

## CHAPTER

## 1

## Introduction

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p0010 1 WinBUGS (Gilks et al., 1994; Spiegelhalter et al., 2003; Lunn et al., 2009)  
 2 is a general-purpose software program to fit statistical models under the  
 3 Bayesian approach to statistics. That is, statistical inference is based on  
 4 the posterior distribution, which expresses all that is known about the  
 5 parameters of a statistical model, given the data and existing knowledge.  
 6 In recent years, the Bayesian paradigm has gained tremendous momentum

- 1 in statistics and its applications, including ecology, so it is natural to wonder  
2 about the reasons for this.

## s0010 1.1 ADVANTAGES OF THE BAYESIAN APPROACH TO STATISTICS

- p0015 3 Key assets of the Bayesian approach and of the associated computa-  
4 tional methods include the following:

### s0015 1.1.1 Numerical Tractability

- p0020 5 Many statistical models are currently too complex to be fitted using  
6 classical statistical methods, but they can be fitted using Bayesian compu-  
7 tational methods (Link et al., 2002). However, it may be reassuring that, in  
8 many cases, Bayesian inference gives answers that numerically closely  
9 match those obtained by classical methods.

### s0020 1.1.2 Absence of Asymptotics

- p0025 10 Asymptotically, that is, for a “large” sample, classical inference based  
11 on maximum likelihood (ML) is unbiased, i.e., in the long run right on  
12 target. However, for finite sample sizes, i.e., for *your data set*, ML may  
13 well be biased (Le Cam, 1990). Similarly, standard errors and confidence  
14 intervals are valid only for “large” samples. Statisticians never say what  
15 “large” exactly means, but you can be assured that typical ecological data  
16 sets aren’t large. In contrast, Bayesian inference is *exact* for any sample  
17 size. This issue is not widely understood by ecological practitioners of sta-  
18 tistics but may be particularly interesting for ecologists since our data sets  
19 are typically small to very small.

### s0025 1.1.3 Ease of Error Propagation

- p0030 20 In classical statistics, computing the uncertainty of functions of random  
21 variables such as parameters is not straightforward and involves approxi-  
22 mations such as the delta method (Williams et al., 2002). For instance,  
23 consider obtaining an estimate for a population growth rate ( $\hat{r}$ ) that is  
24 composed of two estimates of population size in subsequent years  
25 ( $\hat{N}_1, \hat{N}_2$ ). We have  $\hat{N}_1$  and  $\hat{N}_2$  and we want  $\hat{r}$ : what should we do? Getting  
26 the point estimate of  $\hat{r}$  is easy, but what about its standard error? In a  
27 Bayesian analysis with Markov chain Monte Carlo, estimating such, and  
28 much more complex, derived quantities including their uncertainty is

- 1 trivial once we have a random sample from the posterior distribution of  
 2 their constituent parts, such as  $\hat{N}_1$  and  $\hat{N}_2$  in our example.

s0030 **1.1.4 Formal Framework for Combining Information**

p0035 3 By basing inference on both what we knew before (the prior) and what  
 4 we see now (the data at hand), and using solely the laws of probability for  
 5 that combination, Bayesian statistics provides a formal mechanism for  
 6 introducing external knowledge into an analysis. This may greatly  
 7 increase the precision of the estimates (McCarthy and Masters, 2005);  
 8 some parameters may only become estimable through precisely this com-  
 9 bination of information.

p0040 10 Using existing information also appears a very sensible thing to do: after  
 11 all, only rarely don't we know anything at all about the likely magnitude of  
 12 an estimated parameter. For instance, when estimating the annual survival  
 13 rate in a population of some large bird species such as a condor, we would  
 14 be rather surprised to find it to be less than, say, 0.9. Values of less than, say,  
 15 0.5 would appear downright impossible. However, in classical statistics, by  
 16 not using any existing information, we effectively say that the survival rate  
 17 in that population could be just as well 0.1 as 0.9, or even 0 or 1. This is not  
 18 really a sensible attitude since every population ecologists knows very well  
 19 *a priori* that no condor population would ever survive for very long with a  
 20 survival rate of 0.1. In classical statistics, we always feign total ignorance  
 21 about the system under study when we analyze it.

