Prioriteitenprogramma

Niet Lineaire Systemen

Populatiedynamica

News Letter

A newsletter for the project
'Population dynamics, including epidemiology'
being part of the NWO priority program
'Nonlinear Systems'.

June 18, 1999

Visit the Home Page on:
`http://www.bio.vu.nl/thb/users/nls`

This newsletter will appear once every three months during the course of the project. Its content will mainly consist of announcements of activities, such as seminars and workshops. Moreover, information about foreign visitors being in the Netherlands as part of the program will be given.

To make this newsletter as informative as possible we ask you to let us know about activities that are planned and the date visitors are coming and give lectures. Also addresses of persons (in the Netherlands or abroad) who might be interested in receiving this newsletter are welcome.

All correspondence should be sent to: Bob Kooi
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Contents

Contributions to this newsletter were made by: Bas Kooijman, Hans Metz, Sido Mylius.

1 Editorial

The URL of the home-page for the NLS Population Dynamics and Epidemiology project is: `http://www.bio.vu.nl/thb/users/nls` Activities of the programme as well as useful links are given in a Calendar. You can down-load from this home-page the **Newsletter** (4 issues per year) in PostScript and DVI format. For the time being the newsletter will also be send by ordinary mail.

This home-page will be updated four times a year when also the new newsletter is issued. Only the calendar is updated more frequently. Please do not hesitate to contact for updates, improvements, suggestions and so on.

NLS mail-list

If you want to be notified by email when the NLS homepage `http://www.bio.vu.nl/thb/users/nls/` is updated, please send your:

Name + Title	Name company
Name Dept.	Street + number
Zip-code City	Country
E-mail address	Telephone number
Fax number	

to Karin Uyldert, Vrije Universiteit, de Boelelaan 1087, 1081 HV, Amsterdam or email: (`uyldert@bio.vu.nl`)

2 Wanted OIO

Job description: The ALW researcher has to assist in the development of a bifurcation theory for Evolutionarily Stable Strategies, analogous to the existing bifurcation theory for equilibria of dynamical systems. ESSes are equilibria of the evolutionary process of repeated adaptive gene substitutions. The simplest form of the latter process has been formalized under the name of Adaptive Dynamics. Adaptive Dynamics differ from the more usual dynamical systems in that the state space isn't a smooth manifold but consists of contiguous components of different dimension. Moreover, there sometimes is less differentiability than in the usual bifurcation theory for dynamical systems. This is compensated for by a number of consistency conditions which derive from the population dynamics that underlie the substitution process. Info: Hans Metz (`Metz@rulsfb.Leidenuniv.nl`)

3 Summary of PhD-thesis

Summary of the PhD-thesis by **Sido Mylius** Wednesday May 26th 1999, Email: `mylius@bio.uva.nl`

The Good, The Bad and The Fittest: Evolutionary Games in Structured Populations

Introduction and Outline

The mathematical description of biological evolution by means of natural selection is a multi-faceted subject. Disciplines as widely divergent as population genetics, quantitative genetics, evolutionary ecology, game theory and life-history theory provide various methods to tackle evolutionary questions. In recent decades, evolutionary game theory and the analysis of invasibility, which predict the fate of rare mutant types that are numerically dominated by resident types, have gained solid ground for analysing frequency- and density-dependent selection.

Evolution can be seen as the ongoing ousting of resident types by successful novel mutant strategies. Mutants can invade if their fitness is positive, that is, if they can increase in numbers when introduced in an environment that is set by the resident type. Hence, fitness by definition depends on the prevailing environment, which in its turn is determined by the phenotypic composition of the resident population. Recent developments such as the emerging theory of adaptive dynamics integrate classification schemes of evolutionarily stable strategies in dynamical systems theory. By restricting the attention to clonal genetics, and separating the time-scales of convergence to a population-dynamical attractor and of the generation of new successful mutations, the environmental condition can be expressed in terms of the resident genotype. In this way, invasion functions can be derived that depend on the type of the mutant and on the composition of the resident population. These invasion functions serve, together with mutation, as the generators of the dynamical systems describing the evolutionary process.

