

## Gegevens jaarverslag 1998 van sectieleiders ..

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Een algemene beschrijving van het onderzoek van de sectie (zie tekst hieronder)

#### Theoretical Evolutionary 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 co-operation with experimental groups. The theoretical 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.

Een beschrijving van de voortgang van het onderzoek op het niveau van de (sub)projecten

#### 1. Ecological Dynamics (project leader E. Meelis)

**1.1. Development of Sequential Statistical Methods for Data from Environmental Monitoring Systems** (E. Meelis, M. Schipper (AIO )): Environmental monitoring data, by their very nature, arrive sequentially. Sequential statistical methods allow optimal use to be made of such data. However, the existing methods are improper for the specific purposes of monitoring networks as well as due to the nature of the data. Over the past years the section has worked on devising novel sequential techniques better geared to the problem at hand. In 1998 the earlier results for the case of structured covariance matrices were generalised in order to reduce the number of parameters to be estimated.

**1.2. Analysis of Changes in Abundance of Populations** (E. Meelis, M. Dutmer (AIO)): In the wake of the research mentioned under 1.1 a start was made on the development of methods applicable to non-linear processes.

**1.3. Physiologically Structured Populations** (J.A.J. Metz, with O. Diekmann, Utrecht, M. Gyllenberg, Turku, and H. Thieme, Tempe, plus a variable collective of other collaborators): The roots of the general theory of Physiologically Structured Populations go back to the early 1980s. The early developments were mainly concerned with the modelling part. A Partial Differential Equation formalism was used as a vehicle for communication. This naturally led to semi-group approaches. For a special subclass of models an approach based on Volterra integral equations was available. These early developments mainly took place in Leiden and Amsterdam. The work has given rise to a considerable number of applications as well as extensions. However elegant the semi-group developments, within population dynamics the resulting techniques are useful only for a relatively small class of models, essentially equivalent to age based ones. This in stark contrast to the needs brought to the fore by the by now flourishing biological applications. The section collaborates in a small international collective of researchers who try their hand at extending the integral equation approach. At the biological end all the ingredients are the same, but the mathematical end is reached through a different, less classical, route. In previous years it has been shown that an integral equation formalism clearly can do the job in full generality in the linear case, although the required formalism is daunting. The hunt is now on for an extension of this theory to the non-linear case. In 1998 a start was made on an approach based on treating the population as an input-output operator, transforming influences from the environment into effects on the environment. It is expected that in the future the formalism under development will enable very general population models to be treated by the use of fixed point arguments.

**1.4. Graph-based models for Epidemic Processes** (J.A.J. Metz, with O. Diekmann, Utrecht, and M. de Jong, Lelystad): PM; due to lack of time, no effort was spent on this subproject in 1998. It is expected that this project will be discontinued in 1999.

**1.5: The Geometry of Ecological Interactions** (J.A.J. Metz, with U. Dieckmann, Laxenburg, and R. Law, York): Ecological interactions are by their very nature spatial. Yet most population dynamical theory is non-spatial. The technical difficulties of extending the unusual approaches are formidable. In December 1997 the section was involved in organising a workshop with the agenda of taking stock and setting out routes for future mathematical approaches to spatial population dynamics, which should eventually result in a book covering these issues. In 1998 a great deal of work has been spent on this book, and a great deal more work will have to be spent in 1999. The book is expected to appear early in the year 2000 with Cambridge University Press.

#### 2. ESS theory (project leader P. Haccou)

**2.1 Evolutionary Stability of Genetic and Developmental Mechanisms** (P. Haccou, Y. Robbers (AIO), with Y. Iwasa, Fukuoka):

In order to calculate under which circumstances genetic redundancy could evolve, a mathematical model has been constructed. In this model the 'fitness' of a certain genotype is assumed to depend on the concentration of a particular gene product. Increasing this amount beyond a certain threshold does not affect the phenotype, but the costs associated with producing the substance do of course increase. Furthermore it is assumed that during the development of the organism errors can occur that can decrease the amount of gene product effectively available to perform its function. Using this model it has been shown that it is possible for mutants with a second gene coding for the same function to invade the population. The conditions under which this is possible depend on the probability of developmental errors occurring and on the production costs of the substance. This conclusion is surprising because mutants not only have higher production costs than residents, but also a higher variance in the amount of gene product available. Precisely because of this it has always been assumed that for the evolution of gene duplications a period of changes in the environment would be necessary. Our model shows that this is not the case.

**2.2 Development of Butterfly Wing Patterns** (J.A.J. Metz, with A. Monteiro (AIO) and P. Brakefield): Eyespots in *Byciclus* wings are hypothesised to result from the diffusion of a morphogen from central spots, with the wing tissue reacting in a threshold manner to the local morphogen concentration. The mathematical problem of calculating the patterns resulting from grafting experiments was solved and a statistical method was devised to test in a strong way whether the observed patterns are compatible with the hypothesised mechanism.

**2.3. Sperm Precedence** (E. Meelis with P. de Jong): P.M. This project will only properly commence in 1999.

**2.4. Superparasitism and Patch Leaving** (P. Haccou, with C. Cannings, Sheffield, and O. Glazit): In a previous project it has been shown that situations where several individuals are depleting a patch simultaneously can be modelled as a generalised War of Attrition (M. Sjerps, PhD thesis 1994). That analysis showed that when there is no interference between competitors the optimal strategy is to leave at the time predicted by the marginal value theorem. In the current project, the model is extended to include superparasitism. Superparasitism occurs for example when several female parasitic wasps lay eggs in one host, whereas only a limited number (or even only one) offspring can survive. Superparasitism implies that a female's expected number of future descendants from a patch will be affected by her opponents' behaviour AFTER she has left the patch. This complicates the derivation of ESS leaving strategies considerably. We found that this situation can be modelled with an asymmetric generalised War of Attrition, where the asymmetry is caused by differences in arrival time between the competitors. Whereas such differences do not affect results of models without superparasitism, they become crucial in the current case. The model predicts that, when competitors arrive simultaneously there is a fixed optimal leaving time, which is larger than the leaving time derived from the marginal value theorem. When competitors arrive sequentially, optimal patch leaving strategies become stochastic. They depend on whether an individual arrived on the patch first or not.