p0045 22 However, within some limits, it is also possible to specify ignorance in a  
 23 Bayesian analysis. That is, also under the Bayesian paradigm, we can base  
 24 our inference on the observed data alone and thereby obtain inferences  
 25 that are typically very similar numerically to those obtained in a classical  
 26 analysis.

s0035 **1.1.5 Intuitive Appeal**

p0050 27 The *interpretation of probability* in the Bayesian paradigm is much more  
 28 intuitive than in the classical statistical framework; in particular, we directly  
 29 calculate the probability that a parameter has a certain value rather than the  
 30 probability of obtaining a certain kind of data set, given some Null hypo-  
 31 thesis. Hence, popular statements such as "I am 99% sure that ..." are only  
 32 possible in a Bayesian mode of inference, but they are impossible in princi-  
 33 ple under the classical mode of inference. This is because, in the Bayesian  
 34 approach, a probability statement is made about a parameter, whereas in  
 35 the classical approach, it is about a data set.

p0055 36 Furthermore, by drawing conclusions based on a combination of what  
 37 we knew before (the prior, or the "experience" part of learning) and what

1 we see now (the likelihood, or the “current observation” part of learning),  
2 Bayesian statistics represent a *mathematical formalization of the learning*  
3 *process*, i.e., of how we all deal with and process information in science  
4 as well as in our daily life.

#### s0040 1.1.6 Coherence and Intellectual Beauty

p0060 5 The entire Bayesian theory of statistics is based on just three axioms of  
6 probability (Lindley, 1983, 2006). This contrasts with classical statistics  
7 that Bayesians are so fond to criticize for being a patchwork of theory  
8 and *ad hoc* amendments containing plenty of internal contradictions.

### s0045 1.2 SO WHY THEN ISN'T EVERYONE A BAYESIAN?

p0065 9 Given all the advantages of the Bayesian approach to statistics just men-  
10 tioned, it may come as a surprise that currently almost all ecologists still  
11 use classical statistics. Why is this?

p0070 12 Of course, there is some resistance to the Bayesian philosophy with  
13 its perceived subjectivity of prior choice and the challenge of avoiding  
14 to, unknowingly, inject information into an analysis via the priors, see  
15 Chapter 2. However, arguably, the lack of a much more widespread adop-  
16 tion of Bayesian methods in ecology has mostly practical reasons.

p0075 17 First, a Bayesian treatment shines most for complex models, which may  
18 not even be fit in a frequentist mode of inference (Link et al., 2002). Hence,  
19 until very recently, most applications of Bayesian statistics featured rather  
20 complex statistical models. These are neither the easiest to understand in  
21 the first place, nor may they be relevant to the majority of ecologists.  
22 Second, typical introductory books on Bayesian statistics are written in  
23 what is fairly heavy mathematics to most ecologists. Hence, getting to the  
24 entry point of the Bayesian world of statistics has been very difficult for  
25 many ecologists. Third, Bayesian philosophy and computational methods  
26 are not usually taught at universities. Finally, and perhaps most impor-  
27 tantly, the practical implementation of a Bayesian analysis has typically  
28 involved custom-written code in general-purpose computer languages  
29 such as Fortran or C++. Therefore, for someone lacking a solid knowledge  
30 in statistics and computing, Bayesian analyses were essentially out of reach.

### s0050 1.3 WinBUGS

p0080 31 This last point has radically changed with the advent of WinBUGS  
32 (Lunn et al., 2009). Arguably, WinBUGS is the only software that allows  
33 an average numerate ecologist to conduct his own Bayesian analyses of

1 realistically complex, customized statistical models. By customized I mean  
 2 that one is not constrained to run only those models that a program lets  
 3 you select by clicking on a button. However, although WinBUGS has been  
 4 and is increasingly being used in ecology, the paucity of really accessible  
 5 and attractive introductions to WinBUGS for ecologists is a surprise (but  
 6 see McCarthy, 2007). I believe that this is the main reason for why Win-  
 7 BUGS isn't even more widely used in ecology.

