environment if they lower the host's fitness. They have to be beneficial in order to coexist with the host if they are not perfectly transmitted to the seeds, but evolution selects for 100 fidelity of infection inheritance. In this model we want to see in what way mixed strategies (both vertical and horizontal infection) affect the coexistence of uninfected and infected plants at equilibrium; also, what would evolution do for the host, for the symbionts and for their association. We present a detailed classification of the possible equilibria with examples. The (in)stability of the steady states is investigated using resent results by Diekmann, Gyllenberg & Getto (SIAM J. Math. Anal. 2007). This talk is based on joint work with Diana Preoteasa.

**K.P. Hadeler**

### Transport Equations and Quiescent States

Moving organisms perform complicated walks which can be described by transport equations modeling changing velocity, turning events etc. On a larger/longer scale, such movements appear as diffusion. Several mathematical problems appear quite natural: How do the known results on reaction diffusion equations translate into transport equations? How to get diffusion approximations to transport equations and perhaps a hierarchy of intermediate approximating equations.

Transport equations can be seen in the wider framework of coupled systems (velocity states are coupled by turning events) and (some) diffusion approximations can be seen as singular perturbation problems. Also dynamics with quiescent phases fit into this framework of coupled systems (quiescence may appear as absence of motion or absence of any non-trivial dynamics). For systems with quiescent phases an outline of an emerging coherent theory is given.

**Fred Hamelin**

### A differential game theoretical analysis of mechanistic models for territoriality

In this paper, elements of differential game theory are used to analyze a spatially explicit home range model for interacting wolf packs. The model consists of a system of partial differential equations whose parameters reflect the movement behavior of individuals within each pack and whose solutions describe the patterns of space-use associated to each pack. By controlling the behavioral parameters in a spatially-dynamic fashion, packs adjust their patterns of movement so as to find a Nash-optimal balance between spreading their territory and avoiding conflict with hostile neighbors. On the mathematical side, the game let appear some of the few singularities never observed in nonzero-sum games. From the ecological standpoint, one recognizes in the resulting evolutionarily stable equilibrium a buffer-zone, or a no-wolf's land where deers are known to find refuge. Territories overlap arises as a singular solution. Scent-marking is not yet incorporated into the model. (joint with Mark Lewis)

**Alan Hastings**

### Persistence of structured populations

Many populations are structured by space or stage. We derive a biologically interpretable persistence condition for these systems using ideas from M-matrices. We show that persistence of such a population consisting of subpopulations depends on whether the sum of the reproductive gains through all possible closed, between-patch reproductive paths through multiple generations, relative to the shortfall in self-persistence in each path, exceeds unity. This provides the basis for evaluating connectivity and habitat heterogeneity to understand marine reserve design, the collapse of marine fisheries and other conservation issues and understanding of the dynamics of structured populations. We extend these results to look at conditions for growth rates other than 1 (persistence), and for continuous time models. We also consider particular applications of these results.

**Frank Hilker**

### Epidemiological models with Allee effect

Infectious disease models have traditionally focused on epidemics that run over a relatively short time scale. The host population size can therefore be assumed constant. This talk addresses host populations with a strong Allee effect (i.e., there is a critical threshold size below which population growth is negative). Endemic diseases which lead to a reduction in population size could drive the host below the Allee threshold and thus to extinction. The interplay between infection and demographics can lead to a rich dynamical behaviour, including tristability, limit cycle oscillations and homoclinic bifurcations. Due to the model's structural simplicity, it is amenable to phase plane analysis. The bifurcation behaviour is investigated by numerical continuation. Implications for disease control and conservation management are discussed.

**Petra Klepac**

### Matrix models for stage-classified epidemics

Petra Klepac, Hal Caswell, Michel Neubert

The demographic time-scale is usually very different from the epidemic time-scale, so most models focus either on demographic or epidemic questions. But most infectious diseases affect different stages of the host population in a different way, so the model should incorporate both realistic demographic and epidemic detail. To allow for demographic detail in each epidemic compartment, we have constructed a matrix model by generalizing the vec-permutation matrix approach to spatial models, developed by Hunter and Caswell, to a model that classifies individuals by demographic stage and epidemiological status. We find that the combined matrix model changes the dynamics of its building blocks; a simple demographic model and the basic SIR model, and show how to do sensitivity analysis for such a model.