**2.5. Sex Ratio Theory** (E. Meelis, with S. Krakov, Berlin, and I. Hardy, Aarhus: P.M. This project will only properly commence in 1999.

**2.6. Battle of the Sexes** (S. Mylius, guest, ex-OIO): In the classical battle-of-the-sexes game pay-offs are assumed on the basis of some gross phenomenological argument. In this project a more detailed population dynamical model was developed in which the pay-offs can be derived from population dynamical considerations such as the time lost in courtship and in bringing up the young. This subproject ended in 1998 with the last steps in the analytical and numerical exploration of the model and the sending in of the final manuscript.

**2.7. Life History Theory** (J.A.J. Metz, with T. van Dooren, Antwerp, M. Heino, Helsinki, U. Dieckmann, Laxenburg): P.M. There were no new developments in 1998. The plans are to use the results of the previous years as the basis for two grant applications. One goal of this project is to provide concrete models that can serve as a testbed for some of the tools developed in project 3.

### 3. Adaptive Dynamics (project leader J.A.J. Metz)

**3.1. Evolutionarily Singular Points for Higher Dimensional Trait Spaces** (J.A.J. Metz, with S.A.H. Geritz, Turku, E. Kisdi, Budapest, G. Meszner, Budapest, U. Dieckmann, Laxenburg), F.J.A. Jacobs (AIO):

Evolutionarily singular points are the routing points in trait space for the adaptive random walk through that space. Examples are ESSes where the random walk reaches a halt, and branching points where an initially monomorphic population starts to become permanently dimorphic (a process akin to, and probably forming the ecological basis of, speciation). The random walk is a result of the perpetual production but ecologically limited invasiveness of novel mutants. In the case of one-dimensional trait spaces the classification of singular points can be made along classical algebraic lines. However, in higher dimensional trait spaces this is no longer possible as the local invasion criterium no longer allows a polynomial representation. In 1998 we have finally been able to derive a local algebraic form in terms of homogeneous functions which is applicable for completely general equilibrium population dynamics. A second result was a general proof that away from singular points invasion indeed as expected implies fixation of the invading mutant provided the mutational steps are sufficiently small. To reach this result a novel axiomatisation of the generalised population dynamical substrate of the adaptive dynamics process had to be developed, which is a rather nice result in its own right.

**3.2. Bifurcation theory of Evolutionarily Singular Points** (J.A.J. Metz, F.J.A. Jacobs (AIO), with S.A.H. Geritz, Turku, E. Kisdi, Budapest, G. Meszner, Budapest, U. Dieckmann, Laxenburg): Bifurcation points are points in parameter space where the pattern of behavioural options of a dynamical system change in a qualitative manner. At this point in time bifurcation theory forms the most important toolbox for analysing non-linear dynamical systems in an efficient manner. The so-called co-dimension of a bifurcation is the number of parameters that need to be given a special value in order to end up at a bifurcation point of that co-dimension. Evolutionarily Singular Points form the most important markers for the dynamical options of adaptive dynamics. However, the classical bifurcation theory as developed for i.a. differential equations is not immediately applicable due to some mathematical quirks of adaptive dynamics considered as dynamical systems. On our way to the development of a bifurcation theory for evolutionarily singular points 1998 saw the development of a full classification of the co-dimension one bifurcations of the evolutionarily singular points of Lotka-Volterra type population dynamical models.

**3.3. Evolution in Metapopulations** (J.A.J. Metz, G. Mulder (AIO), with M. Gyllenberg, Turku, K. Parvinen, Turku, R. Ferriere, Paris, C. Cadet. Paris, and U. Dieckmann. Laxenburg):

The usual fitness measures at the basis of adaptive dynamics theory are no longer applicable in the case of so-called meta-populations, i.e., populations made up of a very large number of subpopulations coupled by migration. (When the number of subpopulations is small the general fitness concept developed by the section in the early nineties still performs well.) Metapopulations are the simplest paradigms for spatially structured populations. In 1998 we have finally been able to derive a fitness concept applicable to metapopulations consisting of infinitely many equally coupled patches (in practice we may consider the patches to be equally coupled when the interpatch distance is smaller than twice the root mean square dispersal distance).

**3.4. Evolution and development** (F. Galis): The integration of developmental and evolutionary biology into a new field is having a major impact on the understanding of how development influences the direction and rate of evolution. We are studying how developmental processes constrain morphological evolution. In 1998 we have been able to unravel an important part of the developmental constraint that keeps the number of cervical vertebrae in mammals constant at seven.

**3.5. Adaptive and Non-adaptive Speciation** (J.A.J. Metz, with E. van Batenburg, E. Gittenberger, U. Dieckmann, Laxenburg, and M. Doebeli, Basel): P.M. No time was spent on this project in 1998 (but see subproject 3.9). However, we expect to return to it in 1999.

**3.6. Adaptive Dynamics in Context** (J.A.J. Metz and U. Dieckmann, Laxenburg): In 1997 a start was made with an edited volume surveying the state of the art of adaptive dynamics. Steady but slow progress was made in 1998. The work on this book was severely impeded by the much higher than expected workload necessary for the spatial ecology book (subproject 1.5) and on the virulence management book (subproject 3.7).

**3.7. Virulence Management** (J.A.J. Metz, with M. Sabelis, Amsterdam, U. Dieckmann, Laxenburg, and K. Sigmund, Vienna): Evolution of virulence in pathogens is a very fast and relatively well monitored process. As such it provides an ideal testing ground for the ideas of adaptive dynamics. In addition the subject is of great applied importance. In December 1998 the section was involved in organising a workshop on this topic. A book initiated at this workshop will take stock and survey new avenues, stressing the potential applications of the theory. Getting this book on the road entailed a good amount of editorial work.

**3.8. Cultural Evolution** (P. Haccou, with K. Riebel and C. ten Cate): P.M. The preliminary explorations for this subproject will only commence in 1999.

