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Gegevens jaarverslag 1998/99 van sectieleiders

Een algemene beschrijving van het onderzoek van de sectie

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 projecten

Ecological Dynamics
project leader: E. Meelis
This project considers the dynamics of single species as well as processes involving the interaction between several species on ecological time scales. In one direction novel mathematical tools are developed for the translation from complex individual level causes to population dynamical consequences. In the other direction data analytical tools for dealing with observed ecological time series are developed, which increasingly account for the underlying individual level processes.
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. M. Schipper completed her dissertation on this subject. A publication for the case of structured covariance matrices is in preparation.
1.2. **Analysis of Changes in Abundance of Populations** (started end 1998; E. Meelis, M. Dutmer (AIO)): The research mentioned under 1.1 was extended to non-linear processes, in order to account a little better for the population dynamical mechanisms implicitly under consideration. The methods derived earlier could indeed be generalised to the non-linear case. However, it turned out to be difficult to estimate 'natural' parameters such as "carrying capacity" sufficiently accurately in the appropriate sequential context.
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. During 1998/99 the collective developed an approach based on treating the population as an input-output operator, transforming influences from the environment into effects on the environment. The importance if this approach us that it enables very general population models to be treated by the use of fixed point arguments. A paper summarizing the results so far was submitted to the Journal of mathematical Biology.
1.5: **The Geometry of Ecological Interactions** (J.A.J. Metz, with U. Dieckmann, Laxenburg, and R. Law, York; ended end 1999): 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 and 99 a great deal of work has been spent on this book. The book will appear in May 4, 2000 with Cambridge University Press.

1.3 **Branching Process Models** (P. Haccou, with P. Jagers, Gothenburg (a), and Y. Iwasa (Fukuoka) and V. Vatutin, Moscow (b)): Branching processes are stochastic processes that explicitly incorporate stochasticity due to inter-individual variation. Their theory is well developed in that there are theorems available covering very general classes of life histories. However, these results are reached at a cost: individuals are assumed not to influence each other's reproduction, neither directly nor indirectly. This makes that those models have their main use for the analysis of invasions starting with a small population. There branching process tools are very powerful. **(a)** Many results from the mathematical theory of branching processes are eminently relevant for biology. However, they are not known to (mathematical) biologists since they are published in mathematical journals, and are phrased in a highly technical form so that their phrasing needs considerable adjustment before they can be applied. Patsy Haccou and Peter Jagers are trying to bridge the communication gape by organising that a group of mathematicians and mathematical biologists together write a book on branching processes explicitly for a biological audience. **(b)** Real environments are rarely constant. A special area of branching process theory focusses on the consequences of independent reproduction in randomly fluctuating environments. Most results in this area are qualitative. Quatitative results are hard to come by. At an earlier stage of this subproject (with Yoh Iwasa) it was found using computer simulation that in environments where the expected numbers of offspring per individual are Poisson distributed and vary independently over years, the chances of success of subsequent invaders are positively autocorrelated. A conclusion is that in reintroductions in such environments it is better to spread invaders (e.g. seeds) over different patches rather than to introduce them each generation in one and the same patch. It was conjectured that the result might hold in general. Together with Vladimir Vatutin a further theoretical analysis of this conjecture was made; the ultimate objective is providing a formal proof. In addition the scope of the investigation was widened by taking into account the effects of a Markovian dependence in the environment.

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ESS theory

Project leader: P. Haccou

In this project the step in the opposite direction, from population dynamics to properties of individuals, is made through the ESS route. In addition statistical methods are developed for analysing data on individuals in a manner useful for evolutionary theorising.

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 can 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, while the costs associated with production keep increasing. Furthermore, it is assumed that developmental errors can occur, which render the gene product unable to perform its function. Under the assumption that the resident population has evolved to an optimal production strategy, we calculated the optimal amount of gene product. Using this as a starting point we determined the circumstances under which rare mutants with a second gene performing the same function can invade. This second gene is also subject to developmental errors, which may be correlated with the errors affecting the first gene. We have shown that under these circumstances redundancy can evolve and we have also calculated the optimal production of the second gene. This conclusion is surprising, because mutants not only have higher production costs, 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 genetic redundancy a period of change in the environment would be necessary. Our model shows that this is not the case. Another surprising conclusion is that when the first gene already produces the threshold value of the substance, the conditions under which redundancy can arise are less strict than when the first gene produces less than the threshold value. This suggests that full redundancy should be more common in nature than partial redundancy. A paper detailing these results has been submitted.

2.2 **Development of Butterfly Wing Patterns** (J.A.J. Metz, with A. Monteiro (AIO) and P. Brakefield; ended end 1998): 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** (started in 1999; E. Meelis with P. de Jong): An optimal test has been derived for detecting sperm precedence.

2.4 **War of Attrition Models for Food Patch Leaving** (P. Haccou, with C. Cannings, Sheffield, and O. Glaizot): The war of attrition is a model of contest behaviour, where two or more contestants compete for an indivisible resource (Maynard Smith, 1974). Each competitor chooses a persistence time in advance, unknown to the others. The individual with the longest persistence time gets the reward. Each individual pays a cost which is equal to some positive constant (the cost rate) times the duration of the game. In the original model, all

competitors have equal cost rate and reward. In the Asymmetric WOA payoffs of staying and leaving depend on the 'role' of a contestant. One of those roles is 'favoured'; individuals with that role have a smaller cost rate and/or a higher final reward. Hammerstein and Parker showed for the two contestants case that no ESS can exist if both have complete information about their role. However, if mistakes in role perception occur, there is a single ESS characterised by two explicitly expressable probability density functions for the staying time conditional on the perceived role. In the Generalized WOA, analysed by Bishop and Cannings (1981) cost rates and reward are not necessarily constant. Sjerps and Haccou (1994a,b) generalized B&C's results to include cases where costs and rewards may be equal after a finite time and showed that the model can be used to study migration strategies of moth larvae on a host plant. However, they only considered symmetric situations. In the present project we consider a GA-WOA where conditional payoff functions may change in time and after some time are equal. One of the applications is the study patch leaving by moth larvae under competition when there are asymmetries between contestants, e.g. due to age-differences. Some superparasitism models can also be phrased in this manner, with the asymmetry being due to differences in arrival time. We derived the ESS strategy for the situation with two competitors when there are mistakes in role perception, once again in the form of explicit expressions for the distributions of the conditional strategies, together with procedures for calculating numerical approximations.