**Mark Lewis**

**First passage time: insights into animal movement**

Hannah W. Mckenzie, Mark A. Lewis, and Evelyn H. Merrill

Movement plays a role in structuring the interactions between individuals, their environment, and other species. First passage time is a novel way of understanding the effect of the landscape on animal movement and search time. In the context of animal movement, first passage time is the time taken for an animal to reach a specified site for the first time. We derive a general first passage time equation for animal movement that can be connected with empirical data. This equation is related to the Fokker-Planck equation, which is used to describe the distribution of animals in the landscape. To illustrate the first passage time method we consider three examples. First we show how territorial behavior affects the time required for a red fox to locate prey throughout its territory. Second, we discuss the effect of two different searching modes on the functional response and show that random searching leads to a Holling type III functional response. Third we show how detailed GPS data for wolf movement can be coupled to a first passage time model and used to assess the impact of linear habitat features such as roads on the time taken to locate prey. First passage time analysis provides a new tool for studying the influence of animal movement on ecological processes.

**Pierre Magal**

**P-gp transfer and acquired multi-drug resistance in tumors cells**

Pierre Magal, Frank Le Foll, Jennifer Pasquier, Glenn Webb, Peter Hinow

Multi-Drug resistance for cancer cells has been a serious issue since several decades. In the past, many models have been proposed to describe this problem. These models use a discrete structure for the cancer cell population, and they may include some class of resistant, non resistant, and acquired resistant cells. Recently, this problem has received a more detailed biological description, and it turns out that the resistance to treatments is due in 40 of cancers to a protein called P-glycoprotein (P-gp). Moreover it has been proved that P-gp can be transferred from cell to cell by an osmotic phenomenon. This transfers turn to be responsible for the acquired resistance of sensitive cells. The goal of this talk is to introduce this problem, and to present a cell population dynamic model with continuous P-gp structure.

**Andrew Nevai**

**Sluggish susceptibles and the endemic equilibrium in three related disease models**

I will compare and contrast properties of the endemic equilibria in three related SIS disease models. In each model, suspectibles move slower than infectives through spatially heterogeneous habitats.

**Shigui Ruan**

**Travelling Wave Solutions in Multi-group Age-Structured Epidemic Models**

Age-structured epidemic models have been used to describe either the age of individuals or the age of infection of certain diseases and to determine how these characteristics affect the outcomes and consequences of epidemiological processes. Most results on age-structured epidemic models focus on the existence, uniqueness, and convergence to disease equilibrium of solutions. In this paper we investigate the existence of travelling wave solutions in a deterministic age-structured model describing the circulation of a disease within a population of multi-groups. Individuals of each group are able to move with a random walk which is modelled by the classical Fickian diffusion and are classified into two subclasses, susceptible and infective. A susceptible individual in a given group can be criss-cross infected by direct contact with infective individuals of possibly any group. This process of transmission can depend upon the age of the disease of infected individuals. The goal of this paper is to provide sufficient conditions that ensure the existence of travelling wave solutions for the age-structured epidemic model. The case of two population groups is numerically investigated which applies to the criss-cross transmission of certain sexual transmission diseases and feline immunodificiency virus (FIV). (Based on a joint paper with Arnaut Ducrot and Pierre Magal)

**Sebastian Schreiber**

### Persistence of structured populations in random environments

I will present preliminary results on necessary and sufficient criteria for the existence of a positive stationary distribution for discrete time models of the form $x(t+1) = A(\xi(t), x(t))x(t)$ where $A(\xi(t), x(t))$ is a $k \times k$ non-negative matrix depending on the current vector of population densities $x(t)$ and a stationary process $\xi(t)$. Applications to models of spatially structured and stage structured populations will be given. This work is in collaboration with Michel Benaïm.