## 1.4 WHY THIS BOOK?

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p0085 8 This book aims at filling this gap by gently introducing ecologists to  
 9 WinBUGS for exactly those methods they use most often, i.e., the linear,  
 10 generalized linear, linear mixed, and generalized linear mixed model  
 11 (GLMM). Table 1.1 shows how the three latter model classes are all gen-  
 12 eralizations of the simple Normal linear model (LM) in the top left cell of  
 13 the body of the table. They extend the Normal model to contain either  
 14 more than a single random process (represented by the residual in the  
 15 Normal LM) and/or to exponential family distributions other than  
 16 the Normal, e.g., Poisson and Binomial. Alternatively, starting from the  
 17 GLMM in the bottom right cell, the other three model classes can be  
 18 viewed as special cases obtained by imposing restrictions on a general  
 19 GLMM.

p0090 20 These four model classes form the core of modern applied statistics.  
 21 However, even though many ecologists will have applied them often  
 22 using click-and-point programs or even statistics packages with a pro-  
 23 gramming language such as GenStat, R, or SAS, I dare express doubts  
 24 whether they all really always understand the models they have fitted.  
 25 Having to specify a model in the elementary way that one has to in Win-  
 26 BUGS will prove to greatly enhance your understanding of these models,  
 27 whether you fit them by some sort of likelihood analysis (e.g., ML or  
 28 restricted maximum likelihood [REML]) or in a Bayesian analysis.

p0095 29 Apart from the gentle and nonmathematical presentation by examples,  
 30 the unique selling points of this book, which distinguish it from others, are

t0010 **TABLE 1.1** Classification of Some Core Models Used for Applied  
 Statistical Analysis

	Single Random Process	Two or More Random Processes
Normal response	Linear model (LM)	Linear mixed model (LMM)
Exponential family response	Generalized linear model (GLM)	Generalized linear mixed model (GLMM)

- 1 the full integration of all WinBUGS analyses into program R, the parallel
- 2 presentation of classical and Bayesian analyses of all models and the use of
- 3 simulated data sets. Next, I briefly expand on each of these points.

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### 1.4.1 This Is Also an R Book

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- 4 One key feature of this book as an introduction to WinBUGS is that we
- 5 conduct all analyses in WinBUGS fully integrated within program R
- 6 (R Development Core Team, 2007). R has become the *lingua franca* of mod-
- 7 ern statistical computing and conducting your Bayesian analysis in
- 8 WinBUGS from within an R session has great practical benefits. Moreover,
- 9 we also see how to conduct all analyses using common R functions such as
- 10 `lm()`, `glm()`, and `glmer()`. This has the added bonus that this book will
- 11 be useful to you even if you only want to learn to understand and fit the
- 12 models in Table 1 in a classical statistical setting.

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### 1.4.2 Juxtaposition of Classical and Bayesian Analyses

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- 13 Another key feature is the juxtaposition of analyses using the classical
- 14 methods provided for in program R (mostly ML) and the analyses of the
- 15 same models in a Bayesian mode of inference using WinBUGS. Thus, with
- 16 the exception of Chapters 20 and 21, we fit every model in both the clas-
- 17 sical and the Bayesian mode of inference. I have two reasons for creating
- 18 parallel examples. First, this should increase your confidence into the
- 19 “new” (Bayesian) solutions since with vague priors they give numerically
- 20 very similar answers as the “old” solutions (e.g., ML). Second, the analysis
- 21 of a single model by both classical and Bayesian methods should help to
- 22 demystify Bayesian analysis. One sometimes reads statements like “we
- 23 used a Bayesian model,” or “perhaps a Bayesian model should be tried
- 24 on this difficult problem.” This is nonsense! Since any model exists inde-
- 25 pendently of the method we choose to analyze it. For instance, the linear
- 26 regression model is not Bayesian or non-Bayesian; rather, this model may
- 27 be *analyzed* in a Bayesian or in a frequentist mode of inference. Even that
- 28 class of models which has come to be seen as almost synonymous with
- 29 Bayesian inference, hierarchical models which specify a hierarchy of sto-
- 30 chastic processes, is not intrinsically Bayesian; rather, hierarchical models
- 31 can be analyzed by frequentist (de Valpine and Hastings, 2002; Lee et al.,
- 32 2006; de Valpine, 2009; Ponciano et al., 2009) or by Bayesian methods
- 33 (Link and Sauer, 2002; Sauer and Link, 2002; Wikle, 2003; Clark et al.,
- 34 2005). Indeed, many statisticians now use the two modes of inference
- 35 quite opportunistically (Royle and Dorazio, 2006, 2008). Thus, the juxta-
- 36 position of classical and Bayesian analysis of the same models should
- 37 make it very clear that a model is one thing and its analysis another
- 38 and that there really is no such thing as a “Bayesian model.”