**3.9. Adaptive Speciation** (J.A.J. Metz, with U. Dieckmann, Laxenburg, D. Tautz, Cologne, M. Doebeli, Basel): One of the most intriguing phenomena discovered in the context of adaptive dynamics is adaptive branching. This phenomenon provides an abstract underpinning for the process of sympatric and parapatric speciation. The first steps were taken in organising a workshop on sympatric speciation to take stock of the possible connections. This workshop should engender a book on this topic that should set the agenda for future research.

Een overzicht van het in 1998 bij de sectie werkzame personeel (zie hieronder)

#### STAFF

Senior Investigators	Function	Source of Finance	Details
Prof. Dr. J.A.J. Metz	Full Professor	Leiden University	
Dr. F. Galis	Assistant Professor	Leiden University	0.3
Dr. P. Haccou	Assistant Professor	Leiden University	
Drs. E. Meelis	Assistant Professor	Leiden University	

## Postdocs

Junior Investigators	Function	Source of Finance	Details
Ir. M.Y. Dutmer	Research Assistant	Leiden University	from 1-8-98
Drs. F.J.A. Jacobs	Research Assistant	Leiden University	until 31-8-98
Drs. G. Mulder	Research Assistant	Leiden University	0.8
Drs. Y. Robbers	Research Assistant	Leiden University	from 1-4-98
Drs. M. Schipper	Research Assistant	Leiden University	until 1-7-98

## Analytical, Technical and Administrative Staff

E.A. van Ast-Gray	Secretary	Leiden University	from 24-8-98	0.5
H. Regeer-Groenhuijzen	Secretary	Leiden University		0.5
Y.M. Zitman-de Graaf	Secretary	Leiden University	until 31-8-98	0.5

## Guests

Dr. N. v.d. Hoeven	Researcher	volunteer	0.2
Drs. F.J.A. Jacobs	Researcher	volunteer	from 1-9-98
Drs. S.D. Mylius	Researcher	volunteer	p.m.
Drs. M. Schipper	Researcher	volunteer	from 1-7-98
Dr. J. Val	Researcher	volunteer	until 1-7-98
E. Westerveld	Researcher	volunteer	until 1-7-98

Een overzicht van de research output in 1998, volgens de aangegeven indeling

geef telkens aan bij welk project de output hoort

NB1. Kijk naar EEW Annual Report 1997 voor benodigde format bij aangegeven publicaties

NB2. Verschaf bij promoties de volgende informatie: datum promotie, naam promovendus, titel proefschrift, namen promotor(en)/co-promotor, universiteit, aantal pp., project

### *Publications in scientific journals*

Bowmer CT., R.N. Hoofman, A.O. Hanstveit, P.W.M. Venderbosch and N. van der Hoeven. The ecotoxicity and the biodegradability of lactic acid, alkyl lactate esters and lactic acid salts. *Chemosphere* 37 (1998): 1317-1333.(1)

Diekmann O., M. Gyllenberg, J.A.J. Metz and H.R. Thieme. On the formulation and analysis of general deterministic structured population models. I. Linear theory. *Journal of Mathematical Biology* 36 (1998) 349-388. (1)

Diekmann O., M.C.M. de Jong and J.A.J. Metz. A deterministic epidemic model taking account of repeated contacts between the same individuals. *J.App.Prob.* 35 (1998) 448-462. (1)

Galis F. and Metz JAJ. Why are there so many cichlid species? *Trends in Ecology and Evolution* 13 (1) (1998): 1-2. (3)

Geritz S.A.H. Coevolution of seed size and seed predation. *Evolutionary Ecology* (1998) 12: 891-911. (2)

Geritz S.A.H., E. Kisdi, G. Meszéna and J.A.J. Metz. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evolutionary Ecology* 12 (1998) 35-57. (3)

Gerritsen A.A.M., N. van der Hoeven and A. Pielaat. The acute toxicity of selected alkylphenols on young and adult *Daphnia magna*. *Ecotoxicol. Environm. Safety* 39 (1998): 227-232.(1)

Haccou P. and Y. Iwasa Robustness of optimal mixed strategies. *Journal of Mathematical Biology* 36 (1998) 485-496. (2)

Haccou P. and J.M. McNamara Effects of parental survival on clutch size decisions in fluctuating environments. *Evolutionary Ecology* 12 (1998) 459-475. (2)

Heino M., J.A.J. Metz and V. Kaitala. The enigma of frequency-dependent selection. *TREE* 13, No. 9 (1998) 367-370. (2)

Heino M., J.A.J. Metz and V. Kaitala. *TREE* 13, No. 12 (1998) 509. (2)

Hoeven N. van der. Power analysis for the NOEC: What is the probability of detecting small toxic effects on three different species using the appropriate standardized test protocols? *Ecotoxicology* 7 (1998): 355-361.

Van Dooren T.J.M. and J.A.J. Metz Delayed maturation in temporally structured populations with non-equilibrium dynamics. *Journal of Evolutionary Biology* 11 (1998) 41-62. (2/3)

### ***Dissertations***

**Geritz S.A.H.** The evolutionary significance of variation in seed size. 6 January 1998 Leiden Univ. Promotores: Prof. Dr. J.A.J. Metz, Prof. Dr. E. v.d. Meijden 151p. Proefschrift RUL. (3)

Een overzicht van de invited keynote addresses

Geef naam keynote speaker, titel lezing, bij gelegenheid van, plaats, land, datum

**F. Galis** On the homology of structures and Hox genes: the vertebral column. Novartis Foundation Symposium on Homology. London, England, July.

**P. Haccou** Implication of Environmental Fluctuations for Establishment Probability. Workshop population dynamics. Göthenburg, 11 - 15 May.

**P. Haccou** Patch leaving strategies and superparasitism. VII International Congress of Ecology in Florence, 19 - 25 July.

**P. Haccou:** Establishment probability of small populations in fluctuating environments, 4th International conference on difference equations and their applications, Poznan, Poland, 27 - 31 August.

