

## Ecology of Butterflies in Europe

Due to the importance of butterflies as indicators of environmental quality and their usefulness as model systems to address ecological and evolutionary questions, butterfly biology has become a focus of research, especially within Europe. This book synthesizes all relevant and recent knowledge in the field, making this a definite work for those making use of this taxonomic group as a model system. It is divided into five major parts which deal with habitat use, population biology and genetics, evolutionary ecology, distribution and phylogeny, and global change and conservation. There are growing numbers of scientific projects and networks in Europe in which the use of butterflies as tools and targets for conservation is central, and application of knowledge is closely related to European cultural landscapes. However, the material can also be applied to a wide geographic scope. Written by an international team of experts, this timely book is suitable for students, researchers and enthusiasts.

JOSEF SETTELE currently works at the UFZ – Helmholtz Centre for Environmental Research. He is Head of the Animal Ecology section in the Department of Community Ecology, and Adjunct Professor of Ecology at the University of Halle. He was initiator and coordinator of the EU projects ‘MacMan’ (Maculinea butterflies as indicators and tools for conservation management) from 2002 to 2006, and ‘ALARM’ (Assessing LArge scale environmental Risks for biodiversity with tested Methods) from 2004 to 2009. His general research focus is on population and conservation biology of animals (in particular, butterflies). He has published more than 200 scientific papers. He is a Fellow of the Royal Entomological Society and Editor in Chief of the open access journal *BioRisk*. In 2009 he started a 4-year term as chairman of Butterfly Conservation Europe.

TIM SHREEVE is a Reader of Ecology at Oxford Brookes University. His current work in butterfly ecology encompasses three main areas: behaviour and activity in relation to microclimate and climatic constraints on population persistence; the role of wing morphology in relation to predation, mate attraction and thermoregulation; and the analysis of biogeographical patterns of Palaearctic species and the roles of ecological attributes of species and their associated strategies in determining occurrence and conservation status. He is a Fellow of the Royal Entomological Society and Editor in Chief of the *Journal of Insect Conservation*.

MARTIN KONVIČKA is Adjunct Professor at the Institute of Entomology of the Czech Academy of Sciences. He has major interests in butterfly ecology and conservation biology, and in using evolutionary and behavioural information for conserving

endangered species. He uses butterflies as a model for the study of biodiversity. He has participated in many butterfly-related projects launched in the Czech Republic since the mid-1990s, including the butterfly monitoring scheme of the Czech Republic and the publication of the Czech butterfly distribution atlas.

HANS VAN DYCK is a Professor at the Biodiversity Research Centre of the Belgian Université catholique de Louvain (UCL). Since 2004, he has been the head of a new research team, the Behavioural Ecology and Conservation Group. His main interest is to combine both basic and applied research in ecology and evolution in order to better understand changing organisms in changing anthropogenic environments and what this means for conservation. He is also lecturer in behavioural ecology, landscape ecology and entomology.

# Ecology of Butterflies in Europe

Edited by  
Josef Settele  
*Helmholtz Centre for Environmental Research – UFZ, Germany*

Tim Shreeve  
*Oxford Brookes University, UK*

Martin Konvička  
*Czech Academy of Sciences, Czech Republic*

Hans Van Dyck  
*Biodiversity Research Centre (UCL), Belgium*



Cambridge University Press  
978-0-521-76697-5 — Ecology of Butterflies in Europe  
Edited by Josef Settele , Tim Shreeve , Martin Konvička , Hans Van Dyck  
Frontmatter  
[More Information](#)

**CAMBRIDGE**  
UNIVERSITY PRESS

University Printing House, Cambridge CB2 8BS, United Kingdom  
One Liberty Plaza, 20th Floor, New York, NY 10006, USA  
477 Williamstown Road, Port Melbourne, VIC 3207, Australia  
314-321, 3rd Floor, Plot 3, Splendor Forum, Jasola District Centre, New Delhi - 110025, India  
103 Penang Road, #05-06/07, Visioncrest Commercial, Singapore 238467

Cambridge University Press is part of the University of Cambridge.

It furthers the University's mission by disseminating knowledge in the pursuit of education, learning and research at the highest international levels of excellence.