This thesis deals with three problems in the framework of evolutionary game dynamics and complex population dynamics, with invasibility analysis as a unifying principle. It consists of three parts, and each part in turn consists of two chapters. The first part deals with evolutionary game dynamics, where the model *Battle of the Sexes* is taken as an example.

It shows that the evolutionary predictions of traditional game-dynamic models, in which the costs and benefits of a strategy are summarized by simple entries from a payoff matrix, may be quite different from models that explicitly consider the mechanisms controlling mating in a structured population. This part stresses the importance of incorporating life-history information in game-dynamic model building. In part two, the semelparous life-history of Pacific salmon is used to illustrate an analysis of invasion in periodically fluctuating populations. Contrary to the steady-state situation, successful invasion can inevitably lead to an attractor switch, causing the expulsion of the former invader. This intriguing example may prove to be the exception to the rule, but in any case underlines the need for precision when defining invasibility of strategies in the presence of multiple attractors. The third part argues that the strategies brought forth by evolution should be defined as strategies that are both non-invasible and attainable. It raises and answers the question whether (and, if so, how) they can also be found by maximizing simple optimization criteria. This part makes yet another plea for more mechanistic model building, emphasizing the significance of the precise way in which density dependence limits population growth.

Part I: Game Dynamics and the Battle of the Sexes

I extend Dawkins' well-known *Battle of the Sexes*, by introducing a population with mating structure. Previous models of the battle of the sexes are mostly formulated in terms of replicator dynamics. They specify dynamical systems on the basis of the payoff matrices of the evolutionary population-game, by assuming that strategies produce copies of themselves, proportional to their average payoff values. In chapter 1, I model the sex war more mechanistically, by expressing the costs of raising the offspring and performing a prolonged courtship via a time delay for the corresponding individuals, instead of via payoff matrices. I assume that during such a time delay, an individual is not able to have new matings. Only after sitting out the delay, can an individual (and its offspring) reappear on the mating market. From these assumptions I derive a pair-formation submodel, and a system of partial- or delay-differential equations describing the dynamics of the game. The dynamical behaviour of this model is shown to be qualitatively different from that of the traditional models of the battle of the sexes.

The pair-formation model can be reduced by a time-scale argument. This idea is developed in chapter 2, where I present an approximation of the delay-differential equations system in terms of ordinary differential equations. This simplified system can be analysed much more thoroughly than the original delay-differential equations system. A combination of analytical and numerical techniques shows that the model can give rise to two non-trivial asymptotically stable equilibrium points: an asymptotically stable interior equilibrium where both female strategies and both male strategies are present, and a stable boundary equilibrium where only one of the female strategies and both male strategies are present. The traditional approaches of modelling the battle of the sexes lead to a unique interior equilibrium, accompanied by cyclic dynamics. My analysis shows that they miss crucial properties of the pair formation-based dynamics. In other words, the addition of an elementary further assumption about individual life history fundamentally changes the model predictions.

In general, I conclude that in analysing evolutionary games one should pay careful attention to the specific mechanisms involved in the conflict, and to derive simple models for evolutionary games, starting from more complex, mechanistic building blocks. The widespread method of modelling games at a high phenomenological level, through payoff matrices, can be misleading. As far as further research is concerned, an interesting extension would be to study the co-evolution of female preference and male willingness. The quasi-steady state population-dynamical equilibria calculated by means of the time-scaled pair-formation submodel can serve as a basis for such an adaptive dynamics.

Part II: Invincibility despite Invasibility

In chapters 3 and 4, I present the analysis of a simple model for the competition between different ages at reproduction of Pacific salmon, focusing on the situation that the resident population numbers have converged to one of several low-periodic attractors. These different local attractors of the resident population dynamics can have different invasion properties.