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### 1.4.3 The Power of Simulating Data

- p0110** 1 A third key feature of this book is the use of simulated data sets  
 2 throughout (except for one data set used repeatedly in the exercises). At  
 3 first, this may seem artificial, and I have no doubts that some readers may  
 4 be disinterested in an analysis when a problem is perceived as “unreal.”  
 5 However, I would claim that several very important benefits accrue from  
 6 the use of simulated data sets, especially in an introductory book:
- p0115 7 1. For simulated data, truth is known. That is, estimates obtained in the  
 8 analysis of a model can be compared with what we know they should  
 9 be in the long-run average.
- p0120 10 2. When coding an analysis in WinBUGS, especially in more complex  
 11 cases but even for simpler ones, it is very easy to make mistakes.  
 12 Ensuring that an analysis recovers estimates that resemble the known  
 13 input values used to generate a data set can be an important check that  
 14 it has been coded correctly.
- p0125** 15 3. It has been said that one of the most difficult, but absolutely necessary  
 16 statistical concepts to grasp is that of the sampling variation of an  
 17 estimator. For nonstatisticians, I don’t see any other way to grasp the  
 18 meaning of sampling variation other than literally experiencing it by  
 19 repeatedly simulating data under the same model, analyzing them, and  
 20 seeing how estimates differ randomly from one sample to the next: this  
 21 variation is exactly what the standard error of an estimate quantifies. In  
 22 real life, one typically only ever observes a single realization (i.e., data  
 23 set) from the stochastic system about which one wants to make an  
 24 inference in a statistical analysis. Hence, for ecologists it may be hard to  
 25 make the connection with the concept of repeated samples from a  
 26 system, when all we have is a single data set (and related to that, to  
 27 understand the difference between a standard deviation and a standard  
 28 error).
- p0130 29 4. Simulating data can be used to study the long-run average  
 30 characteristics of estimates, given a certain kind of data set, by  
 31 repeating the same data generation-data analysis cycle many times. In  
 32 this way, the (frequentist) operating characteristics of an estimator  
 33 (bias, or “is it on target on average?”; efficiency, or “how far away from  
 34 the target is the individual estimate on average?”) can be studied by  
 35 packaging both the simulation and the analysis into a loop and  
 36 comparing the distribution of the resulting estimates to the known  
 37 truth. Further, required sample sizes to obtain a desired level of  
 38 precision can be investigated, as can issues of parameter estimability.  
 39 All this can be done for exactly the specifications of one’s data set, e.g.,  
 40 replicate data sets can be generated and analyzed with sample size and  
 41 parameter values identical to those in one’s real data set to get an  
 42 impression, say, of the precision of the estimates that one is likely to



1 obtain. This is also the idea behind posterior predictive checks of  
 2 goodness-of-fit, where the “natural” lack of fit for a model is studied  
 3 using ideal data sets and then compared with the lack of fit observed  
 4 for the actual data set (see Section 8.4.2).

p0135 5 5. Simulated data sets can be used to study effects of assumption  
 6 violations. All models embody a set of assumptions that will be  
 7 violated to some degree. Whether this has serious consequences for  
 8 those estimates one is particularly interested in, can be studied using  
 9 simulation.