2.5. **Sex Ratio Theory** (started 1999; E. Meelis, with S. Krakov, Berlin, and I. Hardy, Aarhus). A chapter in the Sex Ratio Handbook edited by I. Hardy was written on the analysis of sex ratio variances and sequences of sex allocation.

2.6. **Battle of the Sexes** (S. Mylius, guest, ex-OIO; ended in 1998): 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. The last steps in the analytical and numerical exploration of the model were made and the final manuscript was sent in.

2.7. **Life History Theory** (J.A.J. Metz, with T. van Dooren, Antwerp, M. Heino, Helsinki, U. Dieckmann, Laxenburg): P.M. 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. There were no new developments in 1998. In 1999 two grant aplications were written (for a large EU project together with 5 other institutions and for an ALW AIO; both successful).

Adaptive Dynamics

project leader: J.A.J. Metz

This project considers evolutionary time-scales and the species level as well as between-species interaction. Our aim here is the construction of an overarching theory of phenotypic evolution, as a direct dynamical extension of the evolutionary statics of ESS theory. This theory also deals with coevolution and with the treelike structure of character evolution through adaptive speciation.

3.1. **Evolutionarily Singular Points for Higher Dimensional Trait Spaces** (J.A.J. Metz, with S.A.H. Geritz, Turku, E. Kisdi, Budapest, G. Meszena, 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 further 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. Meszena, 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 1998/99 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. In the wake of these bifurcation results a new mechanism for evolutionary cycling was discovered in which a branching is followed by the extinction of one of the lines of descent whereupon the population again evolves towards the branching point etc., a situation remniscent of the purported evolutionary history of the Gryphea oysters.

3.3. **Evolution in Metapopulations** (started in 1998; 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). In 1999 this concept was used to derive an analytic expression for the ES conditional dispersal strategy for individuals which can account for the overall patch quality and the instantaneous local population size. Two papers on these subjects were submitted. In addition a number of numerical studies were made of ES unconditional dispersal strategies for various special assumptions about the local population dynamics. These should lead to two further submissions in 2000.

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 1998/99 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. In addition we have started to investigate the developmental constraint that keeps the phylotypic stage constant. Finally, a subproject was started on the role of phenotypic plasticity and genetic assimilation in the process of adaptation and evolutionary change.

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 1998/99 (but see subproject 3.9). However, we expect to return to it in 2000.

3.6. **Adaptive Dynamics in Context** (J.A.J. Metz and U. Dieckmann, Laxenburg; to be ended in 2001): 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 1998/99. 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** (started in 1998; J.A.J. Metz, with M. Sabelis, Amsterdam, U. Dieckmann, Laxenburg, and K. Sigmund, Vienna; to be ended in 2000): 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 takes stock and surveys 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** (started in 1999; P. Haccou, with K. Riebel and C. ten Cate): A grant application entitled 'Sexual imprinting, song learning and gene-culture co-evolution: modelling the evolution of brood parasitism in birds' was submitted to ALW (NWO) and granted. In 2000 the associated PhD project will commence. Outline: Sexual imprinting, the acquisition of mate preferences through learning characteristics of parents or siblings early in life, occurs in many bird species. In this project the role of sexual imprinting and song learning in the evolution of interspecific brood parasitism in birds will be examined by means of models for gene-culture co-evolution and adaptive dynamics. We will consider three families of bird species in which brood parasitism is frequent, i.e. two families of songbirds, the Viduinae and cowbirds, and one family of non-songbirds, the cuckoos. In almost all of the known Viduinae species, males mimic aspects of the song of their foster fathers along with their species specific song and females prefer to mate with males that sing the song of their foster father. It has been suggested that in this family, host song learning and imprinting have an important role in the origin and maintenance of the linkage between host species and brood parasites. This family mainly consists of specialistic parasites and it is believed that host colonisation in this family is a major driving force in rapid speciation. We will first develop models for the Viduinae, to examine the origin of broodparasitism in this family and the subsequent process of host colonisation and speciation. Subsequently we will adjust the models to study these processes in cowbirds and cuckoos and relate the different mechanisms of mate preference and song learning to the different evolutionary history in these three families.

3.9. **Adaptive Speciation** (started in 1999; J.A.J. Metz, with U. Dieckmann, Laxenburg, D. Tautz, Cologne, M. Doebeli, Basel; to be ended in 2002): 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. In December 1999 a workshop on sympatric speciation was organized to

take stock of the possible connections. This workshop should engender a book on this topic, to be edited over 2000 and 2001, that should set the agenda for future research.

controleer de projectnaam, geef aan wie projectleider is; zorg voor een begrijpelijke projectbeschrijving; geef de wetenschappelijke vorderingen aan en maak daarbij gebruik van begrijpelijke, liefst zelfs aantrekkelijke taal; gebruik per project maximaal ½ A4 om de voortgang van het onderzoek te beschrijven.

Een overzicht van het in 1998/9 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	Associate 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	until 31-12-99	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. 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
Dr. S.D. Mylius	Researcher	volunteer	p.m. until 5-99
Dr. M. Schipper	Researcher	volunteer	1-7-98 – 31-5-99
Dr. J. Val	Researcher	volunteer	until 1-7-98

schrap personeel dat in 1999 niet meer aanwezig was
vul aan met personeel dat in 1999 voor het eerst aanwezig was
geef voor personeel dat niet voor het hele kalenderjaar was aangesteld datum aan van aanstelling resp. vertrek
geef per persoon de omvang van de aanstelling op jaarbasis, indien < 1
corrigeer evt. fouten in aangeleverde informatie

Een overzicht van de research output in 1999, volgens de aangegeven indeling

1999:

geef de lijst met publicaties, in 1999 verschenen in scientific journals en scientific reports

Bosch F van den, JAJ Metz and JC Zadoks. Pandemics of Focal Plant Disease, a Model. Phytopathology 89.6 (1999): 495-505. (1)

Diekmann O, Mylius SD, ten Donkelaar JR. Saumon a la Kaitala et Getz, sauce hollandaise. Evolutionary Ecology Research 1 (1999): (3) 261-275. (2)

