

1994 SECTION 1 THEORETICAL BIOLOGY

Section Chair: Prof.dr. J.A.J. Metz

The Section designs unifying frameworks as well as mathematical tools for studying evolutionary and ecological problems, both on an a priori basis and in close cooperation with experimental groups. The research ranges from exploring the consequences of established biological theories to the construction of models for specific biological systems, the latter often with a view to develop data - analytical techniques. In addition the section investigates the nature of key biological concepts, both with a narrow biological focus, and seen against the context of their societal embedding.

Project 1.94.1. Mathematical foundations of individual-based population models.

Heads: Prof.dr. O. Diekmann, Prof.dr. J.A.J. Metz.

Description: The design and examination of mathematical formalisms for stepping from the physiological/behavioural levels to the description of changes in population densities.

Progress: A number of technical aspects have been elucidated of the general mathematical formalism, based on cumulative numbers of births, for the description of physiologically structured populations living in variable environments.

A comparison of a concrete stochastic individual-based model, a continuum approximation of that model, and an approximation by a trait substitution sequence, or "adaptive dynamics", has contributed towards elucidating the conditions under which the various modelling approximations should be applicable. Luckily the adaptive dynamics type models turned out to do a good job.

Project 1.94.2. Population dynamics

Heads: Prof.dr. O. Diekmann, Prof.dr. J.A.J. Metz.

Description: Investigation and classification of the types of dynamical behaviour of populations in dependence on the underlying mechanisms.

Progress: Motivated by the spread of Phocine Distemper Virus among seals, a collection of epidemiological models has been analyzed in which the transmission speed was assumed to be independent of the, changing, population density. This has led to new quantitative insights concerning the relation between mechanisms for the transmission of infection and the total size of an epidemic.

It has been shown by means of a simple spatially structured model for predator prey interactions, that increasing the carrying capacity of the prey need not lead to large fluctuations in the population densities (and therefore to a high risk of extinction of the predator), this in contrast to the spatially unstructured case.

It has been shown that the model for the "battle of the sexes" mentioned in the 1993 Report (under 1.93.3) allows a, fairly representative, limiting case which can be described by but two coupled differential equations and therefore can be analyzed with relative ease.

Project 1.94.3. Adaptive dynamics

Heads: Prof.dr. O. Diekmann, Prof.dr. J.A.J. Metz

Description: The investigation of the process of trait substitutions resulting from the selective filtering of mutational variation, with particular reference to the characterization and classification of singular points such as branching points and Evolutionarily Stable Strategies.

Progress: The heuristic development of an axiom system for adaptive dynamics, mentioned in the 1993 report, has been brought a little further towards a mathematically acceptable end. This has led to sharper insights into a number of points, i.a. about the population dynamically justifiable continuity assumptions about the dependence of the fitness of a mutant type on both its own trait values and the trait values of all the resident types.

A simple model for the evolution of life histories was analyzed for various assumptions about the feedback through the environment to the demographic parameters. It turns out that the population dynamical embedding is more important in determining the ESS life history parameters than is customarily acknowledged.

Project 1.94.4. Phylogeny-reconstruction and analysis of historically associated lineages.

Head: Dr. M.Zandee.

Description: Development of theory, methods and data-analysis in systematical biology, based on the cladistic method.

Progress: In cooperation with H. Turner (RHHB) the behaviour of Goloboff's tree-fitness was investigated and a more effective fitness-measure proposed. ("The behaviour of Goloboff's tree fitness measure F". Ms submitted to and accepted by Cladistics).

Project 1.94.5. Study of the separate effects of evolutionary optimisation and phylogenetic constraints on the variation in behaviour within groups of related species

Heads: Dr. P. Haccou, Dr. M.R. Zandee.

Description: Development of optimality models of behaviour in general, specifically applied to parasitoids of the genus *Leptopilina*. Study of the relationship between phylogeny and behavioural strategies.

Progress: Ir. J. v. Velzen has been appointed (AIO) on 1st July. He started reading the extensive literature. It was proved that in randomly fluctuating environments sequential invasions have a much higher chance of success than simultaneous ones, which has consequences for studies of meta-population dynamics, calculation of optimal life history strategies and biological control programs.

It was shown that mixed strategies with large variances do relatively well in a wide range of stochastic environments. This result indicates that the interpretation of the often-observed variance in behavioural strategies should be reconsidered.

Project 1.94.6. Analysis of speciation through partial reproductive isolation

Head: Dr. F.H.D. van Batenburg.