[www.cambridge.org](http://www.cambridge.org)

Information on this title: [www.cambridge.org/9780521766975](http://www.cambridge.org/9780521766975)

© Cambridge University Press 2009

This publication is in copyright. Subject to statutory exception and to the provisions of relevant collective licensing agreements, no reproduction of any part may take place without the written permission of Cambridge University Press.

First published 2009

*A catalogue record for this publication is available from the British Library*

ISBN 978-0-521-76697-5 Hardback

ISBN 978-0-521-74759-2 Paperback

Additional resources for this publication at [www.cambridge.org/9780521766975](http://www.cambridge.org/9780521766975)

Cambridge University Press has no responsibility for the persistence or accuracy of URLs for external or third-party internet websites referred to in this publication, and does not guarantee that any content on such websites is, or will remain, accurate or appropriate.

## Contents

List of contributors	<i>page</i> vii
Preface	xi
<b>1 Ecology of butterflies in Europe – where are we now and where to go?</b>	<b>1</b>
ROGER L. H. DENNIS	
<b>PART I HABITAT USE: RESOURCES AND CONSTRAINTS</b>	<b>7</b>
<b>2 Adult food resources in butterflies</b>	<b>9</b>
ANDREAS ERHARDT AND JOVANNE MEVI-SCHÜTZ	
<b>3 Mating behaviour in butterflies</b>	<b>17</b>
PER-OLOF WICKMAN	
<b>4 Butterfly oviposition: sites, behaviour and modes</b>	<b>29</b>
ENRIQUE GARCÍA-BARROS AND THOMAS FARTMANN	
<b>5 Butterfly herbivory and larval ecology</b>	<b>43</b>
MIGUEL L. MUNGUIRA, ENRIQUE GARCÍA-BARROS AND JOSÉ MARTÍN CANO	
<b>6 Thermoregulation and habitat use in butterflies</b>	<b>55</b>
PER-OLOF WICKMAN	
<b>7 Predictive species distribution modelling in butterflies</b>	<b>62</b>
BORIS SCHRÖDER, BARBARA STRAUSS, ROBERT BIEDERMANN, BIRGIT BINZENHÖFER AND JOSEF SETTELE	
<b>PART II POPULATION BIOLOGY: POPULATION STRUCTURE, DYNAMICS AND GENETICS</b>	<b>79</b>
<b>8 Butterfly population structure and dynamics</b>	<b>81</b>
ROBERT J. WILSON AND DAVID B. ROY	
<b>9 Costs and benefits of dispersal in butterflies</b>	<b>97</b>
THOMAS HOVESTADT AND MARKO NIEMINEN	
<b>10 Population genetics of butterflies</b>	<b>107</b>
GABRIEL NEVE	
<b>11 Parasitoids of European butterflies</b>	<b>130</b>
MARK R. SHAW, CONSTANTÍ STEFANESCU AND SASKYA VAN NOUHUYS	
<b>PART III EVOLUTIONARY BIOLOGY</b>	<b>157</b>
<b>12 Adaptation and plasticity in butterflies: the interplay of genes and environment</b>	<b>159</b>
HANS VAN DYCK AND JACK J. WINDIG	
<b>13 Functional significance of butterfly wing morphology variation</b>	<b>171</b>
TIM SHREEVE, MARTIN KONVIČKA AND HANS VAN DYCK	
<b>14 Evolutionary ecology of butterfly fecundity</b>	<b>189</b>
BENGT KARLSSON AND HANS VAN DYCK	
<b>15 Gradients in butterfly biology</b>	<b>198</b>
SÖREN NYLIN	