p0140 10 6. Finally, and perhaps most importantly, I would claim that the ultimate  
 11 proof that one has really understood the analysis of a statistical model  
 12 is when one is able to simulate a data set under that very model.  
 13 Analyzing data is a little like fixing a motorbike but in reverse: it  
 14 consists of breaking a data set into its parts (e.g., covariate effects and  
 15 variances), whereas fixing a bike means putting all the parts of a bike  
 16 into the right place. One way to convince yourself that you really  
 17 understand how a bike works is to first dismantle and then reassemble  
 18 it again to a functioning vehicle. Similarly, for data analysis, by first  
 19 assembling a data set and then breaking it apart into recognizable parts  
 20 by analyzing it, you can prove to yourself that you really understand  
 21 the analysis.

p0145 22 In summary, I believe that the value of simulation for analysis and  
 23 understanding of complex stochastic systems can hardly be overstated.  
 24 On a personal note, what has helped me most to understand nonnormal  
 25 GLMs or mixed models, apart from having to specify them in the intuitive  
 26 BUGS language, was to simulate the associated data sets in program R,  
 27 which is great for simulating data.

p0150 28 Finally, I hope that the slightly artificial flavor of my data sets is more  
 29 than made up for by their nice ecological setting and the attractive organ-  
 30 isms we pretend to be studying. I imagine that many ecologists will by far  
 31 prefer learning about new statistical methods using artificial *ecological* data  
 32 sets than using real, but “boring” data sets from the political, social,  
 33 economical, or medical sciences, as one has to do in many excellent intro-  
 34 ductory books.

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## 1.5 WHAT THIS BOOK IS NOT ABOUT: THEORY OF BAYESIAN STATISTICS AND COMPUTATION

p0155 35 The theory of Bayesian inference is treated only very cursorily in this  
 36 book (see Chapter 2). Other authors have done this admirably, and  
 37 I refer you to them. Texts that should be accessible to ecologists include



1 Ellison (1996), Wade (2000), Link et al. (2002), Bernardo (2003), Brooks  
 2 (2003), Gelman et al. (2004), Woodworth (2004), McCarthy (2007), Royle  
 3 and Dorazio (2008), King et al. (2009), and Link and Barker (2010).

p0160 4 Furthermore, I don't dwell on explaining Markov chain Monte Carlo  
 5 (MCMC) or Gibbs sampling, the computational methods most frequently  
 6 used to fit models in the Bayesian framework. Arguably, a deep under-  
 7 standing of the details of MCMC is not required for an ecologist to con-  
 8 duct an adequate Bayesian analysis using WinBUGS. After all, very few  
 9 ecologists who nowadays fit a GLM or a mixed model understand the  
 10 (possibly restricted) likelihood function or the algorithms used to find  
 11 its maximum. (Or can you explain the Newton-Raphson algorithm?  
 12 And how about iteratively reweighted least squares?) Rather, by using  
 13 WinBUGS we are going to experience some of the key features of  
 14 MCMC. This includes the chain's initial transient behavior, the resultant  
 15 need for visual or numerical assessment of convergence that leads to dis-  
 16 carding of initial ("burn-in") parts of a chain, and the fact that successive  
 17 iterations are not independent. If you want to read more on Bayesian com-  
 18 putation, most of the above references may serve as an entry point to a  
 19 rich literature.

## 1.6 FURTHER READING

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p0165 20 If you seriously consider going Bayesian for your statistical modeling,  
 21 you will probably want to purchase more than a single book. McCarthy  
 22 (2007) is an accessible introduction to WinBUGS for beginners, although it  
 23 presents WinBUGS only as a standalone application (i.e., not run from R)  
 24 and the coverage of model classes dealt with is somewhat more limited.  
 25 Gelman and Hill (2007) is an excellent textbook on linear, generalized, and  
 26 mixed (generalized) linear models fit in both the classical and the Bayesian  
 27 mode of inference and using both R and WinBUGS. Thus, its concept is  
 28 somewhat similar to that of this book, though it does not feature the rig-  
 29 orous juxtaposition of both kinds of analysis. All examples are from the  
 30 social and political sciences, which will perhaps not particularly interest  
 31 an ecologist. However, the book contains a wealth of information that  
 32 should be digestible for the audience of this book, as does Gelman et al.  
 33 (2004). Ntzoufras (2009) is a new and comprehensive introduction to Win-  
 34 BUGS focusing on GLMs. It is very useful, but has a higher mathematical  
 35 level and uses WinBUGS as a standalone application only. Woodworth  
 36 (2004) is an entry-level introduction to Bayesian inference and also has  
 37 some WinBUGS code examples.

p0170 38 Link and Barker (2010) is an excellent textbook on Bayesian inference  
 39 specifically for ecologists and featuring numerous WinBUGS examples.