**F.J.A. Jacobs** On the Geometrical Representation of Evolutionary Processes. Applied Mathematics Group of the Faculty of Mathematics, Utrecht, March.

**F.J.A. Jacobs** Bifurcation Analysis for Adaptive Dynamics Based on Lotka-Volterra Models. Budapest, November .

**F.J.A. Jacobs** Workshop Applied Bifurcation Analysis: Bifurcation Analysis for Adaptive Dynamics Based on Lotka-Volterra Models. Antwerp. December.

**J.A.J. Metz** Between Population Dynamics and Adaptive Dynamics. Workshop population dynamics. Göthenburg, 11 - 15 May.

**J.A.J. Metz** Adaptive Dynamics: population dynamics evolutionary twist. Conference on Nonlinear Demography in Rostock, 26 - 29 May.

**J.A.J. Metz** From population dynamics to adaptive dynamics. VII International Congress of Ecology in Florence, 19 - 25 July

**J.A.J. Metz** Adaptive Dynamics, population dynamic's evolutionary twist. Research School SOM, Groningen 4 September.

**J.A.J. Metz** How should we define fitness for general structured metapopulations? Spatial Ecology Workshop on Evolution of Dispersal. Tvärminne, Finland, 15 - 19 October.

**J.A.J. Metz** Adaptive Dynamics: Long Term Phenotypic Evolution from a Population Dynamical Perspective. Stafcolloquium, Applied Mathematics Group of the Faculty of Mathematics, Utrecht, 12 November.

Een overzicht van lidmaatschappen van editorial and advisory boards

**F. Galis**

Member Editorial Board, Journal of Experimental Biology (Molecular Developmental Evolution)

**P. Haccou**

Associate Editor Behavioural Processes

Associate Editor American Naturalist

**J.A.J. Metz**

Consultant Department of Mathematics, Utrecht University

Project Leader Adaptive Dynamics Network, Austria.

Member Steering Committee European Science Foundation Program Theoretical Biology of Adaptation

Member Editorial Board Acta Biotheoretica

**E. Meelis**

schrap lidmaatschappen die in 1998 niet meer bestonden  
vul aan met lidmaatschappen die in (de loop van) 1998 zijn ontstaan  
corrigeer foutieve tekst

Een overzicht van awarded grant support, opgesplitst in personnel en equipment

NWO awarded a grant of DFL. 14,750 to Prof. Dr. . Turchin, Dept. of Ecology and Evol. Biology, University of Connecticut to visit Leiden from 19 March until end June.

Een overzicht van de collaboration

## COLLABORATION

(projectcodes are indicated between brackets)

**National**

- Amsterdam, vg. Zuivere en Toegepaste Oecologie UvA, Prof. Dr. M.W. Sabelis (1,3)
- Lelystad, CDI-DLO, Dr. M.C.M. de Jong (1)
- Utrecht, Mathematisch Instituut, Prof. Dr. O. Diekmann (1,2,3)
- Utrecht, Biostatistiek, Dr. M. Schipper (1)
- Wageningen, vg. Wiskunde LUW, Dr. F. v.d. Bosch (1)
- Wageningen, Dienst Landbouw, wiskunde - DLO, Dr. J.A.P. Heesterbeek (1)
- Wageningen, Experimentele dierkunde, Dr. M. Muller (3)

**International**

- Laxenburg, Austria, ADN-IIASA, Dr. U. Dieckmann (2,3)
- Vienna, Austria, Institut für Mathematik, Prof. Dr. K. Sigmund (3)
- Antwerp, Belgium, UIA, Drs. T. van Dooren (3)
- Diepenbeek, Belgium, Prof. Dr. G. Molenberghs (1)
- Helsinki, Finland, Division of Population Biology, Dr. M. Heino (3)
- Jyväskylä, Finland, University of Jyväskylä, Prof. Dr. V. Kaitala (3)

- Turku, Finland, Math. Inst. Univ. of Turku, Prof. Dr. M. Gyllenberg (1,2)
- Paris, France, Laboratoire d'Ecologie, Ecole Normale Supérieure, Dr. R. Ferrière (3)
- Budapest, Hungary, Eötvös University, Dr. É. Kisdi (3)
- Budapest, Hungary, Eötvös University, Dr. G. Meszner (3)
- Fukuoka, Japan, Kyushu Univ., Prof. Dr. Y. Iwasa (2)
- Göthenborg, Sweden, Chalmers University, Prof. dr. P. Jagers, (2)
- Ascot, UK, Imperial Coll./NERC Centre for Pop. Biol., Dr. Ir. V.A.A. Jansen (3)
- Bristol, UK, Dept. Mathematics Univ. of Bristol, Prof. Dr. J. McNamara (2)
- Cambridge, UK, BioEssays, Dr. A.S. Wilkins (3)
- Edinburgh, Herriot Watt University, UK, Dept. of Agricult. Math. Prof. Dr. D. Mollison (1)
- Southampton, University of Sheffield, UK - Prof. Dr. C. Cannings, (2)
- York, UK, University of York, Dr. R. Law (1)
- Berkeley, USA, Museum of Vertebrate Zoology, Univ. of California, Prof. H.W. Greene (3)
- Cambridge, USA, Museum of Comparative Zoology, Harvard University, Prof. K.F. Liem (3)
- College Park, USA, Dept. of Zoology, Univ. of Maryland, Dr. S.A.H. Geritz (3)
- New Haven, USA, Dept of Ecology and Evolution, Yale University, Prof. G.P. Wagner (3)
- Storrs, USA, University of Connecticut, Dr. K. Schwenk (3)
- Tempe, USA, Arizona State Univ., Prof. Dr. H.R. Thieme (1)

beperk opsomming tot samenwerking die aantoonbaar tot wetenschappelijke output leidt  
 schrap samenwerking die daaraan niet voldoet en/of in 1998 niet meer bestond  
 vul aan met nieuwe samenwerkingsrelaties in 1998  
 geef voor elke relatie aan op welk project(en) de relatie betrekking heeft (nieuwe project-aanduiding)

