Hanna Kokko

Modelling for Field Biologists

and Other Interesting People

CAMBRIDGE

CAMBRIDGE www.cambridge.org/9780521831321

This page intentionally left blank

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.

HANNA KOKKO is a Professor in the Department of Biological and Environmental Science at the University of Helsinki.

Modelling for Field Biologists and Other Interesting People

HANNA KOKKO
Department of Biological and Environmental Science,
University of Helsinki, Finland

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

© Hanna Kokko 2007

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

First published in print format 2007

ISBN-13 978-0-511-33207-4 eBook (Adobe Reader)
ISBN-10 0-511-33207-6 eBook (Adobe Reader)

ISBN-13 978-0-521-83132-1 hardback
ISBN-10 0-521-83132-6 hardback

ISBN-13 978-0-521-53856-5 paperback
ISBN-10 0-521-53856-4 paperback

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.

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

Contents

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.

1

Modelling philosophy

where we get momentarily lost in a forest, but emerge intact

Figure 1.1 shows three different kinds of model. A supermodel like Naomi Campbell presents, to some of us at least, an 'idealized' concept of a human being (Fig. 1.1a). The miniature model shown in Fig. 1.1b was built by my uncle to show what his home town Kuopio looked like in the 1930s. Finally, Fig. 1.1c is a mathematical description of the dynamics of a two-species system of a predator and a prey species.

The models all look very different. They also differ a lot in how scary they look to the average behavioural or evolutionary ecologist – most will have to resist the temptation to close their eyes when encountering Fig. 1.1c, together with its equations, much more than when looking at Fig. 1.1a. My aim in this chapter is to show that there is indeed a reason why the word 'model' is used to describe all these figures, to rectify some common misconceptions about models (especially the mathematical ones), and to make life a little less scary for those who know they should be more familiar with modelling in behavioural or evolutionary ecology than they currently are.

Ecology is defined as a science that investigates the abundance and distribution of organisms. This may first sound a little boring, but it gets more interesting once one notices that interactions between organisms play a crucial role here. This means that ecology must study the causalities that underlie the changes in individual numbers, rather than merely providing us with simplistic methodologies of bookkeeping. When trying to understanding those causalities, evolutionary aspects must be taken into account, because evolution underlies everything that organisms do. Very often, the interactions manifest themselves in the behaviour of the