Well-timed mutant strategies are able to sample the periodically varying environment more efficiently than the resident, and invade successfully when the resident is in certain attractors, whereas they cannot invade in the other attractors. When the mutants are inferior to the resident, in the sense that they have lower viability and/or fertility, they still can invade successfully, provided that the amplitude of the oscillations is high enough. Successful invasion can lead to resonance-mediated co-existence of resident and invader, even if the invader is very inferior to the resident. This also depends on the amplitude of the oscillations, and is impossible when the population is in steady state. On the other hand, for mutants that are less inferior to the resident, successful invasion by a mutant strategy from one attractor will inevitably be followed by extinction of the former invader and concurrent re-establishment of the resident. The expulsion of the invader is accompanied by an invasion-induced attractor switch, or phase shift, of the population dynamics. I call this phenomenon "the resident strikes back". In other words, the invader seems to dig its own grave and the resident strategy is *invasible, yet invincible* by these mutants. After the resident has struck back, other mutants can successfully invade again. It is only on a longer time-scale that this might lead to an intermittent co-existence of superior resident and inferior mutant strategies.

The results show that even in a deterministic setting successful invasion does not necessarily lead to establishment and that mutual invasibility is not always sufficient for co-existence. The interplay of population- and adaptive dynamics might yield wrong predictions about the outcome of competition when based on a steady-state analysis.

Part III: Optimization Principles and Density Dependence

Chapters 5 and 6 deal with the questions which arise when the strategies brought forth by evolution, which we define in terms of non-invasibility, are searched by means of maximizing simple optimization criteria. In other words, when is the fittest (in the environment set by itself) also the best (in a more general sense)?

In chapter 5, I concentrate on monomorphic populations in demographic steady state, and present three different conditions under which the evolutionarily stable life-history strategy can be characterized as the life-history strategy at which a relatively simple function is maximal. Depending on the way density dependence shapes the environmental feedback loop, this function can be the individual lifetime reproductive success (R_0), the intrinsic rate of natural increase (r), or another quantity from a large range of possible optimization criteria. I illustrate this by examining the optimal age at maturity for a hypothetical example organism, showing that the details of the population dynamical embedding may influence our evolutionary predictions to an unexpected extent. This analysis is extended in chapter 6, where I derive necessary and sufficient conditions for the equivalence between non-invasible strategies and maxima of optimization functions.

These results show that optimization functions should be *derived*, using all information available about the precise way in which density dependence limits population growth, instead of *assumed*, as is common practice in evolutionary ecology and life-history theory. If we want to assess the validity of prevalent optimization functions, more empirical research on mechanisms of density dependence is of crucial importance.

Taken together, the six chapters demonstrate that it pays to incorporate detailed information concerning individual life-history or population dynamics in an early stage of evolutionary model building. By taking biologically validated approximations, one can still end up with simple models, but with qualitatively different results than from models arrived at in more phenomenological ways.

4 Report on the minisymposium on Adaptive Dynamics

reported by Hans Metz.

This minisymposium was on the occasion of Sido Mylius' Ph.D. defense, May 26, 1999, at the van der Klaauw Laboratory in Leiden, organised in cooperation with the Netherlands Society for Theoretical Biology (NVTB), and the Institute for Evolutionary and Ecological Sciences (EEW) in Leiden.

The first speaker, **Regis Ferriere** (Ecole Normale Superieure de Paris) presented some results obtained by him and Ulf Dieckmann on the simultaneous evolution of cooperativity and dispersal, using the pair approximation methods developed by David Rand and Minus van Baalen (see e.g. the chapter by David Rand in J. MacGlade (1999) *Advanced ecological Theory*, Blackwell Science, and the chapter by Minus van Baalen in U. Dieckmann, R. Law & J.A.J. Metz (1999) *The Geometry of Ecological Interactions: Simplifying Spatial Complexity*, Cambridge University Press). The main outcome was that if only altruism evolves, it moves to some positive level which decreases (eventually to zero) with increasing dispersal rate. If both parameters are allowed to evolve altruism initially increases (or decreases depending on the initial condition), to the value set by the current dispersal rate, whereupon the dispersal rate starts to increase and the the altruism to decrease on a much slower time scale. The difference in time scales reflects the differences on selective pressure which in the case of the dispersal rate is mainly indirect. For other values of the parameters there also was a possibility for evolutionary branching (characterized by an inequality reminiscent of Hamilton's rule!) which still needs further exploration.