Een overzicht van visiting scientists

geef aan welke buitenlanders bij de sectie op bezoek kwamen (naam bezoeker, functie bezoeker, instituut, plaats, land, data bezoek)

**Prof. Dr. John McNamara**, Dept. Mathematics, Univ. of Bristol, UK. 15 and 16 January.

**Prof. K. Liem**, Museum of Comparative Zoology, Harvard University, Cambridge, USA, 17 March.

**Prof. Dr. P. Turchin**, Dept. of Ecology and Evol. Biology, University of Connecticut, USA. 19 March to end June.

**Prof. Dr. J. Atema**, Marine Research Program, Woodshill, University of Boston, USA. 19 May.

**Dr. E.H. Wu**, Museum of Comparative Zoology, Harvard University, USA, early October .

**Dr. O. Glaizot**, Postdoc, Switzerland, 19 - 25 October.

**Prof. Dr. M.A Lewis**, University of Utah, USA. 2-8 December 1998 under the auspices of NWO Priority Programme on Non-Linear Systems (NWO prioriteitenprogramma NietLineaire Systemen).

Een overzicht van door gasten gehouden lezingen binnen het EEW

geef aan welke gastsprekers een voordracht voor het EEW hielden (datum, naam gastspreker, functie gastspreker, instituut, plaats, land, titel voordracht)

**Prof. Dr. P. Turchin**, Dept. of Ecology and Evol. Biology, University of Connecticut. 10 and 13 March. Nonlinear Ecological Time Series Analysis (two day course of lectures) followed by Workshops (hands on training) on 1, 2 and 3 April.

**Prof. Dr. R. Lande**. University of Oregon, Eugene, USA, 27 August. Non-adaptive speciation, diversity and extinction.

**Dr S.M. Deban**, J.A.J.e Institute for Advanced Study and Brain Research Institute, University of Bremen, 1 December. Co-ordination and plasticity of feeding movements in salamanders.

**Prof. Dr. M.A. Lewis**, University of Utah, 2-8 December 1998. under auspices of NWO Priority Programme on Non-Linear Systems. 1) On the asymptotic speed of a stochastic invasion. 2) Wolf home ranges and prey survival

Een overzicht van externe promotie-begeleiding

Opgave van 1<sup>e</sup> en 2<sup>e</sup> fase onderwijsactiviteiten, w.o. aantal maanden begeleiding stagestudenten en aantal maanden begeleiding interne promovendi

F. Galis organized a symposium “Evolution and Development ” of nine meetings from January – March for 15 students.

F. Galis, together with M. Schilthuizen, organized a monthly speciation luncheon meeting wherein an invited speaker held an introduction.

F.J.A. Jacobs supervised Michiel Koster (stagestudent) for 20 weeks.

F.J.A. Jacobs supervised Evertjan van de Kaa (doctoral student (Drs.)) for 26 weeks.

E. Meelis – Teaching of 2<sup>nd</sup> year Statistics: 16 hours lectures plus 12 hours practical.

E. Meelis Supervisor of PhD students M. Schipper and M.Y. Dutmer.

P. Haccou – Teaching of 1<sup>st</sup> year Basic Mathematics: 10 hours lectures including exercises.

P. Haccou – Teaching of 1<sup>st</sup> year Mathematical Processes in Biology: 18 hours lectures plus 20 hours exercise classes.

J.A.J. – Teaching of 1<sup>st</sup> year Statistics: 14 hours lectures plus 12 hours exercise classes.

J.A.J. Metz Supervisor of PhD students S.D. Mylius, F.J.A. Jacobs, G. Mulder, Y. Robbers .

Een overzicht van georganiseerde meetings

geef aan welke (inter)nationale symposia en congressen (mede) georganiseerd zijn (titel, plaats, data, naam organisator, aantal deelnemers)

**J.A.J. Metz**, Co-organizer, Workshop Evolutionary Conservation Biology, Laxenburg, Austria, 40 participants

**J.A.J. Metz**, Co-organizer, Special Program on Stochastic Processes in Biology at the Stochastic Centre in Gothenburg, Sweden, April-May 1998, including a Workshop on Population Dynamics, 11-15 May, 50 participants

**J.A.J. Metz**, Co-organizer, Workshop of Adaptive Dynamics: Bifurcations, Higher Dimensional Trait Spaces, Budapest, Hungary, 1 - 5 November, 8 participants

Een overzicht van maatschappelijke dienstverlening, w.o. lidmaatschappen externe besturen e.d.

**N. van der Hoeven**

Lid commissie “Bestrijdingsmiddelen en (semi)veldonderzoek” van de Gezondheidsraad.

**E. Meelis**

Secretary Study group Milieubeheer Leiden

**J.A.J. Metz**

Leader Project Adaptive Dynamics Network, IIASA, Austria

Judgement committee D, SLW

Committee Non-linear Population dynamics, NWO Priority Program Nonlinear Systems

Curator LUF endowed chair Philosophy of Biology

Organising Committee Workshop on Virulence Management, IIASA

Co-organizer, Workshop Evolutionary Conservation Biology, Laxenburg, Austria

Project Leader ADN + Curatorship

Een overzicht van toegekende prijzen (distinctions)



geef aan welke wetenschappelijke prijzen of onderscheidingen in de wacht zijn gesleept (naam medewerker, naam prijs, doel prijs, waaruit bestaat de prijs, mening van de jury, datum en van de uitreiking, naam van de uitreiker)

In 1999 Dr. U. Diekmann was presented with the 1998 Kees Bakker Foundation Award.

Het verschaffen van illustratie-materiaal

Verschaf ons wat fraai foto- of teken-materiaal, betrekking hebbend op het onderzoek, vergezeld van korte tekst met uitleg, eventueel in kleur.