vi Contents

PART IV SPECIES IN TIME AND SPACE: DISTRIBUTION AND PHYLOGENY	217
<b>16 Bad species</b>	
HENRI DESCIMON AND JAMES MALLET	219
<b>17 Faunal structures, phylogeography and historical inference</b>	
ROGER L. H. DENNIS AND THOMAS SCHMITT	250
<b>18 Butterfly richness patterns and gradients</b>	
DAVID GUTIÉRREZ	281
<b>19 Ecological genetics and evolutionary ecology in hybrid zones</b>	
ADAM H. PORTER	296
PART V GLOBAL CHANGE AND CONSERVATION	313
<b>20 Climate warming and distribution changes in butterflies</b>	
JANE K. HILL, RALF OHLEMÜLLER, RICHARD FOX AND CHRIS D. THOMAS	315
<b>21 Conservation status of European butterflies</b>	
CHRIS A. M. VAN SWAAY, DIRK MAES AND MARTIN S. WARREN	322
<b>22 (Meta)population viability analysis: a crystal ball for the conservation of endangered butterflies?</b>	
NICOLAS SHTICKZELLE AND MICHEL BAGUETTE	339
<b>23 Butterflies of European ecosystems: impact of land use and options for conservation management</b>	
JOSEF SETTELE, JOHN DOVER, MATTHIAS DOLEK AND MARTIN KONVIČKA	353
References	371
Index of scientific names	471
Keyword index	481

The colour plates are situated between pages 340 and 341.

## Contributors

MICHEL BAGUETTE

Muséum National d'Histoire Naturelle  
 Département Ecologie et Gestion de la Biodiversité  
 France

ROBERT BIEDERMANN

Landscape Ecology Group  
 Institute of Biology and Environmental Sciences  
 University of Oldenburg  
 Germany

BIRGIT BINZENHÖFER

Helmholtz Centre for Environmental Research – UFZ  
 Department of Conservation Biology  
 Germany

ROGER L. H. DENNIS

Institute for Environment, Sustainability and Regeneration  
 Staffordshire University  
 and  
 NERC Centre for Ecology and Hydrology  
 Cambridgeshire  
 UK

HENRI DESCIMON

Marseilles  
 France

MATTHIAS DOLEK

Büro Geyer und Dolek  
 Ecological Research and Planning  
 Germany

JOHN DOVER

Institute for Environment and Sustainability Research  
 Staffordshire University  
 UK

ANDREAS ERHARDT

Department of Environmental Sciences  
 University of Basel  
 Switzerland

THOMAS FARTMANN

Institute of Landscape Ecology  
 University of Münster  
 Germany

RICHARD FOX

Butterfly Conservation  
 UK

ENRIQUE GARCÍA-BARROS

Departamento de Biología (Zoología)  
 Universidad Autónoma de Madrid  
 Spain

DAVID GUTIÉRREZ

Área de Biodiversidad y Conservación  
 Escuela Superior de Ciencias Experimentales y Tecnología  
 Universidad Rey Juan Carlos  
 Spain

JANE K. HILL

Department of Biology  
 University of York  
 UK

THOMAS HOVESTADT

Field Station Fabrikschleichach  
 University of Würzburg  
 Germany

BENGT KARLSSON

Department of Zoology  
 Stockholm University  
 Sweden

MARTIN KONVIČKA

Faculty of Sciences  
 University South Bohemia  
 Institute of Entomology and  
 Czech Academy of Sciences  
 Czech Republic

## viii List of contributors

DIRK MAES

Research Institute for Nature and Forest (INBO)  
 Belgium

JAMES MALLETT

Galton Laboratory  
 Department of Biology  
 University College London  
 UK

JOSÉ MARTÍN CANO

Departamento de Biología (Zoología)  
 Universidad Autónoma de Madrid  
 Spain

JOVANNE MEVI-SCHÜTZ

Department of Integrative Biology  
 University of Basel  
 Switzerland

MIGUEL L. MUNGUIRA

Departamento de Biología (Zoología)  
 Universidad Autónoma de Madrid  
 Spain

GABRIEL NÈVE

Institut Méditerranéen d'écologie et de paléocologie  
 Université de Provence  
 France

MARKO NIEMINEN

Faunatica Oy  
 Lansantie 3 D  
 Finland

SÖREN NYLIN

Department of Zoology  
 Stockholm University  
 Sweden

RALF OHLEMÜLLER

Institute of Hazard and Risk Research (IHRR) and  
 School of Biological and Biomedical Sciences  
 Durham University  
 UK

ADAM PORTER

Department of Plant, Soil and Insect Sciences and  
 Graduate Program in Organismic and Evolutionary Biology  
 University of Massachusetts  
 USA