Description: Analysis of the influence of partial reproductive isolation upon speciation using simulation models.

Progress: just started.

Project 1.94.7. Development of methods for predicting the secondary structure of RNA.

Head: Dr. F.H.D. van Batenburg.

Description: Development of theory, methods and computerprograms for the deduction of the secondary structure of RNA from data on the primary structure.

Progress: It is found that our newly developed algorithm mimics the folding pathway rather than "just computing the final secondary structure". This opens possibilities for research that were impossible previously.

Project 1.94.8. Analysis of the effects of human activities on the development of ecological systems.

Head: Drs. E. Meelis.

Description: Development of methods for the analysis of environmental monitoring data.

Progress: For three monitoring situations of increasing complexity a sequential test has been developed by application of the minimax principle. The result has been applied to a simple practical example.

Project 1.94.9. Relation between reductionist and non-reductionist approaches within biology.

Head: Dr. Th.E. Sprey.

Description: Research into the importance of structuralist and phenomenological approaches for biology, and for the role of biology within society, for instance in relation to the discussion about basic attitudes and the environmental crisis.

Progress: The interaction between structuralists and phenomenologists was intensified in the preparation of a workshop in 1995.

Project 1.94.10. Biological science and the relation between man and nature/animals.

Head: Dr. H. Verhoog.

Description: Analysis of the human (biologist's) attitude and relation towards nature, and the implications of biological thinking for our concept of man.

Progress: A paper was presented at an international conference and a research proposal was written about the moral relevance of 'naturalness'.

Project 1.94.11. Development of the concept of composite species

Head: Prof.dr. D.J. Kornet.

Description: Formal reconstruction of the species concept, especially the determination of species boundaries in the time dimension.

Progress: The mathematical proof that a particular relation INT indeed partitions genealogical networks exhaustively into mutual exclusive entities was refined. Thereby came to light a general validity of the method developed. In addition research is carried out on (a) The structure of the programming language APL

(b) Development of methods for the analysis of behavioural data

STAFF

Prof.dr. O. Diekmann	full professor	Leiden University
Prof.dr. J.A.J. Metz	full professor	Leiden University
Dr. F.H.D. van Batenburg	assistant professor	Leiden University
Dr. P. Haccou	assistant professor	Leiden University
Drs. E. Meelis	assistant professor	Leiden University
Dr. Th.E. Sprey	assistant professor	Leiden University
Dr. H. Verhoog	assistant professor	Leiden University
Dr. M. Zandee	assistant professor	Leiden University

Postdocs

Dr. P. Haccou	researcher	KNAW
Dr. J. Val	researcherš	NWO

Junior investigators

Dr.ir. V.A.A. Jansen	research assistant	Leiden University
Drs. M.J.P. Maas	research assistant	Leiden University
Drs. F.S.A. Jacobs	research assistant	Leiden University
Ir. J. v. Velzen	research assistant	Leiden University
Drs. M. Schipper	research assistant	Leiden University
Drs. S.A.H. Geritz	research assistant	Foundation for Life Sciences
Drs. S.D. Mylius	research assistant	Foundation for Life Sciences

Analytical, technical and administrative staff

H. Regeer - Groenhuijzen	secretary	Leiden University
Y.M. Zitman - de Graaf	secretary	Leiden University

Guests

Drs. W.M.A. Bressers	researcher	volunteer
Prof.dr. P. Dullemeijer	researcher	volunteer
Drs. S.A.H. Geritz	researcher	volunteer

Dr. S. Gulyaev	researcher	NWO/EMBO
Dr.Ir. V.A.A. Jansen	researcher	volunteer
Dr. D.J. Kornet	researcher	volunteer
Dr. M.J. Sjerps	researcher	Ger.lab.È?È?Y
Drs. J. Verboom	researcher	IBN
Dr. M.B.H. Visser	researcher	volunteer
Dr. F. Wemelsfelder	researcher	volunteer

COOPERATIONf

(projectcodes are indicated between brackets)

Leiden

- RHHB, RUL, Prof.dr. C.G. Kalkman (1.94.11)
- RHHB, RUL, Dr. P.C. van Welzen (1.94.4)
- vg. Biochemie RUL, Dr. C. Pley (1.94.7)
- Medische Fac. RUL, Prof.dr. Tj. de Cock Buning (1.94.10)
- Medische Fac. RUL, vg. šEthofarmacologie, Dr. M.R. Kruk (b)
- Fac. Wijsbegeerte RUL, Dr. J.W. McAllister (1.94.11)