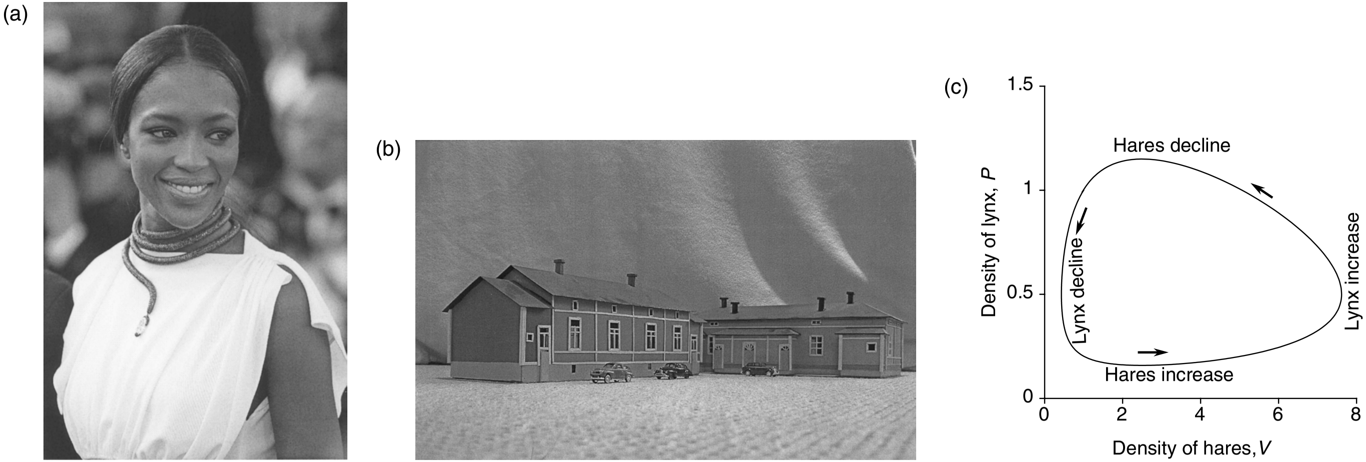

Fig. 1.1 Models. (a) Naomi Campbell; (b) a street corner from a miniature model of Kuopio, a town in Eastern Finland; (c) hare–lynx cycle described by Lotka–Volterra equations $dV/dt = rV - aVP$ and $dP/dt = -qP + baVP$. Here V is hare density; P is lynx density; t marks time such that dV/dt gives the rate of change in the hare density and dP/dt similarly for lynx; r, a, b and q are parameters that determine how quickly hares reproduce (r), how many hares are eaten (a) for a given density of lynx and hare, how efficiently eaten hares are converted into lynx offspring (b) and how quickly lynx die when food is in short supply (q). The limit cycle is drawn using values $r = 0.1$, $a = 0.2$, $b = 0.1$, and $q = 0.1$. The predator–prey cycle shows qualitatively nice cycling, but the model is meant to be conceptual only: parameters are hardly realistic when at the peak of lynx density there are only twice as many hares as there are lynx in the forest. The Lotka–Volterra cycle can be found in almost all textbooks on ecology. I have used the notation of Odenbaugh (2005), who uses the predator–prey cycle to illustrate several important philosophical issues on the need to simplify when modelling ecological phenomena.

organism in question. Behavioural and evolutionary ecology are the sciences that study the evolutionary and ecological causalities that cause individuals to behave the way they do – and while saying this, one should not forget the physiological and physical mechanisms that shape and constrain the ways in which individuals can behave.

This definition places behavioural and evolutionary ecology in a scarily complex web of interactions. It appears that everything interacts with everything else: a migrating bird has to combat weather and winds, manage its energy reserves, find the flight speed that is appropriate for the wing shape the bird has, find its way using perhaps several different orientation mechanisms, avoid predators on the way, find good stopover sites, arrive in a sensible time of the year and compete with conspecifics for breeding localities and possibly mates too. And, all of this is governed by genes that influence the bird's behaviour in a multitude of ways. Why should we ever be interested in modelling such a system – or even if we were, what hope do we have of ever capturing the complexity of the situation the bird finds itself in?

The quick answer is that there is no hope. Our model simply will never be able to deal with such complexity. The perhaps more surprising elaboration of this statement is that if a model did capture all of this – perhaps computers in the future could stomach it all? – the outcome would not be desirable at all. Why? The famed author J. A. Suarez Miranda said it all in his book *Travels of Praiseworthy Men*, already in 1658:

> . . . In that Empire, the craft of Cartography attained such Perfection that the Map of a Single province covered the space of an entire City, and the Map of the Empire itself an entire Province. In the course of Time, these Extensive maps were found somehow wanting, and so the College of Cartographers evolved a Map of the Empire that was of the same Scale as the Empire and that coincided with it point for point. Less attentive to the Study of Cartography, succeeding Generations came to judge a map of such Magnitude cumbersome, and, not without Irreverence, they abandoned it to the Rigours of sun and Rain. In the western Deserts, tattered Fragments of the Map are still to be found, Sheltering an occasional Beast or beggar; in the whole Nation, no other relic is left of the Discipline of Geography.