DAVID B. ROY

NERC Centre for Ecology and Hydrology  
 Oxfordshire  
 UK

THOMAS SCHMITT

Biogeographie, FB VI  
 University of Trier  
 Germany

BORIS SCHRÖDER

Institute of Geocology  
 University of Potsdam  
 Germany

NICOLAS SHTICKZELLE

Quantitative Conservation Biology Group  
 Biodiversity Research Centre  
 Université catholique de Louvain  
 Belgium

JOSEF SETTELE

Helmholtz Centre for Environmental Research – UFZ  
 Department of Community Ecology  
 Germany

MARK SHAW

Honorary Research Associate  
 National Museums of Scotland  
 UK

TIM SHREEVE

School of Life Sciences  
 Oxford Brookes University  
 UK

CONSTANTI STEFANESCU

Butterfly Monitoring Scheme  
 Museu de Granollers–Ciències Naturals  
 Spain

BARBARA STRAUSS

Landscape Ecology Group  
 Institute of Biology and Environmental Sciences  
 University of Oldenburg  
 Germany

CHRIS D. THOMAS

Department of Biology  
 University of York  
 UK



HANS VAN DYCK

Behavioural Ecology and Conservation Group  
Biodiversity Research Centre  
Université catholique de Louvain  
Belgium

SASKYA VAN NOUHUYS

Department Biological and Environmental Sciences  
University of Helsinki  
Finland  
and  
Department of Ecology and Evolutionary Biology  
Cornell University  
USA

CHRIS A. M. VAN SWAAY

Dutch Butterfly Conservation  
The Netherlands

MARTIN S. WARREN

Butterfly Conservation  
UK

PER-OLOF WICKMAN

Department of Education in Mathematics and Science  
Stockholm University  
Sweden

ROBERT J. WILSON

Centre for Ecology and Conservation  
University of Exeter  
UK

JACK J. WINDIG

Animal Breeding and Genomics Centre (ABGC)  
Animal Sciences Group  
The Netherlands

## Preface

### WHY?

The last 20 years has seen a dramatic increase in research on butterflies, driven from two directions. The first has been academic, with a realisation that butterflies can be model organisms to study evolutionary, behavioural and biogeographic processes. The second has been, and continues to be, an urgency to tackle extensive declines in butterfly species, a phenomenon not just restricted to Europe. As recently as 50 years ago there were no major issues concerning the conservation of butterflies and biodiversity was not regarded as an issue, though even at that time a few species of butterfly were in decline within Europe. About 30 years ago the study of butterflies was often regarded as an academic sideline, since when the contribution of butterfly biologists to mainstream biology has increased in importance. Over the last 10 years there has been a remarkable synthesis of ideas and an increasing realisation that academic studies can contribute much to conservation. The science of conservation is becoming increasingly evidence-based and a true dialogue between academics and conservationists is emerging, including a scientific approach to using butterflies as biodiversity indicators. It is thus timely to produce a European-scale book about butterfly ecology, with the potential to make a clear statement about the 'state of the art' and the emerging issues. Not least, such a text should clearly indicate where the current research is taking place and which scientists and research teams are focusing on what. In producing this book it has been our intention to do just this.

### WHO?

The idea for this book was conceived by Roger Dennis almost 10 years ago in September 1999 at the time of 3rd International Symposium of Butterfly Conservation, organised by Butterfly Conservation in Oxford, UK. The original three editors were Roger Dennis, Tim Shreeve and Andrew Pullin. For health reasons Roger Dennis stepped down from his lead role and the team was then joined by

Josef Settele. Andrew Pullin left because of other commitments and the editorial team 'evolved' into a combination of colleagues from four different European countries, namely Josef Settele, Tim Shreeve, Martin Konvička and Hans Van Dyck. During the gestation period, chapter authors changed, with the majority of author combinations reflecting the international dimension of butterfly ecology in Europe. Surprisingly, the editorial team as a whole physically only met once, to finalise arrangements, at Wageningen (Netherlands) in April 2008 during the 'Future of Butterflies II' conference, organised by the Dutch Butterfly Conservation. All other communication between the editors has been electronic.

Although Roger Dennis left the editorial team, all the editors thought it appropriate that he be asked to write an introductory overview, firstly as a tribute for his originating the concept and secondly for his long-standing contribution to the development of butterfly ecology.