National

- Amsterdam, CWI, Drs. Th. Hantke (1.94.2)
- Amsterdam, CWI, Drs. A. de Koeyer (1.94.2)
- Amsterdam, UvA, Prof.Dr. S.A.L.M. Kooijman ontbreekt jv 1993 en 1994
- Amsterdam, CWI, Dr. Yu.A. Kuznetsov (1.94.2)
- Amsterdam, vg. Zuivere en Toegepaste Oecologie UvA, Dr. A.M. de Roos (1.94.1/2)
- Amsterdam, vg. Zuivere en Toegepaste Oecologie UvA, Prof.dr. M.W. Sabelis (1.94.2/3)
- Amsterdam, UvA, Dr. S.M. Verduijn Lunel (1.94.1)
- Amsterdam, vg. Theoretische Biologie VU, Drs. C.v.d. Weele (1.94.9)
- Bakkeveen, Volkshogeschool Allardsoog, G. Wring (1.94.9)
- Bilthoven, RIVM, Dr. E.J.M. Veling (1.94.2)
- Bilthoven, RIVM, Dr. M. Kretzschmar (1.94.2)
- Den Haag, BSO (ASWI standaards), Drs. H. van Loon (a)
- Driebergen, Vrije Hogeschool, B. Siepman v.d. Berg (1.94.9)
- Eindhoven, Reuter (ASWI standaards), Drs. L. van Geldrop (a)
- Enschede, TU Twente, Dr. S.A. van Gils (1.94.2)
- Enschede, TU Twente, ASWI, Ir. F. Bonnema (a)
- Leersum, IBN DLO, Dr. P. Opdam (1.94.2)

- Lelystad, CDI - DLO, Dr. M.C.M. de Jong (1.94.1/2)
- Lexmond, Adfee (ASWI standaards), B. Smoor (a)
- Texel, IBN - DLO, Dr. P.J.H. Reijnders (1.94.2)
- Wageningen, vg. Fytopathologie LUW, Prof.dr. J.C. Zadoks (1.94.2)
- Wageningen, Alternatieve Landbouw LUW, J.D. van Mansvelt (1.94.9)
- Wageningen, Alternatieve Landbouw LUW, W. Beekman (1.94.9)
- Wageningen, vg. Wiskunde LUW, Dr. F. v.d. Bosch (1.94.2)
- Wageningen, Dienst Landbouw, wiskunde - DLO, Dr. J.A.P. Heesterbeek (1.94.2)
- Wageningen, IBN CBS, Dr. A.J. van Strien (1.94.8)

International

- Ascot, UK, Imperial Coll./NERC Centre for Pop. Biol., Dr. H.C.J. Godfray (1.94.3)
- Ascot, UK, Imperial Coll./NERC Centre for Pop. Biol., H. Wilson (1.94.3)
- Bristol, UK, Dept. Mathematics Univ. of Bristol, Dr. J. McNamara (1.94.5)
- Glasgow, UK, Univ. of Strathclyde, Dr. D. Greenhalgh (1.94.2)
- Milton Keynes, UK, Open Univ., Prof.dr. B.C. Goodwin (1.94.9)
- York, UK, University of York, Dr. R. Law (1.94.3)
- Boedapest, Hongary, Eo?Àtvo?Às University, Dr. À(?À. Kisdi (1.94.3/5)
- Boedapest, Hongary, Eo?Àtvo?Às University, Drs. G. Meszena (1.94.3)
- Boedapest, Hongary, Eo?Àtvo?Às University, Dr. L. Pasztor (1.94.3)
- Diepenbeek, Belgium, Limburgs Universitair Centrum, Drs. E. Nuyts (1.94.3)
- Fukuoka, Japan, Kyushu Univ., Prof.dr. Y. Iwasa (1.94.5)
- Hanoi, Vietnam, Univ. of Hanoi, Dr. Nguien Ba (1.94.9)
- Jerusalem, IsraÀ-?Àl, Hebrew University, D. Cohen (1.94.3)
- JÀG?Àlich, Germany, Forschungszentrum JÀG?Àlich, Drs. U. Dieckmann (1.94.3)
- Lyon, France, Dr. C. Bernstein (1.94.5)
- Paris, France, À(?Àquipe de Logique MathÀ)?Àmatique, Univ. Paris VII, Dr. H.A.J.M. Schellinx (1.94.11)
- Milaan, Italy, Politecnico di Milano, M. Gatto (1.94.3)
- Prague, TsjechiÀ-?À, Filosofie Natw., Dr. S. Neubauer (1.94.10)
- Prague, TsjechiÀ-?À, Filosofie Natw., Dr. S. Komarek (1.94.10)
- Santa Barbara, USA, Univ. of California, Prof.dr. R.M. Nisbet (1.94.1)
- Stanford, USA, Stanford University, Prof.dr. S. Tuljapurkar (1.94.5)
- Tempe, USA, Arizona State Univ., Dr. H.R. Thieme (1.94.1)
- Tucson, USA, Univ. of Arizona, Drs. R. FerriÀ/?Àre (1.94.1/3)