If this passage makes you want to find the rest of Suarez Miranda's book in a library (instead of learning more about modelling), prepare to be disappointed. The book or its author never existed except in the above quote written by Jorge Luis Borges and Adolfo Bioy Casares (see Borges

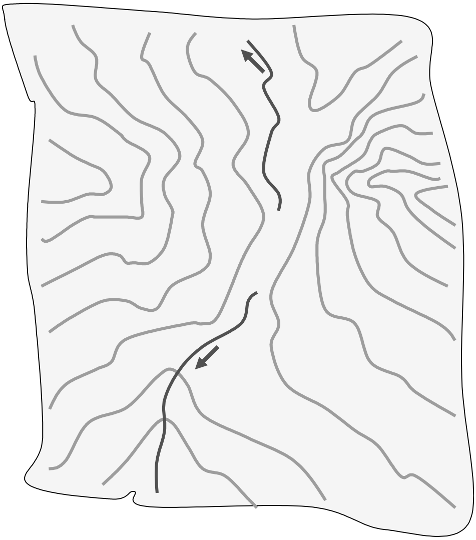

Fig. 1.2 A map is a model too. How would you plan your route in this landscape?

1975). Nevertheless, it marks a perfect beginning for a tour of the virtual world of modelling.

Why do we make maps of landscapes? These exist at a range of different scales, and the detail included may also vary irrespective of scale: a mining company probably requires different information about an area than a passing tourist or a hiker. Using the map in Fig. 1.2, a hiker is probably quite keen to have a look at the contour lines: they tell her the easiest route through a mountain pass and predict the direction of the flow of the river she will encounter. This can be important for a variety of reasons, including orientation purposes. Now, to predict the flow of the river, it is not necessary to mark every tuft of grass that borders the river, or every tree in the forest our hiker is passing through, on the map. These would only make it more difficult to grasp the overall shape of the landscape. Taken to the extreme, if the ultimate goal was to include all the detail of the forest in the map, our poor hiker would have to carry the whole landscape with her. Even if this was physically possible, the gain from doing so would be zero: if lost in a forest, she would not become any wiser by looking at a too vastly detailed map than by staring at the original forest. Such maps indeed deserve to be left rotting in the rain.

This, of course, is exactly the reason why models are 'not real'. They are idealized versions of the real world. My uncle is now building a street with shops in his miniature model of Kuopio. He knows that to create the visual impression one would get by looking down a particular street in Kuopio, it is important to shape the fonts in shop windows to match the original ones, and he has made countless visits to the local library's archives to verify all this detail. However, it is far less important to use exactly the same chemical composition of the paint. This is the art of modelling: to know which aspects of reality one can sacrifice, and which ones are crucial to retain. Any medical simulation of drug concentrations in various tissues of the human body is likely to include the fact that the blood vessels from the gut lead to the liver, since that organ rids us of strange compounds in the bloodstream. The whole machinery involved is never included. For example, the developmental fact that the DNA in of our cells contain instructions on how to build the blood vessels is simply not relevant – until, perhaps, we find patients who have a genetic disorder that disrupts this process and makes them react to medicines in surprising ways. But even then, we should not go to the other extreme and start including every possible gene action in the model, from eye colour determination to how fast one's toenails grow.

George Box, a well-known statistician, once quipped 'All models are false, but some models are useful'. Have a look again at Fig. 1.1c. Here, V might denote the numbers of hares in an area, and P are lynx. The equations may look scary, but all they do is to describe some numerical rules of species interaction: $\mathrm{d}V/\mathrm{d}t$ is the change of hare numbers over time, and this is larger if there are lots of hares (large V) – since many hares can produce more leverets (baby hares) than few hares can. Likewise, lots of lynx can produce lots of new lynx. How lynx and hare populations respond to each other, however, differs between the species. Lynx populations tend to increase when hares are abundant, but hare populations respond negatively to the abundance of lynx, for rather obvious reasons. This is reflected in a negative sign in front of P in the hare equation, and in a positive sign in front of V in the lynx equation. The squiggles in Fig. 1.1c are called Lotka–Volterra equations, and they predict – when solved – that lynx and hare numbers will cycle up and down, hares always declining before their predators do.