**Hal Smith**

### Models of Virulent Phage Growth with application to Phage Therapy

We modify existing models of bacteriophage growth on an exponentially growing bacterial population by including (1) density dependent phage attack rates and (2) loss to phage due to adsorption to both infected and uninfected bacteria. The effects of these modifications on key pharmacokinetic parameters associated with phage therapy are examined. More general phage growth models are explored which account for infection-age of bacteria, bacteria-phage complex formation, and decoupling phage progeny release from host cell lysis.

**Rebecca Tyson**

### Modelling the Dynamics of the Canada Lynx and Snowshoe Hare Population Cycle

The population cycle of the Snowshoe Hare (SH) has been a focus of scientific interest for the past century. These populations are characterized by striking high amplitude multi-year cycles with a period of 8-11 years. For many years, the SH cycle was thought to be a classical predator-prey interaction between the hare and the lynx. Existing models have shown the importance of the predator-prey interaction, and have approximately captured many traits of the cycle. None however, have been able to simultaneously capture all of the five main cycle characteristics, namely the maximum population, minimum population, cycle amplitude and cycle period for both the lynx and hare. In particular, models generally predict minimum hare densities that are much higher than those observed in the field. Our first objective is to develop a model of the lynx-hare population dynamics that generates cycles with realistic boreal values for all five cycle probes mentioned above. We then use this model to investigate possible sources of the difference in dynamics between northern and southern hare populations: the northern populations exhibit large multiannual cycles, while the southern populations exhibit little to no cycling. In particular, we study the effect of generalist predation and of habitat fragmentation.

**Hans Weinberger**

### A multi-age-stage fish model

I have been looking at the application of some recent work with Nanako Shigesada and Kohkichi Kawasaki to a multi-age-stage fish model. The idea is to model the situation envisioned by Ricker by a reaction-diffusion system in which there is predation of the juveniles by the adults when the adult population is large. One finds that the system is partially cooperative, in the sense that is is cooperative when the population densities are small, but not when they are large. This fact leads to spreading results of the kind introduced by H.R. Thieme in a 1979 paper on epidemic models. Everything works nicely for the 2-stage model, and I have begun to think about the corresponding 3-stage model with eggs in addition to juveniles and adults.

**Xiaoqiang Zhao**

### Spreading Speeds and Traveling Waves for Non-monotone Integrodifference Equations

The invasion speed is a fundamental characteristic of biological invasions, since it describes the speed at which the geographic range of the population expands. The theory of spreading speeds and monostable traveling waves for monotone semiflows has been well developed in such a way that it can be applied to various discrete- and continuous-time evolution equations admitting the comparison principle. However, there are only a few works on spreading speeds for non-monotone biological evolution systems.

In this talk, I will report our recent research on a class of non-monotone discrete-time integrodifference equation models. We obtain a set of sufficient conditions for the existence of the spreading speed, and the existence and nonexistence of traveling waves. It turns out that the spreading speed is linearly determinate and coincides with the minimal wave speed of traveling waves.

**Huaiping Zhu**
**Modeling the West Nile Virus with corvids and non-corvids**
There have been mathematical modeling studies for the West Nile virus among mosquitoes and avian species. In all of the existing models, the avian species were treated as one family. Also for the first several years since its first appearance in North America, the dead birds, especially the dead American crows due to the infection of the virus were used as an indication of the virus activity in a given region. I will first introduce and summarize the existing models and related results. The surveillance data for West Nile virus in southern Ontario, Canada, suggests that corvids and non-corvids have different infection-induced rates. By taking corvids and non-corvids as multiple-reservoirs hosts and mosquitoes as vector, we propose a single-season ordinary differential equations model to model the transmission dynamics of WNV in the mosquito-bird cycle. The eight-dimensional system of differential equations can have up to 2 positive equilibria. We will study the local stability and bifurcations of the model. The existence of the backward bifurcation gives a further sub-threshold condition beyond the reproduction number for the control of the virus. The existence of the backward bifurcation also suggests that the West Nile virus activity in a given region is initial-size dependent. The result of this study also suggests that even though the dead American crow may not be seen in a given region, there might be still a possibility of an outbreak due to the existence of the non-corvids as a reservoir.