The second speaker, **Sido Mylius** (sectie Populatiebiologie, UvA), explained how the invasion by a mutant may result in a jump between population-dynamical attractors resulting in the invader being ousted again, for which he coined the phrase: The Resident Strikes Back. The most intriguing case occurred in a model originally devised to study the evolution of the return to the spawning grounds of Pacific salmon. Here a population of individuals reproducing in their third year may be invaded by individuals reproducing in their fourth year even when the product of the incurred mortality over the years and the basic fertility of the latter is smaller, and the competition, assumed to occur only upstream, is fully symmetrical. The point is that the 3-year salmon may oscillate in density in such a manner that 4-year salmon invading at the right phase of the oscillation sample a majority of low-density years, where the 3-year salmon always sample equal proportions of good and bad years. However, the introduction of the 4-year salmon produces a phase shift in the oscillation such that from then on the 4-year salmon actually sample a majority of bad years. In other words, the 4-year invader seems to dig its own grave and the 3-year resident strategy is invasible, yet invincible. He further analysed this problem using a toy-model of 1-year and 2-year salmon that he could analyse in great detail. This way he could analyse the transition to the resident-strikes-back scenario by way of a heteroclinic bifurcation.

The third speaker, **Karl Sigmund** (Institut für Mathematik, Universität Wien), started by classifying two strategy games on the basis of the relative sizes of the pay-offs, in a small number of qualitative equivalence classes. Within this framework he then considered repeated games and strategies with particular simple sorts of memories, for which the strategy for the next move is set by the outcomes of the previous move relative to some aspiration level, plus some updating rule for the aspiration level, also depending on the outcome of the moves and the present aspiration level. First he showed results for the case of fixed aspiration levels, with an emphasis on when such aspiration levels can lead to good outcomes when once in a while, but only rarely, a player mistakenly makes a wrong move. As a next step he considered the class of convex update rules, where the new aspiration level is set by a convex combination of the present aspiration level and a perceived pay-off. He only had full results for the two extreme cases, to wit a full switch to the received pay-off (or of the pay-off received by the opponent) or a small adaptation. In the latter case the time-evolution of the system can be approximated by a differential equation (or rather a differential inclusion) with a piecewise constant right hand side. In the former case the problem can be analyzed by combinatorial and Markov chain methods. One intriguing outcome was that envy, i.e., set your aspiration level equal to what your opponent got, can actually lead to a rather good overall pay-off.

The last speaker, **Odo Diekmann** (Mathematisch Instituut, UU), discussed the case of the missing year classes: when can in a semelparous organism maturating at age exactly k, a population dynamics be such that the dynamics with only one year class present is uninvadable by other year classes. To this end he further analysed a model first conceived by Michael Bulmer in order to analyse the periodic cicada problem. The main feature of the model is that all interactions take place through a single variable I, a weighted (and gauged to include some basic, environment independent, survival probabilities) sum of the population sizes in all year classes. In good Ricker tradition this variable then feeds through in an exponential manner to the survival of the year classes (and/or multiplicatively to the reproduction), with a different sensitivity for each year class, like $\exp[-gI]$, with g the, year-class specific, sensitivity. For the simplest case of $k = 2$ he could fully analyze this model, provided the basic reproduction ratio is sufficiently small so that no complicated dynamics occurs. It turns out that there was a nice complete dichotomy where there exists either an interior equilibrium with both year classes present, or the boundary equilibrium with only one year class present is uninvadable. The latter case i.a. occurred when the two weights decreased with age and the sensitivities increased with age. The full necessary and sufficient conditions were a little more complicated, but could be written as explicit inequalities in the parameters. The weaker result that the fulfilment of two ordering rules in opposite direction for the weights and sensitivities precludes an invasion by the missing year classes holds true in general for arbitrary k.

5 Report of visit Konstadia Lika

reported by Bas Kooijman.