- Toronto, Canada, Dept. Zoology Univ. Toronto, Prof.dr. D.R. Brooks (1.94.4)
- Turku, Finland, Math. Inst. Univ. of Turku, Prof.dr. M. Gyllenberg (1.94.1)
- Vancouver, Canada, Simon Fraser University, Prof.dr. B. Roitberg (1.94.5)
- Wenen, Austria, Institut für Mathematik, K. Sigmund (1.94.3)

PUBLICATIONS

- FHD van Batenburg Creating the APL extended standard. APL Quote Quad 25: 21 (a)
- FHD van Batenburg et al. ASWI programming standards for APL programs. APL - Cam 16: 567 - 584 (a)
- FHD van Batenburg APL94 workshop "Programming style and APL". APL - CAM 16: 552 - 560 (a)
- FHD van Batenburg Restriction riddance: more power to parentheses. APL Quote Quad 25: 220 - 224 (a)
- FHD van Batenburg APL complaints (out) of control. APL Quote Quad 24: 36 - 37 (a)
- F van den Bosch, JC Zadoks, JAJ Metz Continental expansion of plant disease: A survey of some recent results. In: J Grasman and G van Straten (eds.), Predictability and Nonlinear Modelling in Natural Sciences and Economics. Dordrecht, Boston, London, Kluwer Acad. (1.94.2)
- IC Cuthill, P Haccou, A Kacelnik Starlings ("Sturnus vulgaris") exploiting patches: response to long - term changes in travel time. Behavioral Ecology 5: 81 - 90 (1.94.5)
- O Diekmann, M Gyllenberg, JAJ Metz, HR Thieme The 'cumulative' formulation of (physiologically) structured population models. In: P Clément and G Lumer (eds.) Evolution equations, control theory, and biomathematics. Lecture notes in pure and applied mathematics vol. 155, New York, Marcel Dekker, Inc. p. 145-154 (1.94.1)
- O Diekmann, JAJ Metz On the reciprocal relationship between life histories and population dynamics. In: SA Levin (ed.) Frontiers in Mathematical Biology, Springer Lecture Notes in Biomathematics 100 (1994): 263 - 279 (1.94.1)
- AP Gulyaev, E van Batenburg, CWA Pleij Similarities between the secondary structure of satellite tobacco mosaic virus and tobamovirus RNAs. Journal of General Virology 75: 2851 - 2856 (1.94.7)
- P Haccou, E Meelis Statistical analysis of behavioural data. Paperback ed. (1994) Oxford University press, 396 pp. (b)
- Y Iwasa, P Haccou ESS emergence pattern of male butterflies in stochastic environments. Evolutionary Ecology 8: 503 - 523 (1.94.5)
- MCM de Jong, O Diekmann, JAP Heesterbeek The computation of R_0 for discrete - time epidemic models with dynamic heterogeneity. Math Biosci 119: 97 - 114 (1.94.2)
- PGL Klinkhamer, TJ de Jong, JAJ Metz Why plants can be too attractive - a discussion of measures to estimate male fitness. J Ecol 82: 191 - 194 (1.94.3)
- JAJ Metz, P Haccou, E Meelis On the Shapiro - Wilk test and Darling's test for exponentiality. Biometrics 50: 527 - 530 (b)
- E de Ridder, E van Batenburg APL & the Halstead analysis. APL CAM 16: 421 - 423 (a)

MJ Sjerps, P Haccou A war of attrition between larvae on the same host plant: stay and starve or leave and be eaten? *Evolutionary Ecology* 8: 269 - 287 (1.94.5)

MJ Sjerps, P Haccou Effects of competition on optimal patch leaving: A war of attrition. *Theor Popul Biol* 46: 300 - 318 (1.94.5)

ThE Sprey General generative principles: A phenomenological study. *Acta biotheoretica* 41 (1993): 481 – 494 (1.94.9)

H Verhoog Animals in education and the structure of science. *Global Bioethics* 6 (1993): 177 - 185 (1.94.10)

H Verhoog Reduktionistisches und Organisches Denken in der Wissenschaft. In: R Amons et al. (Hrsg.) *Genmanipulation an Pflanze, Tier und Mensch* (1994) 23 - 48. Stuttgart, Verlag Freies Geistesleben. (1.94.9)

H Verhoog Ecologie in het spanningsveld tussen gegeven en gemaakte natuur. *Econieuws* 22: 1 - 9 (1.94.10)

DISSERTATIONS

MJ Sjerps ESS's at different life stages applied to the cinnabar moth. Promotores: Prof.dr. J.A.J. Metz, Prof.dr.

