Modelling for Field Biologists and Other Interesting People

Students of evolutionary and behavioural ecology are often unfamiliar with mathematical techniques, even though much of biology relies on mathematics. Evolutionary ideas are often complex, meaning that the logic of hypotheses proposed should be tested not only empirically but also mathematically. There are numerous different modelling tools used by ecologists, ranging from population genetic 'bookkeeping' to game theory and individual-based computer simulations. Due to the many different modelling options available, it is often difficult to know where to start. Hanna Kokko has designed this book to help with these decisions. Each method described is illustrated with one or two biologically interesting examples that have been chosen to help to overcome the fears of many biologists when faced with mathematical work, while also providing the programming code (MATLAB®) for each problem. Aimed primarily at students of evolutionary and behavioural ecology, this book will be of use to any biologist interested in mathematical modelling.

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CAMBRIDGE UNIVERSITY PRESS

CAMBRIDGE UNIVERSITY PRESS
Cambridge, New York, Melbourne, Madrid, Cape Town, Singapore, São Paulo

Cambridge University Press
The Edinburgh Building, Cambridge CB2 8RU, UK

Published in the United States of America by Cambridge University Press, New York

www.cambridge.org
Information on this title: www.cambridge.org/9780521831321

First published 2007

Printed in the United Kingdom at the University Press, Cambridge

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

ISBN 978-0-521-83132-1 hardback
ISBN 978-0-521-53856-5 paperback

To my parents,
who gave me all those Moomin books to read,
and to the memory of Tove Jansson,
who wrote them

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Preface

This book arose from far too many queries addressed to me in the past 10 years by behavioural or evolutionary ecologists: 'If I wanted to learn to model, what book should I read?' I could not give a straightforward answer to this question, and neither could I choose a course book to cover modelling in behavioural or evolutionary ecology at a beginner's level for the courses I have been teaching. There are many books available that delve into particular methods, but grabbing them requires that one knows a priori that the particular method will be useful. I was looking for a book that would provide a gentle enough introduction for people who might range from keen undergraduates to experienced researchers, but share one thing in common: no hands-on experience with mathematical modelling so far. I found some very good texts for population ecologists, but nothing similar for evolutionary or behavioural ecologists.

This book is an attempt to fill in this gap. My intention is not to provide full coverage of all mathematical tools used in evolutionary studies today – that would be far too much to ask from a volume of this size. Instead, my intention is to present an entry-level 'toolbox' for those people who lack nothing but a kick-start to add modelling techniques to their repertoire of scientific skills. The subtitle 'and other interesting people' reflects the attitude that I have tried to follow in this book: there is no need for anyone to be intimidated by modelling work, let alone by people who possess this apparently magical skill. Working with real-life questions can be so much more interesting – and adding some modelling skills can be much fun. Whether the reader is an undergraduate or a senior scientist, my intention is to show how one might approach a problem, and – if one particular method grabs their attention – give suggestions where to read on to learn more.

I have also been lucky to learn that there are now more books that are devoted to teaching modelling to biologists than there were 10 years ago, which makes my task of pointing to other sources vastly easier. My goal is not to supersede the superb introductions that now exist for many, perhaps most, of the methods presented here. Instead, my intention is to give a glimpse of what is available, through the use of examples. Each chapter illustrates the use of a particular method: say, dynamic optimization, or quantitative genetics. I present the simplest example that I could think of that is complex enough to interest people who probably already lead exciting lives studying the wonders of nature, or are simply keen to learn more.

Absolutely no prior knowledge of any of the methods is required, while familiarity with evolutionary thinking in general will be assumed. My style is intentionally informal and 'chatty'. This is to appreciate what I imagine a likely reader of my book to be like: an engaged and intelligent person, who has probably spent more time wearing muddy boots or rainforest-mouldy T-shirts than staring at books heavily laden with mathematical expressions – these being either too dry or too scary in his or her opinion. To keep to this style, I will have to disappoint those who look for a full treatment of the methods. In my experience, formal definitions of mathematical concepts are far easier to find in the literature than friendly, entry-level explanations of what they mean. For this reason, I am concentrating on providing the latter type of information, with a focus on illustrative examples, while also giving pointers to the mathematically more complete texts in which the full derivations are given. The aim of this book is, therefore, to fill in the gap between the would-be modeller and the beginning level of other, more complete and thorough texts available. Finally, I am hoping to provide some food for thought for those scientists who have some experience with building models but are not familiar with too many different techniques.