Konstadia Lika (Dept of Biology, University of Crete) visited the Dept. of Theoretical Biology of the Vrije Universiteit (22-27 March 1999) within the framework of the NWO priority program NLS. She worked for 6 years with Tom Hallam (Knoxville, Tennessee), and 2 years with Roger Nisbet (Santa Barbara, California), on Dynamic Energy Budgets of the production type. In this class of models, maintenance requirements are first subtracted from assimilation, before allocation to growth and/or reproduction. Kooijman is working on assimilation models, where assimilation feeds a buffer that is subsequently used for maintenance, development, growth and reproduction. She will talk about this work in the coming TMBM99 conference in Amsterdam. She worked with Kooijman on the comparison of reproduction in animals that sport determinate or indeterminate growth. The topic originated from Roger Nisbet, who suggested that animals that allocate a constant fraction of energy made available from reserves to maintenance plus growth (standard assumption in DEB model), would soon be out-competed by animals that first grow and then reproduce. The analyses by Like and Kooijman show that this is not true; the reverse is to be expected in practice. They are working on a paper with the following provisional title:

Life history implications of allocation to growth versus reproduction in Dynamic Energy Budgets

Abstract: We compare the implications of determinate versus indeterminate growth of a parthenogenetic iteroparous ectotherm at constant food density in the context of the Dynamic Energy Budget theory, which specifies the tight links between life history traits, such as feeding, aging, growth and reproduction. The allocation of a constant fraction of the catabolic power to somatic maintenance and growth leads to a higher life span reproduction and a longer life span, while a bang-bang allocation leads to a higher reproduction just after maturation, and a higher population growth rate. We suggest an evolutionary link between allocation strategies and expected life span.

6 Calendar

29 June- 3 July, 1999

Final Announcement: Theory and Mathematics in Biology and Medicine 1999 Vrije Universiteit Amsterdam, The Netherlands June 29 - July 3, 1999.
Invited lectures by:

Prof. Karl P. Hadeler (Tuebingen University, Germany) Competition, Variability, and Exclusion: Elimination of some and survival for many.
Prof. Dr. Bruce R. Levin (Emory University, USA): Mathematical models of the within and between host population biology of antibiotic treatment and resistance
Prof. Dr. Karl Sigmund (University of Vienna, Austria) Reciprocal altruism, direct and indirect
Prof. Dr. Bela Novak (Technical University Budapest, Hungary) Modelling the cell division cycle
Prof. Dr. Eshel Ben-Jacob (Tel-Aviv University, Israel) Bacterial wisdom and the challenge of antibiotic resistance
Prof. Dr. Lila Kari (The University of Western Ontario, Canada) DNA computing in vitro and in vivo
Honorary lecture by the laureate of the first Prof. Akira Okubo award: Prof. Martin W. Nowak (Institute for Advanced Study, Princeton, USA)

Martin Nowak studied Biochemistry and Mathematics at the University of Vienna where he received his Ph-D (sub auspiciis praesidentis) in 1989. His Diploma thesis was with Peter Schuster on quasi-species theory, his Ph-D thesis with Karl Sigmund on evolution of cooperation. In 1989 Nowak moved to Oxford where he held Junior Research Fellowships at Wolfson College and Keble College and later became a Wellcome Trust Senior Research Fellow and Professor of Mathematical Biology. In his various collaborations with Robert May, he worked on HIV, other viruses, the immune system, the evolution of virulence, metapopulation dynamics, 12log2-8, spatial games, prions and the meaning of life. In 1998, he moved to Princeton to head the first initiative in Theoretical Biology at the Institute for Advanced Study

Registration Registration is possible through our web-site. You can find the instructions on the following web-site: `http://www.bio.vu.nl/tmbm99`

Important Addresses

- For the most complete source of the latest information: The conference web-site `http://www.bio.vu.nl/tmbm99/`
- For answers to some Frequently Asked Questions: `http://toranaga.bio.uva.nl/~aroos/tmbm99-faq.html`
- For information concerning registration, abstract forms, etc.:

VU Conference Service	Phone :	+31-(0)20-4446790
De Boelelaan 1105	Fax :	+31-(0)20-4445825
NL 1081 HV Amsterdam	Email :	`vu_conference@dienst.vu.nl`
The Netherlands		

- For contacting the organising committee: e-mail: `tmbm99@bio.vu.nl`

July 14 - 19, 1999

Biomathematics - Bioinformatics and Applications of Functional Differential Difference Equations Akdeniz University, Antalya, Turkey, July 14 - 19, 1999.