Galis F. On the homology of structures and Hox genes: the vertebral column. Homology (1999) (Novartis Foundation symposium 222): 80-94. (3)

Galis F. Why Do Almost All Mammals Have Seven Cervical Vertebrae? Developmental Constraints, Hox Genes, and Cancer. Journal of Experimental Zoology (Mol Dev Evol) (1999) 285: 19-26. (3)

Geritz, SAH, E van der Meijden and JAJ Metz. Evolutionary Dynamics of Seed Size and Seedling Competitive Ability. Theoretical Population Biology 55 (1999): 324-343. (3)

Gyllenberg, M. and J.A.J. Metz. On Fitness in Structured Metapopulations. IIASA Studies in Adaptive Dynamics 37 (1999): 1-13 (preprints). (3)

Gyllenberg, M. and J.A.J. Metz. On fitness in structured metapopulations. Research Report (1999) A38, University of Turku, Institute of Applied Mathematics, ISBN 951-29-1441-7. (3)

Meszéna, G. and J.A.J. Metz. Species Diversity and Population Regulation: The Importance of Environmental Feedback Dimensionality. IIASA Studies in Adaptive Dynamics 38 (1999): 1-24 (preprints). (3)

Jansen, V.A.A. and Mulder, G.S.E.E. Evolving biodiversity. Ecology Letters (1999) 2: 379-386. (3)

Metz, J.A.J. and M. Gyllenberg. How Should We Define Fitness in Structured Metapopulation Models? Including an Application to the Calculation of Evolutionarily Stable Dispersal Strategies. IIASA Studies in Adaptive Dynamics 36 (1999): 1-18(preprints). (3)

Metz, J.A.J. and M. Gyllenberg. How should we define fitness in structured metapopulation models? Including an application to the calculation of ES dispersal strategies. Research Report (1999) A39, University of Turku, Institute of Applied Mathematics. (3)

Mylius, S.D. What Pair Formation Can Do to the Battle of the Sexes: Towards More Realistic Game Dynamics. Journal of Theoretical Biology (1999) 197: 469-485. (2)

Pappers, S.M., T.J. de Jong, P.G.L. Klinkhamer and E. Meelis (1999). Effects of nectar contents on the number of bumblebee approaches and the length of visitation sequences in Echium vulgare (Boraginaceae). Oikos 87: 580-586. (1)

Seehausen, O., F. Galis and N. Bouton. Cichliden in Oost-Afrika. Evolutie betrapt. Natuur & Techniek 67(1999): 6-15. (3)

geef de lijst met books and book chapters

Haccou, P., M. Sjerps and E. van der Meijden. To leave or to stay, that is the question: predictions from models of patch-leaving strategies. In: H Olff, VK Brown and RH Drent eds. Herbivores: between Plants and Predators. Blackwell Science, Oxford (1999), pp.85-108. (2)

Seehausen, O., F. Galis and N. Bouton. Soortvorming en het ontstaan van verscheidenheid bij cichlide vissen. In: Evolutie betrapt. Eds. Van Strien et al. KNNV. (1999). (3)

geef de lijst met professional publications

reeds aanwezig

geef de lijst met editorial output

reeds aanwezig

geef aan welke promoties plaatsvonden

Schipper, M. Towards a Sequential Analysis of Environmental Monitoring Data. 12 May. Leiden University. Promotor: Prof. Dr. J.A.J. Metz. 179 pp. Proefschrift UL. (1)

Mylius, S.D. The Good The Bad and The Fittest. Evolutionary Games in Structured Populations. 26 May. Leiden University. Promotors: Prof. Dr. O. Diekmann, Prof. Dr. J.A.J. Metz. 157 pp. Proefschrift UL. (2)

1998:

Publications in scientific journals

Bowmer CT., R.N. Hooftman, 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 1998.

F. Galis. Why do almost all mammals have seven cervical vertebrae? Developmental constraints, Hox genes and cancer. Utrecht Genetics Seminars (Human and veterinary geneticists), University of Utrecht. 16 September 1999.

F. Galis. Why do almost all mammals have seven cervical vertebrae? Developmental constraints, Hox genes and cancer. Symposium 'Société des Neurosciences', Luik, Belgium. 7-8 October 1999.

P. Haccou Implication of Environmental Fluctuations for Establishment Probability. Workshop population dynamics. Göthenburg, 11 - 15 May 1998.

P. Haccou Patch leaving strategies and superparasitism. VII International Congres of Ecology in Florence, 19 - 25 July 1998.

P. Haccou: Establishment probability of small populations in fluctuating environments, 4th International conference on difference equations and their applications, Poznan, Poland, 27 - 31 August 1998.

P. Haccou, Chalmers University, Gothenberg, 16-22 August 1999.
P. Haccou. IIASA, Laxenburg, 20 September – 2 October 1999.

F.J.A. Jacobs On the Geometrical Representation of Evolutionary Processes. Applied Mathematics Group of the Faculty of Mathematics, Utrecht, March 1998.

F.J.A. Jacobs Bifurcation Analysis for Adaptive Dynamics Based on Lotka-Volterra Models. Budapest, November 1998.

F.J.A. Jacobs Workshop Applied Bifurcation Analysis: Bifurcation Analysis for Adaptive Dynamics Based on Lotka-Volterra Models. Antwerp. December 1998.

F.J.A. Jacobs. Bifurcation Analysis for Adaptive Dynamics Based on Lotka-Volterra Models. Annual Meeting Nederlandse Vereniging voor Theoretische Biologie, Texel,. 22 - 23 April 1999.

F.J.A. Jacobs. Bifurcation Analysis for Adaptive Dynamics Based on Lotka-Volterra Competition Models. Session: Evolution, Game Theory and Adaptive Dynamics, Congress Theory and Mathematics in Biology and Medicine, Amsterdam 29 June - 3 July 1999.

J.A.J. Metz Between Population Dynamics and Adaptive Dynamics. Workshop population dynamics. Göthenburg, 11 - 15 May 1998.

J.A.J. Metz Adaptive Dynamics: population dynamics evolutionary twist. Conference on Nonlinear Demography in Rostock, 26 - 29 May 1998.

J.A.J. Metz From population dynamics to adaptive dynamics. VII International Congres of Ecology in Florence, 19 - 25 July 1998.