## 3 Scientific Progress and Open Questions

The presentations stimulated lively discussions. These discussions helped to clarify the interaction of space, stage, and time scales. The different approaches that the participants presented allowed for a synthesis of different concepts and methods. Out of these discussions emerged new research challenges (see list below). In addition to the scheduled program, participants spontaneously organized two breakout session:

- Discussion on $R_0$ in stage-structured models. This discussion clarified similarities and differences in threshold values in ecological and epidemiological models.
- Discussion of spatial disease with Allee effect. Importance of demographic factors in epidemic models. Discussion of the strong and weak Allee effect, its mechanistic underpinning and its dynamic consequences (e.g. disease cycles, invasion fronts).

**List of Open Problems:**

1. Theory of Structured Populations
   (a) Unified approach (in which all the classical approaches of linearization and stability analysis work)
   (b) Role and calculation of $R_0$
   (c) Apply sensitivity results and find patterns in biological systems
   (d) Include stochasticity with large deviations
   (e) Blending the abstract and concrete for equations with infinite delay.
   (f) Investigate the effect of quiescent dynamics on the qualitative behavior of a dynamical system
2. Spatial Models
   (a) Include stochasticity in spread models
   (b) Rate of convergence for traveling waves
   (c) Traveling waves and spread rates for nonmonotone systems
   (d) Advance and retreat of population fronts in systems with multiple equilibria
3. Epidemiology and Diseases

(a) Including several serotypes
(b) Vaccination policy when secondary infection can be more harmful
(c) Seasonal forcing in stochastic systems with periodic solutions
(d) How does the disease transmission term influence the dynamics
(e) Final size distribution when $R_0$ is close to one
(f) What is the probability of a disease going extinct after the first outbreak ?
(g) Phage treatment models
(h) Vertical transmission in WNV models
(i) Backwards bifurcations in epidemic models: what features give rise to them ?
(j) Including demographic functions in epidemic models

## 4 Outcome of the Meeting

The workshop fostered new contacts, and collaborations. Participants learned about new techniques. Young researchers had the opportunity to meet experienced colleagues and receive valuable feedback. Mutual future collaborative research visits and workshops were envisioned and discussed. Many participants expressed the wish to continue the spirit of this workshop in future meetings. To demonstrate the impact of the meeting we list some quotes from a survey collected from the participants.

- *For the first time, I truly started to grasp the connections between matrix models and continuous models, epidemic models and predator prey models, delay equations and stage structured models.*
- *Everyone of the workshop was supportive and willing to share their experience and ideas with the more junior researchers.*
- *I am in the process of looking for a postdoc. This was a terrific experience to know what other opportunities there are for research and collaboration in the future. I learned about analytic methods about structured populations, sensitivity analysis, and to formulate age structured models as delay equations.*
- *I began two new projects, resulting from meeting people whom I would not have otherwise met.*
- *I received many useful commends from others after my talk which will improve my future modelling efforts.*
- *I received excellent feedback on first passage time problems (discussed ellipticity of operators and nonlinear averaging of stochastic process) ... will result in improved revision of two current papers.*
- *This is a very valuable meeting for me - my first broad acquaintance with this community.*
- *Increased my overview, which is helpful, among other things, for editorial work.*
- *I am a PhD student and this was my first scientific meeting ever. The research presented is overwhelming, and I am very impressed how friendly and supportive the participants are.*
- *I got into contact with possible future postdocs and arranged possible co-supervision of graduate students.*

The meeting has given impulse to an area that covers topics in mathematics as well as in field biology and that is significant for resource management and preservation and for disease prevention and control. From a strictly mathematical point of view, population dynamics as presented here provides new results and questions in particular in the qualitative analysis of ordinary and partial differential equations, difference equations and stochastic processes. We thank BIRS for this great opportunity and for outstanding hospitality.