Of course, the model is incomplete. It is wrong. It does not include density-dependent responses in the absence of predation: even if hares bred like, well, rabbits, neither species can in reality fill every square metre of the world with their offspring – food would run out long before that. Also, the model does not include the fact that both hares and lynx need some time before they mature. Or that both species reproduce sexually. Or that hares could possess antipredator responses. Or that lynx might use different hunting techniques in the summer and the winter. And so on ad infinitum. All these points are true, but the important point is: would one have predicted that the simple statements "hares beget hares; lynx beget lynx; and lynx eat hares" can, *by themselves*, lead to predator–prey cycles? Perhaps some people's intuition tells them immediately that this is the case. But perhaps someone else disagrees and argues that some other process, perhaps some cyclic weather pattern, must interfere before cycles can occur. How could we ever solve the case, without writing the matter down in equations? By carefully looking at patterns in nature? Not easy: we simply cannot find idealized hare and lynx populations that would not have interfering factors of all sorts. By conducting clever experiments? Yes, this definitely plays a large part: experiments very typically try to strip down the messy nature of reality to get at the pure effect of a particular biological factor. Nevertheless, there is always the chance that some other factor that we did not think about at all was influencing our results. In the end, the only way to find out if an argument 'from X follows Y' is a valid statement to offer, one has to put it in a mathematical form.

The analogy with an experimenter's work is very important here. Experiments could also be (and often indeed are) criticized for being unrealistic, as they do not fully reflect the natural setting. For example, a subordinate male fish might prefer large females over small ones in a simultaneous choice test, yet in nature this could be irrelevant if large fecund females tend to be paired to dominant males who defend their territory (and mate) vigorously. The defence of the experimenter to this challenge is similar to that of the modeller, too: the whole point of the experiment is to tell us that, *all other things being equal*, the large female is preferred over the small one. Likewise, the hare–lynx dynamics assumes that, all other things being equal, more lynx are bad news to hare populations, and this can run cyclic dynamics.

But there is an important distinction to be made between experimental approaches and modelling studies. An experimentalist is trying to find out if something (say, a male preference for large females) really does occur in nature. A modeller will never achieve this, which is good news to field ecologists were they scared of modellers taking over the scientific world. Models do not investigate nature. Instead, they investigate the validity of our own thinking, i.e. whether the logic behind an argument is correct. Are you interested in finding out if the simple fact that predators eat prey can *in principle* lead to population cycles? If so, go and model it. But whether this fact actually does cause cycles in real populations in Canada or Scandinavia or the vicinity of Kuopio must be investigated out there in nature – perhaps by removing predators from an area, or seeing if cycles are more often seen where the assumptions of this model appear to be better met, or by some other clever methods that the author of this book is not an expert on.

Once one begins to think of models as ‘thinking aids’ rather than investigations of natural phenomena, one could even go as far as to say that we only need models because our brains suffer from too many limitations and are not able to consider all sides of a complicated argument in a balanced way. Take, for example, R. A. Fisher’s (1930) idea that sexually selected traits such as extravagantly long tails in birds exist because the following has happened. Initially a longer than average tail could have conferred a viability benefit to the male, perhaps because it improves flight performance. This means that females who prefer long-tailed males as mates will have offspring who have inherited a nice long tail. The genes for female preferences have now become statistically linked with longer tails in males, and long-tailed male offspring now have the additional advantage of being preferred by females. So, even if too long tails no longer give the viability benefit but instead diminish male offspring survival, the system may end up in a ‘runaway’ where both preferences and tail lengths evolve to ever more extreme values . . . Is it all now crystal clear in your head?

Don’t worry, the confused feeling is shared by countless others who have read Fisher’s account of the process. If only we all had brains capable of mathematically accurate split-second imagination, keeping precise track of all the relevant pros and cons of these genes – then Fisher would just have had to state his idea, and every person in the world would instantly have seen his point. Perhaps Fisher was like that, but most of us are certainly not. We rely on intuition and common sense, both of which can sometimes perform dismally badly.[1] This is why we

---

[1] For anyone interested in a wonderful account of mistakes of reason that are very hard to get rid of: read the book *Inevitable Illusions: How Mistakes of Reason Rule Our Minds* (Piattelli-Palmarini 1994).

end up arguing about whether from X really follows Y or not, and it is the same reason why the modelling niche in ecology is such a good one.[2] Modellers are not more intelligent than the rest, instead they simply gain their living by having learnt a mindset (plus a few mathematical tricks) that allows them to break the problem down into small pieces. This makes the assumptions explicit, and then one can derive the outcome in such small steps – often taken care of by a computer – that they, and everyone else, can trace the steps without suffering a brain overload like that suffered when encountering Fisher's work for the first time.