J.A.J. Metz Adaptive Dynamics, population dynamic's evolutionary twist. Research School SOM, Groningen 4 September 1998.

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 1998.

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 1998.

J.A.J. Metz. Adaptive dynamics of seed size: branching and bifurcations. Ecole Normale Supérieure, Paris. During a symposium on "The mathematics of Biological Adaptation". 29 January 1999.

J.A.J. Metz. Adaptive dynamics in multidimensional trait spaces. Ecole Normale Supérieure in Paris. During a symposium on "The mathematics of Biological Adaptation". 29 January 1999.

J.A.J. Metz. Adaptieve Dynamica: een wiskundige opstap van populatie dynamica naar lange termijn evolutie. 34e Nederlands Mathematisch Congress, Utrecht. 8-9 April 1999.

J.A.J. Metz. From Population Dynamics to Adaptive Dynamics. NATO Advanced Study Institute on Mathematical Problems Arising from Biology. Fields Institute for Research in Mathematics, Toronto, 14-24 June 1999.

J.A.J. Metz (co-author S.Geritz). Bifurcations of Evolutionarily Singular Points exemplified by a model for Seed Size Evolution (and some further applications). NATO Advanced Study Institute on Mathematical Problems Arising from Biology. Fields Institute for Research in Mathematics, Toronto. 14-24 June 1999.

J.A.J. Metz (co-author S.Geritz). Adaptive Dynamics, Population Dynamics' Evolutionary Twist. 4th European Conference on Theory and Mathematics in Biology and Medicine. Amsterdam. 29 June - 3 July 1999.

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

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
Editor Evolutionary Ecology
Editor Cambridge Series: Adaptive Dynamics

E. Meelis
Treasurer of the Institute
schrap lidmaatschappen die in 1999 niet meer bestonden
vul aan met lidmaatschappen die in (de loop van) 1999 zijn ontstaan
corrigeer foutieve tekst

Een overzicht van externally supported projects

NB. Het gaat hier om een nieuw overzicht van alle toegewezen (nog lopende) projecten.
Gevraagd wordt aan te geven:

- de naam van het project (NB.: het begrip project is hier anders dan bij vraag 2)
- omvang van de steun (aanduiding positie en/of aanduiding materieel krediet in k*f*)
- tijdsduur project (bijv. 1998-2001)
- subsidiërende instantie

NWO awarded a grant of DFL. 14,750 to Prof. Dr. P. Turchin, Dept. of Ecology and Evol. Biology, University of Connecticut to visit Leiden from 19 March until end June 1998.

Grant for one OIO from ALW (not appointed yet due to lack of suitable candidates).

Grant for one Postdoc (by EU as part of a programme together with IIASA, Turku, Bergen and Paris for research on "Modern Life-History Theory and Its Application to the Management of Natural Resources") for three years (to be appointed in 2000). Euro 36,300 plus Euro 5,000/year.

Yuri Robbers was awarded a grant by NATO to attend the NATO ASI on Mathematical Problems arising from Biology held at the Fields Institute at the University of Toronto, Canada from June 11 till June 24 1999.

Een overzicht van door gasten gehouden lezingen binnen het EEW

geef aan welke gastsprekers een voordracht voor het EEW hielden (datum, naam gastspreker, funktie 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 1998.

Prof. Dr. R. Lande. University of Oregon, Eugene, USA, 27 August 1998. 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 1998. 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

Dr. Arne Mooers, UvA, 4 February 1999. Bottleneck-mediated speciation – Wright, Fisher, Mayr and the young Turks. During his lecture he also discussed Coyne *et al*.'s 1997 article "A Critique of Sewall Wright's shifting balance theory of evolution".

Dr. Adam S. Wilkins, Cambridge, UK. 26 April 1999. The evolution of sex determination pathways: are there general rules?

Prof. Russ Lande, University of California, San Diego, USA. 27 April 1999. Sex-ratio meiotic drive and sexual selection in stalk-eyed flies.

Mark Purnell, Bursar of Novartis Foundation, University of Leicester, England, 31 May – 19 June 1999.

Prof. Mike Bell, State University of New York, Stony Brook, 17 - 18 August 1999.

Dr. Arne Mooers, UvA, 12 November 1999. The influence of extinction on evolutionary history.

Lauren Chapman, University of Florida, Gainsville, USA. 6 December 1999, Refuges, Barriers, and Biological Sieves: Swamps and Fish Diversity in East Africa.

Vladimir Vatutin, Dept. of Discrete Mathematics, Steklov Mathematical Institute, Moskow, Russia, 21 December 1999, Branching processes and genetic divergence.

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

Geef aan voor 1e fase:
- naam van het vak met aantal college-uren
- naam van het vak met aantal practicum-uren + aantal practicanten
- naam van vak(ken) met tentamen + aantal tentamendeelnemers
- naam cursus met cursusduur in weken en aantal cursisten
- aantal maanden begeleiding stagestudenten.

Geef aan voor 2e fase:
- aantal maanden begeleiding interne promovendi
- naam cursus met cursusduur in weken en aantal cursisten

1998:

M. Dutmer. Assisting 2nd year Statistics, 12 hours practical.

F. Galis (together with J.A.J. Metz). Seminarium Evolution and Development. 14 students. 3-4 months.
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 2nd year Statistics: 16 hours lectures plus 12 hours practial.
E. Meelis Supervisor of PhD students M. Schipper and M.Y. Dutmer.

P. Haccou. Teaching of 1st year Basic Mathematics: 10 hours lectures including exercises.
P. Haccou. Teaching of 1st year Mathematical Processes in Biology: 18 hours lectures plus 20 hours exercise classes.
P. Haccou. Supervision of PhD student: Y. Robbers.

P. Haccou. EEW Curriculum Committee
P. Haccou. Education Committee, Research School Functional Ecology.
P. Haccou. COBIOL (Coo Biologie)

J.A.J. Metz. Teaching of 1st 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 .

Y. Robbers. Assisting workgroups 1st year Maths, 20 hours; 1st year Statistics including revision, 3 weeks; 2nd year Statistics, 12 hours.

1999:

M. Dutmer. Assisting 1st year Statistics.
P. Haccou. Teaching of 1st year Basic Mathematics: 6 hours practical.
P. Haccou. Teaching of 1st year Mathematical Processes in Biology: 16 hours lectures plus 32 hours exercise classes.