Frans stelt voor een van de figuren uit de bifurcatieanalyse te nemen (deze zitten in de iMac van Hans)

Aanvullende gegevens van D. Kornet volgen rechtstreeks

### Theoretical Biology and Phylogenetics

Section Chair: E. Gittenberger

The section studies patterns and processes involved in evolutionary change. Macroevolution, speciation in particular, is the major area of interest. Evolutionary and ecological issues are investigated by use of theoretical and experimental research. Gastropods are used as model system in the experimental research. The theoretical research ranges from exploring the consequences of established biological theories to the construction of models for specific biological systems. In addition the section investigates the nature of key biological concepts and cooperates with researchers in the National Museum of Natural History (NNM) in projects on evolutionary aspects of past and present biodiversity.

#### 1. Foundations of Phylogenetics.

Chair D.J. Kornet

#### 2. Grondslagen

Chair D.J. Kornet

#### 3. Molecular and Morphological Phylogenetics

Chair E. Gittenberger

a. Molecular systematics of *Albinaria*. This project aims at a more profound knowledge of the systematic and phylogenetic patterns within the genus *Albinaria*, to also achieve a better understanding of the evolutionary processes that resulted in the actual, bewildering variation that characterizes this group of over 100 species. Various aspects of the generic evolutionary history are studied with a variety of morphological, molecular and biogeographical methods. Doing so, the complicated geological history of the generic range, an area with frequent changes in the distribution of water and land, is also taken into account. The phenomena in hybrid zones, in particular mutation rate, selection and introgression, and their potential relevance for speciation are also studied.

Dr. M. Schilthuizen, while analysing DNA fragments from hybrid zones, discovered that next to the well-known hybrid zones, high concentrations of an uncommon variant of an intron may be found. The meaning of this discovery is further investigated. With several co-authors, a phylogeography of *A. hippolyti* was finished; the molecular data show that long distance dispersal has to be accepted next to allopatry on paleo-islands as relevant in (sub)speciation. Drs. C. van Moorsel developed a novel method for DNA extraction in snails. She spent much time in investigating the intra- and interindividual variation of rDNA ITS1; the preliminary results point at more variation than expected, which may lower the usefulness of this frequently used DNA for phylogeny reconstruction. A manuscript was finished on convergent evolution in shell characters among *Albinaria* and *Isabellaria* species in S. Greece; a phylogeny was proposed on the basis of rDNA ITS1&2. Drs. M. Graafland continued investigating the occurrence of a peculiar, still undescribed, anatomical detail in a group of *Albinaria* species.

b. Phylogeny of *Albinaria*, *Sericata* and *Isabellaria*. This project is closely related to the previous one, with more emphasis on phenomena in higher taxa. It aims at a reconstruction of the phylogeny of a clade formed by

the species of the nominal genera *Albinaria*, *Isabellaria*, *Sericata* and maybe additional ones, with absolute dating of the major splitting events. Convergent evolution and maybe reversals in the bauplan of the apertural closing device will be derived from the cladogram. The relevance of the location of paleo-islands, actual islands and limestone islands will also be investigated.

Drs. D. Uit de Weerd started this project, which is still in its infancy.

c. Population history of *Arianta* in Alpine refugia. The ranges of some morphologically aberrant populations of Alpine *Arianta* are concentrated in areas that have not completely been covered by the ice during the Pleistocene glaciations. The question is whether the subspecies in question differentiated in isolation on the island-like nunataks.

In a pilot study ITS1 rDNA was used to investigate the question. Some populations were studied, but without unequivocal results. Fieldwork in N. Austria and N. Italy brought important new research material. The project will be continued with molecular methods. Cytochrome 1 will additionally be used to study the relationships between the alleged nunatak forms and those that are supposed to have invaded the Alpine lowlands postglacially.

d. *Mastus* radiation in Crete. Is the genus *Mastus* speciose, showing a radiation in Crete comparable to that in *Albinaria*, and triggered by the past occurrence of various paleo-islands, or should we accept only a few very variable species with another evolutionary history. Both views have been defended in the literature.

During the 2nd year students course 'Biodiversity and Pattern Analysis', some students studied samples of *Mastus* shells from ca. 50 localities in Crete. They largely confirmed the view that there are several separate entities occupying separate coherent ranges in the island. The project will be continued. Live material will be collected for DNA sequencing and phylogeny reconstruction and dating using the sequential data.

e. RNA and phylogeny reconstruction. The potential use of RNA structures (primary, secondary and tertiary) and structuring pathways in phylogeny reconstruction is investigated in *Albinaria* as a model taxon. The hypothesis is tested that the folding pathways of the molecules, analogous to ontogeny, contain traces of the phylogenetic history of the taxa.

Despite fascinating discussions among the participants (F.H.D. van Batenburg, E. Gittenberger, S. Gulyaev, C.W.A. Pleij, and students) this subproject made only little progress. The value for phylogeny reconstruction of the primary and to a lesser extent the secondary structure has already been demonstrated convincingly, but the informative content of the folding pathway is still a matter of dispute.

f. Speciation by non-adaptive radiation. In a joint theoretical subproject with Section 8 (H. Metz), a computer experiment, the question is investigated whether allopatric speciation may occur in the absence of environmental differences in the separate subranges. What conditions may favour speciation under equal selective regimes in two subpopulations, differing primarily because of independent random mutations only. A simulation model was developed by F.H.D. van Batenburg and its relation with reality discussed with E. Gittenberger and H. Metz. The model contains already realistic variables like mutation rate, environmental condition, selection pressure, etc., and will be further improved. The experiment starts with a single gene-pool, which is subdivided into two by the introduction of a more or less complete barrier to gene-flow. What happens when the barrier is removed after a series of generations that have lived under the same constant or fluctuating selective pressure. Under particular conditions two separate gene-pools seem to persist after removal of the barrier. The participants could spend only little time on this subproject, which will be continued to be concluded with a publication.

#### 4. Past and Present Biodiversity

Under this heading the various research projects that are partly initiated and supervised by curators of the National Museum of Natural History *Naturalis* (= NNM) are listed. These projects have elements of systematics and phylogenetics and are related to biodiversity. For each of the following researchers, Prof. dr. E. Gittenberger will be responsible as promotor.