So, models only exist because we need them to help us: none of us are born with such supercomputer brains that we could evaluate arbitrarily complex arguments immediately and without external help. What is the optimal complexity of a model, then? Once again, it depends on the question. Reflect for a moment that there are maps with different scales. In the context of scientific models, it is useful to be reminded of the ultimate reason we do science: it is the joy of understanding something. If we could visualize and memorize much more detailed maps than we currently do, useful maps would include more detail than they currently do. Exactly analogously, if we could grasp much more complex processes without getting headaches than we currently do, models would look different too. Given the way our brains are built, a good guideline is that a model should include all the relevant details for the particular question at hand, but it should be kept so simple that it can be understood (if with joy, then still better). In other words, a model is not particularly helpful if it predicts that under conditions A the animal should do X, while under conditions B it should do X 30% of the time and Y in the rest of instances, and then there are 17 other parameters that interact with each other in producing a diversity of outcomes – but when asked why the model produces these effects of A and B, we still have no answer that can be expressed in a language that anyone's intuition can understand. Removing some additional detail from the model can then be surprisingly helpful: the effects of A and B could still be the same, but with far simpler equations.

For example, we might have spent a lot of time modelling the distribution of body condition in a population of migratory birds, ending up with very cumbersome equations, when a far simpler way to grasp

---

[2] Endless collaboration prospects – so you can pick the ones in the countries with the best food and weather. Field trips are to sites with already nicely established facilities, can usually be arranged in the best time of the year too, and someone else is doing all the tedious aspects of the data collection. Cool.

the conceptual issue is to divide up the population into two classes of individuals, 'hungry' and 'satisfied'. To show a conceptual point, this might be sufficient. Results could be far simpler to derive this way than with a more complete model, and if our understanding of the biology advances faster this way, the simplification is justified. But how to know, then, that the division has not caused some artifacts? Perhaps an exact shape of the body condition distribution would have produced a totally different answer? The answer is . . . we don't really know, unless we build the more complicated model too. (Which means that modellers rarely run out of models to study.[3]) Alternatively, it is often the case that the simple model has dealt with most of the thinking load, so that extrapolating to the last step can (fairly reliably) be achieved using imagination and verbal argumentation. This may sound unsatisfactory, but at least it provides a reason why any modelling quest should start with a fairly simple setting: effects of new added interactions are hard to judge otherwise.

In the above – and indeed in the rest of this book – I am mainly dealing with conceptual models. They are typically models that aim to answer questions, 'Does from A follow B?' Or in a little more complicated way: 'Under which biologically relevant conditions can we claim that from A follows B?' Such models usually aim at relatively broad taxonomic applicability, which also means that details of the behaviour of a specific species, no matter how exciting and important they appear, should usually be considered irrelevant. A modeller should not necessarily be judged as arrogant or ignorant if she brushes over such detail. When we want to know under what conditions, in general, one expects female preferences to evolve based on indirect genetic benefits, it is not very wise to consider details of the energetics of black grouse leks. Predictions of conceptual models, therefore, tend to be qualitative rather than quantitative. For example, we may predict that sexually selected male traits can be very costly to their bearer, whereas large costs of female preferences are not expected (because if we assume such costs, preferences evolve to zero, see Kokko *et al.* (2006a) for a review). The model is not intended to predict exactly how costly the trait will be in the case of a male black grouse.

---

[3] There is a real danger of becoming addicted to a problem. This leads to building towers of models on top of each other, adding this or that feature, until the meaning of it all becomes totally obscure to any outsider. If you intend to pursue the modelling path seriously, beware of this danger. It helps to go to conferences and listen mistakenly to talks of the session you did not intend to attend.