J.A.J. Metz. Teaching of 1st year Statistics: 22 hours lectures including exercise classes.

E. Meelis. Teaching of 2nd year Statistics: 16 hours lectures plus 12 hours practical.

Y. Robbers. Assisting 1st year Maths (32 hours practical); 2nd year Statistics (12 hours practical).
Y. Robbers. Developing and teaching advanced course in theoretical biology "van data naar werkelijkheid" with G. Mulder and various guest lecturers (12 day course, 2 months development).

Een overzicht van externe promotie-begeleiding

P. Haccou. External Examiner, Greg Colbert, University of Adelaide.
P. Haccou. External Examiner, Marcel Luiz Hernandez, University of Bristol

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. 1998, 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 1998, 8 participants

J.A.J. Metz . Organising Committee Workshop on Virulence Management, IIASA 1998. ?????

J.A.J. Metz, VIITH Congress of the European Society for Evolutionary Biology, Barcelona, Spain (visited and together with Ulf Dieckmann and Michael Doebeli organized a one day sympsosium "Linking Ecology to Evolution: Non-Equilibrium Processes and Adaptive Dynamics"). 24-28 August 1999.

J.A.J. Metz together with Ulf Dieckmann (Adaptive Dynamics Network, IIASA), Michael Doebeli (formerly at Basel, now UBC, Vancouver) and Diethard Tautz (U Koeln) organized a Workshop "The formation of biodiversity through adaptive speciation",at IIASA, Laxenburg, Austria. 10 - 13 December 1999.

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

P. Haccou.
Judging Committee ALW

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 (2 months sabbatical time)
Committee Non-linear Population dynamics, NWO Priority Program Nonlinear Systems
Curator LUF endowed chair Philosophy of Biology
Project Leader ADN + Curatorship

schrap lidmaatschappen die in 1999 niet meer bestonden
vul aan met lidmaatschappen die in (de loop van) 1999 zijn ontstaan
corrigeer foutieve tekst

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 plaats van de uitreiking, naam van de uitreiker)

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

Do the following need to be included anywhere?

F. Galis. Newsfeature in Science, 23 July 1999 by Elisabeth Pennisi after Evolution Congress in June in Madison: E. Pennisi, 1999. Development shapes evolution. Science 285: 518-519.

Yuri Robbers Congress Nederlandse Vereniging voor Gedragsbiologie (NVG), Dalfsen. 15-17 December.

Version at 6 July 2000

Gegevens jaarverslag 1998-1999 van sectieleiders

1. Een algemene beschrijving van het onderzoek van de sectie

Theoretical Biology and Phylogenetics
Section Chair: E. Gittenberger
The section studies patterns and processes involved in evolutionary change. Macroevolution, speciation in particular, is a major area of interest. Evolutionary and ecological issues are investigated by use of theoretical and experimental research. Gastropods and arachnids are used as model systems 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 co-operates with researchers in the National Museum of Natural History (NNM) in projects on evolutionary aspects of past and present biodiversity.

2. Een beschrijving van de voortgang van het onderzoek op het niveau van de projecten

I. Conceptual and Methodological Foundations of Phylogenetics
project leader: D.J. Kornet
This project aims to contribute to the development of conceptual and methodological issues in the theory of Phylogenetic Systematics.

Ia. Title: Keyconcepts in Phylogenetics. (D.J. Kornet)
The interpretation of terminal entities of phylogenies as Composite Species (defined by cladogenesis and character fixation as primary and secondary criteria) entails various methodological implications. Methods for coding character states of polymorphic taxa as used in practice were detected, analysed, and evaluated. Ignoring the demand of fixation appears to lead to the artificial introduction of reversals, overruling or dimming the phylogenetic signal. A taxon should by coded by the ancestral of its polymorphic character states, or by a question mark if the polarity of the states is unknown. A manuscript on polymorphism coding methods was submitted to Systematic Biology.

Ib. Title: Phylogeny Reconstruction and Analysis of Historical Associations. (M. Zandee)
Progress: Ir. M.G.P. van Veller and his supervisors Dr. M. Zandee and Prof. Dr. D.J. Kornet studied the role of methodological assumptions in the analysis of biogeographical patterns. It was discovered that sets of such assumptions must be inclusive, otherwise the resulting historical patterns are internally inconsistent. A manuscript was prepared and submitted to Cladistics (accepted and published in 1999; http://wwwbio.leidenuniv.nl/~zandee/include.pdf). It was discovered that most methods and respective computer implementations for the analysis of biogeographic patterns do not obey the requirement of inclusion. A manuscript was prepared and submitted to Cladistics (accepted in 1999; http://wwwbio.leidenuniv.nl/~zandee/methods.pdf). Most of the methods (and some computer implementations) can be changed and remedied in a way such that all requirements to make them internally consistent are fulfilled. A manuscript was prepared and submitted to Cladistics (http://wwwbio.leidenuniv.nl/~zandee/remedies.pdf).

II. Bioinformatics and Self-Organizing Systems
project leader: D.J. Kornet (F.H.D. van Batenburg, A.P. Gultyaev, D.J. Kornet)
This project aims to contribute to the field of Bioinformatics by data-mining and the simulation of complex systems, and to the theory of self-organizing complex systems.

With respect to the simulation of folding of elements of RNA tertiary structures, the data on the known functional RNA pseudoknots are being collected in the database, available on the Internet (manuscript accepted in 1999). An approximation for thermodynamic stabilities of RNA pseudoknots, based on the general polymer theory, is developed (manuscript published). A phylogenetically conserved structure, important for discontinuous RNA transcription, is revealed in the arterivirus group (manuscript published in Proc.Natl.Acad.USA together with the group of Eric Snijder, LUMC). A version of the program for predicting single-stranded DNA folding has been developed (in particular, used for analysis of RNA-DNA annealing during HIV replication - manuscript published with the group of Ben Berkhout, AMC Amsterdam).