Modelling relies heavily on computers nowadays. The development of ideas in the book is not specific to any particular programming language, but to help readers who might be interested in the programming aspect. All the examples in the book are available electronically, with the programming code for reproducing all the figures at www.helsinki.fi/~hmkokko/modelling. For this I have used MATLAB (www.mathworks.com), as it is a versatile tool that works well for ecologists. For university students or staff, it is worth knowing that universities have licences for this program more often than biologists seem to realise. Nevertheless, not all readers of this book will have access to this particular program. They

might also like to stick to another program for some other reason – or use the old-fashioned but often surprisingly useful pen and paper method. I strongly encourage such readers to read on: the programming language is a side issue here, used in technical side boxes only. It really does not matter if Hamilton's rule is expressed as if `b*r>c` (MATLAB) or as `=IF(A1*A2>A3;1;0)` (Microsoft Excel, assuming that values of *b, r* and *c* are stored in cells A1, A2 and A3, respectively). Therefore the examples can all be translated across programming languages, although spreadsheet programs may become cumbersome to use for more extensive calculations. Two examples of freeware programs very similar to MATLAB are SysQuake LE (www.calerga.com), and the somewhat more statistically oriented R (www.r-project.org). A "free" version of MATLAB is Scilab (http://www.scilab.org/). Many prefer 'traditional' programming languages such as C or Basic (nowadays often in the version VisualBasic), which is also fine. Ideas are important, not the programming platform used. An open source platform called Scilab (www.scilab.org) is also available.

An additional reason why the programming language does not matter is that often the goal is to derive analytical expressions. These are general solutions such as $br > c$, as opposed to extensive lists of numerical values. This means that programming languages are not always even needed to find out expected evolutionary outcomes. Even here, the software industry has been busy producing equation-solving beasts such as MAPLE (www.maplesoft.com) or MATHEMATICA (www.wolfram.com), but the humble combination of pen and paper surprisingly often retains its centuries-old effectiveness. I still very often find the neatest presentation of an equation fastest by scribbling all those squiggles on paper, and few of the examples presented in this book are computing intensive at all.

Books are rarely created alone, and this one is no exception. My sincere thanks go to my Cambridge University Press editor Dominic Lewis, who allowed and encouraged me to write in a relaxed style that would make any editor of a scientific journal cringe. His help and support was absolutely crucial as was the editing work by Jane Ward. The other important support group is students. This book is heavily based on courses I have given at Jyväskylä University and Helsinki University in the years 2002–2006. My very warm thanks go to all the participants: it is incredible to see such active and enthusiastic students, and the feedback helped me more than you may believe in this project. Some of the feedback diaries you produced should have been called works of art, and I have ruthlessly exploited all the insights they contained. Andrés López-Sepulcre and Daniel Rankin helped me a lot with the courses – thank you.

A number of people read individual chapters with great care, some of them even commented on the whole manuscript in impressive detail. The feedback has been truly indispensable. Patricia Backwell, Mats Björklund, Anders Brodin, Rob Brooks, Jakob Bro-Jørgensen, Johanna Eklund, Kevin Foster, Nika Galic, Phillip Gienapp, Ilkka Hanski, Wade Hazel, Mikko Heino, Alasdair Houston, Michael Jennions, Jonathan Jeschke, Jussi Lehtonen, Anna Lindholm, Jan Lindström, Andrés López-Sepulcre, Martim Melo, Hans Metz, Lesley Morrell, Päivi Paavilainen, Janne Pyykkö, Esa Ranta, Ian Rickard, Walter Rydman, Franziska Schädelin, Toomas Tammaru, Andrea Townsend, Wouter Vahl, and a number of students whose views were transmitted to me via the above-mentioned people: thank you! Michael Jennions deserves a special mention for coming up with the title of the book, and Martim Melo for the quote from *Travels of Praiseworthy Men*. The book has immensely benefited from all these comments, but any errors that remain, as well as any less than perfect choices regarding style and content, are obviously mine.

Finally, thank you Liisa and Ilkka.