Instead, a good model should in the end say: these are the conditions that have to be met before we believe we have a logically consistent argument that explains male trait evolution; now go and find out if it really is the case. The need to test assumptions and not just predictions of a model can hardly be overemphasized. But as we have just learnt, assumptions never reflect the system completely faithfully, and that is perhaps the most important reason why an empiricist should have some grasp of mathematical modelling, even if not interested in pursuing it as a career. A model that is based on the assumption that the moon is a flat Roquefort cheese is obviously so out of this world that any conclusions drawn from it, no matter how mathematically solid, will have no relevance whatsoever. But a good and useful model will still appear 'false' in the sense that many aspects of reality are necessarily ignored, and here one must be able to judge if the assumptions nevertheless capture the essence of the biological argument.

Not all models refrain from making numerically explicit predictions, however. Some are much more applied and number oriented; perhaps we are not interested in the causalities at all, but we would really like to predict the number of rats left in an area after an eradication programme, extrapolating from past knowledge of rat behaviour. In such a case, it is probably not particularly important to know exactly why rats retain memories of bad food experiences for as long a time as they do. We can simply assume this happens, take an exact numerical value from experiments and build this into our model. Such models are predictive and may be precise (if we are lucky), but they do not try to aid our conceptual understanding of evolutionary processes. Of course, if we are really lucky, we might get at that too; some famous success stories where evolutionary insight combines with numerically accurate predictions come from studies that link sex ratios to local mate competition. There are some others too.

There are also models that fail to be simple enough for us to understand fully their inner workings when they churn out results, yet they are not precise either in the sense of predicting the numbers of rats on an island. Often such models are complex computer simulations, tracking the state and behaviour of a large number of virtual individuals, and examining the emergent properties of the system. Such results can be fascinating to watch – who wouldn't like to play god, or have their own study species repeating their fascinating behaviour on a computer screen – but I would like to warn against the overuse of such methods. It is quite easy to become lost in the virtual world: the computer will be happy producing results night after night, and the data can be summarized in a vast number of graphs – but did we really gain an understanding of why this or that curve went up or down when varying one of the umpteen parameters? Rarely. Very complicated individual-based models are perhaps most useful if they try to answer a question such as 'X can happen.' For example, when introducing spatial structure, altruism can spread in local subpopulations; or, an emergent property does exist that is interesting in its own right. They are useless when trying to show that 'X cannot happen', because this would require simulating an infinite number of possible parameter combinations. Not being causally transparent, the outcome of such models could, in the worst case, increase the thinking time required to understand the matter at hand.

Finally, there are models that, for lack of a better term, I call 'mathematically beautiful' models. These are often published in journals that empiricists rarely read, and they look particularly scary to the average ecologist with their theorems and proofs. This book will not cover them. It is good to realize, though, that many of them exist for a rather different purpose than advancing the understanding of a biological system: it is the advancement of mathematics per se. The authors of such papers typically share a love for mathematical beauty, which is a powerful concept that is exceptionally hard to define and not immediately clear to anyone who finds integrals petrifying. Nevertheless, biology abounds with processes that inspire mathematical thinking. Naturally, in an ideal world there should be free flow of information all the way from the extremely theoretical and beautiful results to the ugly and messy nature of ecological data. In practice, there are trade-offs: sometimes mathematical beauty has to be sacrificed for biological relevance, or vice versa. Also, some researchers find the views of the 'other side' fairly incomprehensible. Some gentle advice for the readers of this book with a very strong sense of mathematical beauty: some forgiveness in this respect usually helps a lot if your goal is to make biologists listen. And for the majority of behavioural ecologists: stop being afraid. Nobody masters every mathematical technique; therefore, do not ever be afraid of asking stupid-sounding questions, or beginning your own modelling career somewhere – a paper that maximizes the scariness of the squiggles involved is never a goal in its own right.

Finally, before turning to the actual modelling techniques, it is worth asking yourself: why do you want to build a model? If it is just to have a