The folding dynamics of viroids (plant pathogens, consisting of RNA) has been studied by computer simulations. The evolutionary conserved metastable hairpins are revealed in replicative intermediates of negative polarity. It has been shown that the formation of viroid RNA structure (and hence replication efficiency) is determined by dynamics of competition between alternative structures with different folding pathway requirements for plus- and minus-strand RNAs. Analysis of natural and forced evolution of viroid replicons demonstrates a high flexibility of RNA adaptation for such structural requirements (manuscript published). A conserved metastable hairpin, predicted earlier to be functionally important in the family of plasmid-encoded genes, was experimentally proven in the group of C.W.A. Pleij (manuscript published).

The prime example of scientific theories referring to universal categories is the atomic theory referring to the category of atoms. Progress has been made in extending this model for scientific theories to all categories of self-organizing complex systems that emerge spontaneously as stable configurations of matter, including living matter.

Molecular and Morphological Phylogenetics
Project-leader: E. Gittenberger
Description:
Progress:

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 hybrizymes, high concentrations of an otherwise uncommon variant of an intron may also be found in hybrids. 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, which was accepted for publication. She investigated the intra- and interindividual variation of rDNA ITS1; the results point at more variation than expected, which lowers the usefulness of this frequently used DNA for phylogeny reconstruction. The same DNA segment was studied in cooperation with Dr. G. Armbruster (Leipzig): parts of it turned out to be phylogenetically informative at quite different taxonomic levels. Manuscripts were finished on these two subjects and on convergent evolution in shell characters among *Albinaria* and *Isabellaria* species in S. Greece. Drs. M. Graafland investigated the occurrence of a peculiar, still undescribed, anatomical detail in a group of *Albinaria* species. The results, will be used in a broader context. They support the phylogeny of the taxa suggested by molecular methods, indicating convergence in shell characters.

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 (= CA) 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 by sequencing CO1 mtDNA for about 50 taxa. The preliminary results suggest that both convergence and reversals have occurred in the development of the CA. During extensive fieldwork in Greece much additional research material was collected.

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 or whether these populations simply reinvaded the Alps following the glacial retreat.
In a pilot study ITS1 rDNA had been used to investigate the question. Some populations were studied, but without unequivocal results. Fieldwork in N. Austria, N. Italy, SE. France and NE. Spain brought important new research material. The project was continued in 1999 by W. H. Piel and his student D. Groenenberg using mitochondrial markers. CO1 mtDNA was used to study the relationships between the alleged nunatak forms and those that are supposed to have invaded the Alpine lowlands postglacially. The project will be submitted for publication in mid 2000. The preliminary results suggest a.o. that Pleistocene survival in nunatak-like refugia in the Alps is a realistic scenario for *Arianta*.

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. A sufficient amount of potentially decisive live material for DNA sequencing and subsequent phylogeny reconstruction and dating was collected but could not yet be investigated. The molecular aspects of this project will be studied in the year 2000.

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. Gultyaev, 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 (J.A.J. Metz) using computer modelling, 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 J.A.J. 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.

g. Web evolution in orb-weaving spiders. The advent of the orb-web in spiders caused an explosion of diversity, innovation, and adaptation. Many evolutionary theories concerning everything from web architecture to sexual size dimorphism have been developed from hypotheses of spider phylogeny – yet our understanding of their evolutionary history is poor. W. H. Piel is collecting mitochondrial and nuclear sequence data to produce, for the first time, a molecular phylogeny of orb-weaving spiders. Currently two mitochondrial and three nuclear gene regions are being sequenced. When this on-going project is complete, evolutionary adaptive hypotheses will be studied in light of this new phylogeny.

Past and Present Biodiversity
Project-leader: E. Gittenberger
Description: 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 AIOs in this project, Prof. dr. E. Gittenberger is responsible as promotor.
Progress:

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, Platycnemidiae), the role of West Malaysia and the Philippines'. A third, relatively large part of the thesis came close to completion.
Ir. H.J. Megens, 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. After having spent much time in a search for useful molecular markers, most of the sequencing could be finished in 1999.
Dr. W.H. Piel, in collaboration with Dr. P.J. van Helsdingen, started sequencing mitochondrial markers in order to detect whether speciation has occurred in *Enoplognatha* spiders. Two closely related spider species exhibit almost complete overlap in their distribution and habitat preference, yet they independently maintain nearly identical polymorphic colour patterns. Numerous papers have sought to explain this anomalous case, but always assuming that the species are separate. Current results with CO1 do not show any consistent genetic differences between the two species. Piel will continue to look for other, faster evolving genetic markers.
Drs. C.J.H.M. Fransen, Drs. J. van Tol, and Drs. F.P. Wesseling, curators at the NNM continued 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 and on-going tasks as museum curators. Several concept articles were discussed.

3. Een overzicht van het in 1999 bij de sectie werkzame personeel (zie hieronder)

STAFF

Senior Investigators	Function	Source of Finance	Details
Prof. Dr. E. Gittenberger	Professor		0.3 (0.7 NNM)
Prof. Dr. D.J. Kornet	Endowed Professor	LUF	
Dr. F.H.D. van Batenburg	Associate Professor	Leiden University	
Dr. M. Zandee	Associate Professor	Leiden University	

Postdocs

Dr. R. v.d. Bos	Researcher	NWO	0.8 until 31-3-98
Dr. A.P. Gultyaev	Researcher	NWO	until 18-2-98
Dr. W. Piel	Researcher		from 1-3-99
Dr. M. Schilthuizen	Researcher		till ?-1998
Dr. H. Turner	Researcher	NWO	untill 30-4-98

Junior Investigators			
D.W.K. Gassmann, Dipl. Biol.	Research Assistant	SLW	until 31-12-98
Ir. H.J.W.C. Megens	Research Assistant	SLW	
Drs. C.H.M. van Moorsel	Research Assistant		until 28-2-99
Drs. T.A.C. Reydon	Research Assistant		from 1-12-99
Ir. M.G.P. van Veller	Research Assistant	SLW	
Drs. D. Uit de Weerd	Research Assistant		from 15-11-98

Analytical, Technical and Administrative Staff

E.A. van Ast-Gray	Secretary	Leiden University	from 24-8-98	0.5
H. Groenhuijzen	Secretary	Leiden University		0.5
Dr. A.P. Gultyaev	Scientific Programmer	Leiden Univeristy	from 19-2-98	0.5
Y.M. Zitman-de Graaf	Secretary	Leiden University	until 31-8-98	0.5