The conference on the Theory of Difference and Differential Equations with Applications to Biology and Medicine aims to stimulate collaboration between mathematicians and bioscientists and to act as a forum for the exchange of recent research results and new perspectives in those fields. In addition, the conference is devoted to a rapidly growing, interdisciplinary domain of science where experimental biology and medicine, biochemistry, functional differential and difference equations, stochastic functional differential equations and stochastic processing, functional analysis, evolution equations, operator theory, computational mathematics, and various fields of technology all come together.

Scientific program The scientific program will include one-hour plenary lectures, half-an-hour lectures and poster contributions. We also plan to publish the Conference Proceedings. The conference will cover the theory of difference and differential equations with applications to related disciplines within Biology and Medicine, including immunology, epidemiology, evolution, population dynamics and ecology, molecular biology, cell signalling, tumour growth and treatment, metabolic modeling, neuromodeling, computational biology, cardiovascular modeling, and biomechanics.

Information:

Haydar Akca , King Fahd University of Petroleum and Minerals, Mathematical Sciences Department P.O.Box 1071 Dhahran 31261 Saudi Arabia

Telephone:	966 3 860 2279	(Office)
	966 3 860 6377	(Home)
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e-mail :	`akca@kfupm.edu.sa`	

13-17 December 1999 and 17-21 January 2000

Mathematical methods in oceanology deterministic and stochastic approaches. Marseilles - France.

Information:

Jean-Christophe Poggiale	Email : `poggiale@com.univ-mrs.fr`
C. d'Ocanologie de Marseille	Laboratoire d'Ocanographie et de Biogochimie
Campus de Luminy	13288 Marseille Cedex 09
France	`http://www.com.univ-mrs.fr/LOB/colloque/intro.html`

January 5-9, 2000

Third Winter school on Population Dynamics Woudschoten, The Netherlands, January 5-9, 2000.

Please feel free to pass this message on to anyone you think would be interested in modelling population dynamics.

This will be the third edition of this event, organised by Odo Diekmann, Hans Heesterbeek, Fleur Kelpin and Bob Kooi. The previous schools in January 1996 and January 1998 each attracted more than 50 PhD-students from a broad range of countries and population biological subjects. Reports by participants about these schools can be found in the BioMathematical Newsletter 13 and BMN 17.

As in the previous editions we emphasise the word 'school' and aim to give PhD students in population biology a good understanding of the way mathematics is applied to study problems in their field as well as a thorough background in relevant deterministic and stochastic mathematical techniques. Five lecturers who will each give a series of 4 or 5 lectures. These lecture series start at an elementary level and connect to recent research topics towards the end. Basic techniques receive attention, and lecture notes accompany the presentation.

In addition we retain a successful part of the 1996 and 1998 editions in that participants team up in small groups around one or two papers of their choice from a list we provide. The papers cover the same areas as the lecture topics but go beyond the basic material. We look for stimulating and challenging papers that are allowed to be more difficult than usual, provided they have a rewarding message once you understand them. The groups then study these papers together during several periods of a few hours scattered throughout the week (the idea being that five know more than one and one learns to read more advanced papers). On Saturday one person from each group then gives a short presentation about the findings, ideas, criticism, comments etc.

The speakers are:

Fred Adler	ecology and evolution
Rob de Boer	immunology, virology
Bas Kooijman	dynamic energy budgets, ecotoxicology
Roger Nisbet	stage structured populations, numerics and applications
Horst Thieme	mathematics of physiologically structured population models

More details will be announced in the next issue of the newsletter. Registration forms will become available in early 1999. If you wish to be put on a preliminary list of participants, please send an e-mail with your details (including area of research) to Fleur Kelpin at the address below. There is a limit of 55 participants.

Information:

Fleur Kelpin	Email : `fleur@bio.vu.nl`
Theoretical Biology	Vrije Universiteit
De Boelelaan 1087	NL 1081 HV Amsterdam
The Netherlands	`http://www.bio.vu.nl/thb/users/nls`

August 23-27, 2000

Second international conference on deterministic and stochastic modeling of biointeraction

Information:

Fabio Augusto Milner	Email : `destobio@math.purdue.edu`
West Lafayette, Indiana, USA	`http://www.math.purdue.edu/~milner/DESTOBIO_2000.html`