Drs. D. Gassmann, supervised by Drs. J. van Tol, finished two papers for his doctoral thesis, on a project in the ALW Research Programme 'Pathways from Asia to New Guinea: the origin of non-Australian elements of the Papuan flora and fauna, III. The origin of the Papuan damselflies of the subfamily Calicnemidinae (Odonata, Platycnemididae), the role of West Malaysia and the Philippines'.

Drs. H. J. Meegens, supervised by Dr. R. de Jong, continued his research in the NWO Priority Programme 'Biodiversity in disturbed ecosystems', Role of butterfly-plant and butterfly-ant interactions in the biodiversity of rain forests in South East Asia in different stages of degeneration and regeneration. Much time was spent in a search for useful molecular markers.

Drs. C.J.H.M. Fransen, Drs. J. van Tol, and Drs. F.P. Wesseling, curators at the NNM, could go on again with their doctoral research on Odonata, Crustacea, and Miocene Amazonian freshwater Mollusca, respectively. Their work had slowed down considerably because of the time-consuming removal of the NNM to another building. Several concept articles were discussed.

1. Een overzicht van het in 1998 bij de sectie werkzame personeel (zie hieronder)

### STAFF

Senior investigators	function	source of finance	details
Prof.dr. E. Gittenberger	full professor	Leiden University/NNM	0.3/0.7
Dr. J.C. von Vaupel Klein	associate professor	Leiden University	
Prof.dr. D.J. Kornet	endowed professor	LUF	
Dr. F.H.D. van Batenburg	assistant professor	Leiden University	
Dr. Th.E. Sprey	assistant professor	Leiden University	
Dr. H. Verhoog	assistant professor	Leiden University	
Dr. M.B.H. Visser	researcher	NWO	0.2
Dr. M. Zandee	assistant professor	Leiden University	

#### Postdocs

Dr. R. v.d. Bos	researcher	NWO	0.8 from 1/7
Dr. S. Gulyaev	researcher	NWO/EMBO	
Dr. H. Turner	researcher	NWO	till 1/10

#### Junior investigators

D.W.K. Gassmann, Dipl. Biol.	research assistant	SLW	
Ir. H.J.W.C. Megens	research assistant	SLW	
Drs. C.H.M. van Moorsel	research assistant	Leiden University	
Drs. D. Uit de Weerd	research assistant	Leiden University	from 15.11
Ir. M.G.P. van Veller	research assistant	SLW	

#### Analytical, technical and administrative staff

H. Regeer-Groenhuijzen	secretary	Leiden University	0.5
Y.M. Zitman-de Graaf	secretary	Leiden University	0.5

#### Guests

Dr. A.C. van Bruggen	researcher	volunteer	
Dr. B.W. Hoeksema	researcher	volunteer	
P.J. Kuijten	researcher	volunteer	
Prof.dr. P. Dullemeijer	researcher	volunteer	0.1

2. Een overzicht van de research output in 1998, volgens de aangegeven indeling
3. Een overzicht van de invited keynote addresses
4. Een overzicht van lidmaatschappen van editorial and advisory boards

#### H Verhoog

Subcommittee Ethics and societal aspects, committee Genetic Modification (VROM)  
Committee Ethical testing genetic modification of animals (LNV)

**MBH Visser**

Committee Biotechnology IMPULS: Technology Museum NINT, Amsterdam  
External advisory committee Education Animal Management, Van Hall Institute  
'Re-use', Primate Research Centre TNO  
Dierexperimenten commissie DEC-consult

**AC van Bruggen**

IUCN Species Survival Commission Molluscs  
Chief-editor Achatina  
Chief-editor Bacteria  
Chief-editor Mededelingen Nederlandse Commissie voor Internationale Natuurbescherming  
Editorial board of the 'Revue de Zoologie Africaine/African Journal of Zoology'  
Editorial board of the 'Belgian Journal of Zoology'  
Editorial board of 'Tropical Zoology'  
Editorial board of 'Lutra'

**E Gittenberger**

Editorial board of the 'Bollettino Malacologico', Milano  
Editorial board of 'BIOS', Thessaloniki  
Editorial board of 'Basteria', Leiden  
Editorial board of 'Malacologia', Philadelphia  
Editorial board of 'Zoologischer Anzeiger', Jena

**JC von Vaupel Klein**

Page-charges Commissioner for the 'Netherlands Journal of Zoology'.

5. Een overzicht van awarded grant support, opgesplitst in personnel en equipment
6. Een overzicht van de collaboration

**COLLABORATION**

(projectcodes are indicated between brackets)

**Leiden**

- Bloedbank, Dr. R. Schippers (1.94.7)
- Fac. Wijsbegeerte RUL, Dr. J.W. McAllister (1.94.11)
- LIC RUL, Prof.dr. J.P. Abrahams (1.94.7)
- LIC RUL, Prof.dr. C. Pley (1.94.7)
- Medische Fac. RUL, Prof.dr. Tj. de Cock Buning (1.94.10)
- RHHB, RUL, Dr. P.C. van Welzen (1.94.11)
- NNM, Drs. C.J.H.M. Fransen, Prof.dr. L.B. Holthuis, Dr. R. Hoogmoed, Dr. R. de Jong, Drs. F. Slik, Dr. C. Smeenk, Drs. J. van Tol, Prof.dr. W. Vervoort, Dr.Ir. A.J. de Winter (2.94.7-8)
- RHHB, Dr. P. Kessler, Dr. P. van Welzen (2.94.8)

**National**

- Amsterdam, Filosofie, Prof.dr. W. Achterberg (1.94.10)
- Amsterdam, VUA, S. Kasanmoentalib (1.94.10)
- Amsterdam, ISP, UvA, Dr. H. Turner (1.94.11)
- Driebergen, L. Bolk Instituut, I. E. Lammerts (1.94.10)
- Enschede, TU Twente, ASWI, Ir. F. Bonnema (a)
- Lexmond, Adfee (ASWI standaards), B. Smoor (a)
- Nieuwegein, OASIS (ASWI standaards), Th. Zwart (a)
- Nijmegen, Filosofie, Dr. H. Zwart (1.94.10)
- Utrecht, RUU, Dr. M. Schilder (1.94.11)
- Utrecht, RUU, Drs. H. de Vries (1.94.11)
- Utrecht, Biostatistiek, Drs. M. Schipper (1.94.8)