Guests

Dr AC van Bruggen	researcher	volunteer		
Prof. Dr. P. Dullemeijer	researcher	volunteer	0.1	
D.W.K. Gassmann, Dipl. Biol.	Research Assistant	SLW	from 1-1-99	
Dr. Y.S.D.M. de Jong	researcher		from 1-10-98	
P.J. Kuijten	researcher	volunteer		
Drs. C.H.M. van Moorsel	Research		from 1-3-99	

	Assistant			
T. Pieters	research assistant	NWO	2-6-98 – 1-9-98	
Dr. H. Turner	researcher	NWO	from 1-11-98	
Dr. M.B.H. Visser	researcher	NWO	until 31-5-99	0.2
Dr. Ir. A.J. de Winter	researcher			

Lecturers

Drs. L.E. Paula		Leiden University	from 1-10-99
Dr. Th.E. Sprey	Assistant Professor	Leiden University	until ?-1999
Dr JC von Vaupel Klein	Associate Professor		
Dr. H. Verhoog	Assistant Professor	Leiden University	until 31-10-99

schrap personeel dat in 1999 niet meer aanwezig was
vul aan met personeel dat in 1999 voor het eerst aanwezig was
geef voor personeel dat niet voor het hele kalenderjaar was aangesteld datum aan van aanstelling resp. vertrek
geef per persoon de omvang van de aanstelling op jaarbasis, indien < 1
corrigeer evt. fouten in aangeleverde informatie

4. Een overzicht van de research output in 1999, volgens de aangegeven indeling 1998:

Publications in scientific journals

Aartsen J.J. van, **E. Gittenberger** and J. Goud. Pyramidellidae (Mollusca, Gastropoda, Heterobranchia) collected during the Dutch CANCAP and MAURITANIA expeditions in the south-eastern part of the North Atlantic Ocean (part 1). Zoo. Verh. Leiden 321 (1998): 1-57. **III**

Batenburg, F.H.D. van. Powerful and Easy Business Graphics: Is Rain the Answer? APL Quote Quad 28,1 (September 1977): 16-27. (verschenen in 1998) **II**

Batenburg F.H.D. van, E de Ridder and J de Kerf. APL Extended Compared With Other Languages According to Halstead's Theory. ACM Sigplan 33 (1998): 54-60. **II**

Bos R. van den. Post-conflict stress-response in confined group-living cats (Felis silvestris catus). Applied Animal Behaviour Sci. 59 (1998): 323-330.**I**

Bos R. van den. The Function of Allogrooming in Domestic Cats (Felis silvestris catus); a Study in a Group of Cats Living in Confinement. J.Ethol. 16 (1998): 1-13.**I**

Bos R. van den, C. Nolten and **M.G.P. van Veller**. Phylogenetic reconstruction of a neural network underlying theory of mind in primates. Europ. J. of Neurosci. 10 (suppl.10) (1998): 197.**I**

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Hutterer R. and **E. Gittenberger**. A dwarf on the rocks: Ripkeniella petrophila gen. et spec. nov. (Gastropoda Pulmonata: Hygromiidae), a tiny petrophilous snail from La Gomera, Canary Islands. Basteria 62 (1998): 117-122. **III**
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Bos, R. van den. Welzijn van Dieren en Dierenwelzijnsbeleid: een kritische inleiding. Tilburg University Press (1997): 1-18. (verschenen in 1998)**I**
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5. Een overzicht van de invited keynote addresses

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

E. Gittenberger. The Non-Adaptive Zonitid Radiation. 8th International Congress on the Zoogeography and Ecology of Greece and Adjacent Regions, Kavala, Greece. 17-21 May 1999.

A.P. Gultyaev. Thermodynamics of bulge-pseudoknots and pseudoknot stalks upstream of tRNA-like structues in plant viral RNAs. EU Consortium on 'RNA Structure and Function', (under the Framework of EU project), Midterm Meeting, Rome, 23-25 September 1999.

D.J. Kornet. Coding Polymorphic Taxa for Phylogeny reconstruction. Assessing Historical Biogeographic and Coevolutionary Associations: A Workshop, Department of Zoology, University of Toronto, Canada, 24 October 1998.

D.J. Kornet The overestimation (by society) and underestimation (by scientists) of the role of the subject in science. State of the World Forum, San Francisco. 30 October 1998.

D.J. Kornet. Micro-evolutionary species as Natural Kinds of selforganising systems. Summer Seminar: "Paradigm Shifts In Bioscience", Konrad Lorentz Institut, Altenberg, Vienna, Austria. 28 May 1999.
.
D.J. Kornet. Selforganised things, Natural Kinds, and Theoretical Categories. Workshop Selforganisation and Natural Kinds, International Symposium on Philosophy of Natural Sciences, Lorentz Centre, Leiden. 2 June 1999.

W.H. Piel. TreeBASE: a database of phylogenetic knowledge. The 2nd International Workshop of Species 2000, Tsukuba, Japan. 14-16 July 1999.

W.H. Piel. TreeBASE: a database of phylogenetic knowledge. Species Diversity Information Systems on the Internet symposium, XVI International Botanical Congress, St. Louis, Missouri. 1-7 August 1999.

H. Turner, P. Hovenkamp and P.C. van Welzen, 1999. Biogeography of SE Asia and the W Pacific. XVI Int. Bot. Congr., St. Louis, MO, U.S.A., 1-7 August 1999.

D. Uit de Weerd. Phylogenetically Endangered Genera of Greek Clausilids. 8th International Congress on the Zoogeography and Ecology of Greece and Adjacent Regions, Kavala, Greece, 17-21 May 1999.

M.G.P. van Veller. 1) Empirical Properties of Different Methods under Assumptions Zero, 1, and 2 in vicariance biogeography; 2) Component Analysis (CA). Assessing Historical Biogeographic and

Coevolutionary Associations: A Workshop, Department of Zoology, University of Toronto, Canada, 24 October 1998.

M.G.P. van Veller. 1) Assessment of methods in vicariance biogeography for obtaining inclusive solution sets under assumptions zero (A0), 1 (A1) and 2 (A2), oral presentation; 2) Common patterns in vicariance biogeography: a priori versus a posteriori methods, poster presentation. XVIIIth Meeting of the Willi Hennig Society in Goettingen, Germany. 12-17 September 1999.