E.v.d.Meijden, copromotor, Dr. P. Haccou, Leiden University, 146 pp. (1.94.5)

VAA Jansen Theoretical aspects of metapopulation dynamics. Promotor: Prof.dr. O. Diekmann en Prof.dr.ir.

M.W. Sabelis. Leiden University, 125 pp. (1.94.2)

E Nuyts Modelling in behavioural ecology: the optimal copulation duration in insects and the fighting strategy in the black - headed gull. Promotor: Prof.dr. J.A.J. Metz en Prof.dr. E. Schockaert. Limburgs Universitair Centrum, Diepenbeek, België, 183 pp. (1.94.3)

INVITED LECTURES

O Diekmann Reflections on structured population model. Séminaire Aubin - Frankowska, Paris France, Februari

7

O Diekmann The cumulative formulation of structured population models. NLS population dynamics, seminar, VUA, Amsterdam The Netherlands, March 11

O Diekmann On biological populations and semigroups of operators. Belgisch - šNiederšndischšNordrheinwestfšlisches Sonderkolloquium, Köln Germany, April 22

O Diekmann On biological populations and semigroups of operators. Operator Theory Day, TUD, Delft The Netherlands, April 29

O Diekmann Semigroups of operators describing biological populations. 4th International Conference on Evolution Equations and Semigroups, Pisa Italy, October 1

O Diekmann Semigroups of operators describing biological populations. Mathematical Analysis Seminar, Charles' University, Prague Czechie, November 2

O Diekmann Reflections on contact structure, Mathematical Models for Infectious Diseases. Oberwolfach Germany, November 30

P Haccou Analysis of behavioural data, based on time - structured models. 2nd International Conference on Social Science Information Technology, Amsterdam The Netherlands, December 7 - 9

JAJ Metz Adaptive dynamics. Math. Institute, Warwick UK, February 16

JAJ Metz, JJM van Alphen Have theoreticians taught us something about evolution? Symposium opening Van der Klaauwlaboratory, Leiden The Netherlands, April 22

JAJ Metz Adaptive dynamics. Ecole de Physique, Les Houches France, May 12

JAJ Metz Ecology and the adaptive generation of evolutionary trees. Med. Campus, Pau France, October 24

JAJ Metz Ecology and the adaptive generation of evolutionary trees. 3rd Annual Symposium EEW, Leiden The Netherlands, November 17

M Schipper Sequentiële analyse van meetgegevens: een eenvoudig voorbeeld. Centraal Bureau voor de Statistiek, Voorburg The Netherlands, September 28

TMH Verhoog Ecologie in het spanningsveld tussen gegeven en gemaakte natuur. Symposium Ned. Ecologen

Vereniging over De Milieucrisis en de Grondslagen van de Ecologie, Amsterdam The Netherlands, February 4

TH Verhoog Ethiek en het maakbare dier. Schouwburg Middelburg, February 18

H Verhoog Reading in the book of nature, From stewardship to partnership with nature. Symposium Agriculture and Spirituality, LUW, Wageningen The Netherlands, March 9

H Verhoog Ecologie en Eco - sofie, Stafcolloquium EEW, Leiden The Netherlands, April 27

H Verhoog The social responsibility of ecologists. Paper, EASST - conference Science, technology and change, Budapest Hungary, August 28 - 31

MBH Visser Autonomy and Personal Integrity as an Expression of Intrinsic Value in the Human – Animal Relationship. 10th World Congress on Medical Law, Jerusalem Israel, August 29

5 MEMBERSHIP OF EXTERNAL BOARDS^f

FHD van Batenburg

- Board Dutch APL Association
- APL Study group International Standards Organisation

O Diekmann

- National coordinator EU twinning project 'evolutionary systems'
- Coordinating committee ESF project 'dynamics of complex systems in bio - sciences'
- Chair NWO committee Priorityprogramm 'Non - Linear Systems'