- Wageningen, LUW, Dr. A. Hemerik (1.94.8)
- Amsterdam, ITZ, UvA, Prof.dr. S.B.J. Menken, Prof.dr. F.R. Schram, Dr. S.A. Ulenberg (2.94.6/7)
- Nijmegen, KUN, Prof.dr. G. v.d. Velde (2.94.7)
- Texel, NIOZ, Prof.dr. R.P.M. Bak, Dr. D.H. Spaargaren (2.94.7)

### **International**

- Toronto, Canada, Dept. Zoology Univ. Toronto, Prof.dr. D.R. Brooks (1.94.4)
- Vancouver, Canada, Simon Fraser University, Prof.dr. B. Roitberg (1.94.4)
- Odense, Denmark, Odense University, Dr. K. Gerdes (1.94.7)
- Cambridge, UK, Univ. of Cambridge, Dr. A. Dickinson (1.94.11)
- Southampton, UK, Univ. of Southampton, Dr. J.W.S. Bradshaw (1.94.11)
- Stanford, USA, Stanford University, Prof.dr. S. Tuljapurkar (1.94.4)
- RHHB, RUL, Dr. P.C. van Welzen (1.94.11)
- La Plata, Argentina, Zoöl. Mus., Mrs. Dr. M.C. Coscarón (2.94.6/7/8)
- Brussel, Belgium, KBIN, Dr. J.L. van Goethem, Dr. F. Fiers (2.94.7/9)
- Gent, Belgium, Rijksuniversiteit, Prof.dr. K. Martens, Dr. L. van Brendonck (2.94.7)
- Paris, France, MNHN, Prof.dr. J. Forest, Dr. A. Crosnier, Dr. D. Defaye, Dr. P.Y. Noël (2.94.7)
- Frankfurt, Germany, SMF, Dr. R. Janssen (2.94.6/8/9)
- Hamburg, Germany, Univ. of Hamburg, Prof. Dr. A. Brandt (2.94.7)
- Stuttgart, Germany, Staatl. Mus. für Naturkunde, Dr. H.J. Niederhöfer (2.94.6)
- Wanariset, Kalimantan, Indonesia, Tropenbos Site, Dr. W. Smits (2.95.1)
- Florence, Italy, Univ. of Florence, Prof. Dr. A.M. Simonetta (2.94.7)
- Siena, Italy, IBE, Dr. F. Giusti (2.94.6)
- Padua, Italy, Univ., Prof.dr. A. Minelli (2.94.6/7)
- Tokyo, Japan, Univ. of Fisheries, Prof. Dr. M. Omori, Dr. S. Nishida (2.94.7)
- London, UK, BM(NH), Dr. R. Huys, Dr. P.B. Mordan, Dr. F. Naggs, Dr. J. Taylor (2.94.6/7/8/9)
- Atlanta, USA, CDS, Dr. S. Meredith (2.94.5)
- Cambridge, USA, Harvard University, Prof. Dr. N.E. Pierce (2.95.1)
- Philadelphia, USA, ANSP, Dr. G.M. Davis (2.94.6)
- Washington D.C., USA, Smithsonian Inst., Dr. F. Ferrari (2.94.7)

7. Een overzicht van visiting scientists
8. Een overzicht van door gasten gehouden lezingen binnen het EEW
9. Een overzicht van externe promotie-begeleiding  
[? , museale promovendi?]
10. Opgave van 1<sup>e</sup> en 2<sup>e</sup> fase onderwijsactiviteiten, w.o. aantal maanden begeleiding stagestudenten en aantal maanden begeleiding interne promovendi

[Elders al eerder opgegeven]

11. Een overzicht van georganiseerde meetings
12. Een overzicht van maatschappelijke dienstverlening, w.o. lidmaatschappen externe besturen e.d.

### **R van den Bos**

External Board Animals in Philosophy and Science, Van Gorcum, Assen

### **H Verhoog**

NIBI Committee Professional Code for Biologists

Study group intensive cattle farming (animal protection society)

### **MBH Visser**

Dutch Association for Bio-ethics

Committee Biotechnology IMPULS: Technology Museum NINT, Amsterdam

'Re-use', Primate Research Centre TNO

### **AC van Bruggen**

Nederlandse Commissie voor Internationale Natuurbescherming

Stichting Van Tienhovenfonds (chairman)

Foundation for Life Sciences SEZ Continentale Biogeografie (head of the workgroup)

Commissie Begeleiding Nieuw Dierenpark Eindhoven

Honorair Wetenschappelijk Medewerker Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels

**E Gittenberger**

Unitas Malacologica (Secretary-General)

Board of Directors of the Institute of Malacology, Philadelphia (Participating Member)

Board Onderzoeksinstituut Rijksherbarium-Hortus Botanicus

Board Onderzoekschool Biodiversiteit

Board Wissenschaftlicher Beirat Museum Alexander Koenig, Bonn.

Board Internationaler Redaktionelle Beirat der Senckenbergischen Naturforschenden Gesellschaft, Frankfurt

Foundation for Life Sciences-Werkgemeinschaft Systematische en Evolutionaire Zoölogie (chairman)

Jan Joost ter Pelkwijkfonds (chairman)

**JC von Vaupel Klein**

Secretary of the Editorial Board and Managing Editor of 'Crustaceana, International Journal of Crustacean Research'

Member of the Organizing Committee, Chairman of the Scientific Committee on Larval Biology and Developmental History, and Proceedings Commissioner of the Fourth International Crustacean Congress, due at Amsterdam, July, 1998.

13. Een overzicht van toegekende prijzen (distinctions)

14. Het verschaffen van illustratie-materiaal

Vershaf ons wat fraai foto- of teken-materiaal, betrekking hebbend op het onderzoek, vergezeld van korte tekst met uitleg, eventueel in kleur.