M. Zandee. 1) The use of canonical correlation analysis in coevolutionary studies. 2) The analysis of historical associations by means of component compatibility analysis. Assessing Historical Biogeographic and Coevolutionary Associations: A Workshop, Department of Zoology, University of Toronto, Canada, 24 October 1998.

6. Een overzicht van lidmaatschappen van editorial and advisory boards

F.H.D. van Batenburg
Board Dutch APL Association
APL group (WG3) of International Standards Organisation
Nederlands Normalisatie Instituut afd. programmeertalen
Editor of "WhatsWhere" Column in Quote Quad

R. van den Bos
External Board Animals in Philosophy and Science, Van Gorcum, Assen

AC van Bruggen
IUCN Species Survival Commission Molluscs
Chief-editor Achatina
Chief-editor Basteria
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

DJ Kornet
Director, Prof. Dr. Jan van der Hoeven Stichting.
Member Steering Committee Symposium on Philosophy of Science, Faculty W&N and Faculty of Philosophy
Member Committee Summer University Supplementary Education Secondary School Teachers General Sciences in co-operation with Studium Generale and ICLON.
Member of the Board Research School Biodiversity per 1 May 1999

JC von Vaupel Klein
Page-charges Commissioner for the 'Netherlands Journal of Zoology'.

H Verhoog
Subcommittee Ethics and societal aspects, committee Genetic Modification (VROM)
Committee Ethical testing genetic modification of animals (LNV)
NIBI Committee Professional Code for Biologists
Study group intensive cattle farming (animal protection society)

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
Dutch Association for Bio-ethics

7. Een overzicht van externally supported projects

NB. Het gaat hier om een nieuw overzicht van alle toegewezen (nog lopende) projecten.
Gevraagd wordt aan te geven:

- de naam van het project (NB.: het begrip project is hier anders dan bij vraag 2)
- omvang van de steun (aanduiding positie en/of aanduiding materieel krediet in k*f*)
- tijdsduur project (bijv. 1998-2001)
- subsidiërende instantie

D.J. Kornet awarded dfl. 577,000 from the Education Stimulation Fund of the University Board (College van Bestuur) via Faculty of W&N and Faculty of Philosophy for Curriculum Development of "Foundations of Biology" for a period of four years.

8. Een overzicht van door gasten gehouden lezingen binnen het EEW

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

Stanislav Komarek, Karelsuniversiteit van Praag of Praag, Chair "Filosofie en Geschiedenis van de Natuurwetenschappen", 2-9 June 1998.

9. **Opgave van 1e en 2e fase onderwijsactiviteiten, w.o. aantal maanden begeleiding stagestudenten en aantal maanden begeleiding interne promovendi**

Geef aan voor 1e fase:

- naam van het vak met aantal college-uren
- naam van het vak met aantal practicum-uren + aantal practicanten
- naam van vak(ken) met tentamen + aantal tentamendeelnemers
- naam cursus met cursusduur in weken en aantal cursisten
- aantal maanden begeleiding stagestudenten.

Geef aan voor 2e fase:

- aantal maanden begeleiding interne promovendi
- naam cursus met cursusduur in weken en aantal cursisten

1998:

F.H.D. van Batenburg, Course "Programming, Modelling en Simulation"
F.H.D. van Batenburg, Course "Software Engineering"
F.H.D. van Batenburg, Supplementary Courses "Simulation", "APL".
F.H.D. van Batenburg, Doctoral Students: Sjoerd Ypema, Jan Oliehoek, Wouter Ent.

R. van den Bos, Co-Supervisor, Doctoral Student: Cynthia Nolten.

D.J. Kornet, 1st years teaching: Foundations of Biology – 12 hours lectures.
D.J. Kornet, Doctoral Students: Course Pattern Analysis and Biodiversity – 4 hours.
D.J. Kornet, Doctoral Students: Chris Henkels, Michel van Heijningen, Cynthia Nolten.
D.J. Kornet, Graduates: Foundations of Phylogenetic Systematics (Course) - (two weeks).
D.J. Kornet, Graduates: Biodiversity (Course) – 4 hours.

M.G.P. van Veller, Graduates: Historical Biogeography Course (one week).
M.G.P. van Veller, Co-Supervisor, Doctoral Student: Cynthia Nolten.

M. Zandee, 1st years teaching: Algorithmics for Biologists – 12 hours lectures + 2 day parts practical.
M. Zandee, Graduates: Foundations of Phylogenetic Systematics Course (two weeks).
M. Zandee, Graduates: Historical Biogeography Course (one week).

1999:
D.J. Kornet. Course on Foundations of Species Concepts. (Lectures, literature study, discussion, essays, presentations). 15-26 March 1999.

10. Een overzicht van externe promotie-begeleiding

11. Een overzicht van georganiseerde meetings

D.J. Kornet organized the International Symposium on Philosophy of Natural Sciences together with Physicists and Astro-Physicists from FW&N and Philosophers from the Faculty of Philosophy, Lorentz Centre, Leiden. 2-4 June 1999.
D.J. Kornet organized the Workshop Selforganisation and Natural Kinds, with o.a. keynote speakers Philip Ball (Senior Editor Nature) and Brian Goodwin, together with James McAllister, International Symposium on Philosophy of Natural Sciences, Lorentz Centre, Leiden. 3 June 1999.

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

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
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
Board of Directors of the Institute of Malacology, Philadelphia (Participating Member)
Board Onderzoekinstituut Rijksherbarium-Hortus Botanicus
Board Wissenschaftlicher Beirat Museum Alexander Koenig, Bonn.
Board Internationaler Redaktionelle Beirat der Senckenbergischen Naturforschenden Gesellschaft, Frankfurt
Foundation for Life Sciences-Werkgemeenschap 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.
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

schrap lidmaatschappen die in 1999 niet meer bestonden
vul aan met lidmaatschappen die in (de loop van) 1999 zijn ontstaan
corrigeer foutieve tekst

13. 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 plaats van de uitreiking, naam van de uitreiker)

On April 14 1999 **W.H. Piel** was awarded the "Harvard University Certificate of Distinction in Teaching" for the course "Ethology" in the academic year 1998.

14. Het verschaffen van illustratie-materiaal

D.J. Kornet Expert, Nationale Wetenschapsquiz Junior (VPRO/NWO), 26 December 1999. (Video Band)