### WHAT?

Within this book there is occasional evidence of differences of opinion and interpretation between the authors of some chapters. These differences are a healthy sign that there is room for debate, and as editors we have taken the view that authors are experts and that the differences of opinion reveal that the science of butterfly ecology is permanently developing and in a productive state. The subjects within each chapter cannot be viewed in isolation; there is thus an element of necessary overlap between some chapter parts. As editors, we have had to make decisions on some points; we have added cross-referencing between chapters to indicate where different areas merge; and for nomenclature, which is not consistent over Europe, we have been relatively conservative and adopted Karsholt & Razowski (1996) as the core reference.

We have attempted to provide a wide coverage of the many aspects of butterfly ecology that are being undertaken by European researchers. The text is broadly thematic and clearly states where there are knowledge gaps. Where

xii Preface

appropriate authors also indicate where cross-disciplinary studies can contribute to the advancement of knowledge. It is, however, inevitable in a text of this size that some areas have not received as much attention as some readers would prefer. Reference to these areas, such as the major advances being made in the study of ant–lycaenid interactions, or the painstakingly detailed work on metapopulation models using *Melitaea* species, is made where relevant but we also think that these topics either warrant complete new exhaustive treatments or are covered elsewhere.

WHERE TO IN FUTURE?

It is evident from the contributions to this book that there are emerging new areas of butterfly research and we hope that the synthesis provided within the chapters will provide a stimulus to further work. Each chapter raises important questions. Despite extensive research there are many gaps in our existing knowledge; for example, we do not even know the host-plant ranges of many species, our grip on what determines a habitat for most species is rather limited, and our knowledge of population dynamic processes and interactions at the community level is in its infancy. We now have a range of techniques for studying processes from the molecular to the community and biogeographic levels. Integration of these techniques to provide novel approaches to studying academic questions and addressing immediate conservation issues is now possible and the levels of co-operation between different research groups to achieve these goals are also clear from the contributions to this book.

Research on butterflies within Europe is now transnational, and it is surprising how much has been achieved within the last two decades, often with limited financial resources. The emergence of Butterfly Conservation Europe, as yet poorly funded, provides a potential future mechanism for increasing European co-operation, in providing a forum for raising key issues and bringing subject experts and end-users together. Our plea to politicians and grant-awarding bodies is to guarantee the continuation of basic research and enhance funding for future collaborations. Within Europe there is a

wealth of talent working on the ecology of butterflies, and their work is making major contributions to understanding the state of biodiversity, the mechanisms controlling it, and increasing the power of predictive models in a rapidly changing world. The work contained in this book is a testimonial to what has already been achieved. It is our hope that this book provides a stimulus for further work, in particular that it encourages the next generation of butterfly ecologists. Our one hope is that theory and practice can combine quickly enough to ensure a secure future for butterflies and the species they are associated with in a dynamic European landscape.

ACKNOWLEDGEMENTS

Throughout the years numerous colleagues have been involved in the making of this book. At the risk of having forgotten a few of them – for which we want to apologise – we want to mention at least those who have volunteered as referees of one or more chapters: Andreas Erhardt, Bengt Karlsson, Chris van Swaay, Christer Wiklund, Constanti Stefanescu, Darrell Kemp, Dirk Maes, Enrique García-Barros, Gabriel Nève, Henri Descimon, James Mallet, Jane Hill, Jens Roland, Klaus Fischer, Martin Warren, Michel Baguette, Michiel WallisDeVries, Miguel L. Munguira, Nicolas Schtickzelle, Niklas Wahlberg, Per-Olof Wickman, Robert B. Srygley, Roger L.H. Dennis, Sören Nylin, Thomas Merckx, Thomas Fartmann, Thomas Hovestadt, Thomas Schmitt and Tim New.

Furthermore we are indebted to Mandy Riemer and Alexander Harpke for their continuous technical support in the finalisation as well as the different book editors of Cambridge University Press for their never-ending patience and positive attitude throughout the genesis of the book, we are particularly indebted to Richard Marley and Dominic Lewis.

Josef Settele  
 Tim Shreeve  
 Martin Konvička  
 Hans Van Dyck