1 As an introduction to Bayesianism written mostly in everyday language,  
2 Lindley, an influential Bayesian thinker, has written a delightful book,  
3 where he argues, among others, that *probability is the extension of logic to*  
4 *all events, both certain (like classical logic) and uncertain* (Lindley, 2006,  
5 p. 66). His book is not about practical aspects of Bayesian analysis, but  
6 very informative, quite amusing and above all, written in an accessible  
7 way.

p0175 8 In this book, we run WinBUGS from within program R; hence, some  
9 knowledge of R is required. Your level of knowledge of R only needs to  
10 be minimal and any simple introduction to R would probably suffice to  
11 enable you to use this book. I like Dalgaard (2001) as a very accessible  
12 introduction that focuses mostly on linear models, and at a slightly  
13 higher level, featuring mostly GLMs, Crawley (2005) and Aitkin et al.  
14 (2009). More comprehensive R books will also contain everything  
15 required, e.g., Venables and Ripley (2002), Clark (2007), and Bolker  
16 (2008).

p0180 17 This book barely touches some of the statistical models that one  
18 would perhaps particularly expect to see in a statistics book for ecolo-  
19 gists, namely, Chapters 20 and 21. I say nothing on such core topics in  
20 ecological statistics such as the estimation of population density, survi-  
21 val and other vital rates, or community parameters (Buckland et al.,  
22 2001; Borchers et al., 2002; Williams et al., 2002). This is intentional. I  
23 hope that my book lays the groundwork for a much better understand-  
24 ing of statistical modeling using WinBUGS. This will allow you to better  
25 tackle more complex and specialized analyses, including those featured  
26 in books like Royle and Dorazio (2008), King et al. (2009), and Link and  
27 Barker (2010).

p0185 28 Free documentation for WinBUGS abounds, see <http://www.mrc-bsu>  
29 [.cam.ac.uk/bugs/winbugs/contents.shtml](http://www.mrc-bsu.cam.ac.uk/bugs/winbugs/contents.shtml). The manual comes along with  
30 the program; within WinBUGS go Help > User Manual or press F1 and  
31 then scroll down. Recently, an open-source version of BUGS has been  
32 developed under the name of OpenBugs, see <http://mathstat.helsinki>  
33 [.fi/openbugs/](http://mathstat.helsinki.fi/openbugs/), and the latest release contains a set of ecological example  
34 analyses including those featured in Chapters 20 and 21. WinBUGS can  
35 be run in combination with other programs such as R, GenStat, Matlab,  
36 SAS; see the main WinBUGS Web site. There is even an Excel front-end  
37 (see <http://www.axrf86.dsl.pipex.com/>) that allows you to fit a wide range  
38 of complex models without even knowing the BUGS language. However,  
39 most serious WinBUGS users I know run it from R (see Chapter 5). It turns  
40 out that one of the main challenges for the budding WinBUGS program-  
41 mer is to really understand the linear model (see Chapter 6). One particu-  
42 larly good introduction to the linear model in the context of survival and  
43 population estimation is Chapter 6 in Evan Cooch's *Gentle introduction to*  
44 *MARK* (see <http://www.phidot.org/software/mark/docs/book/pdf/chap6.pdf>).

## 1.7 SUMMARY

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- p0190 1 This book attempts the following:
- p0195 2 1. *demystify Bayesian analyses* by showing their application in the most  
3 widely used general-purpose Bayesian software WinBUGS, in a gentle  
4 tutorial-like style and in parallel with classical analyses using program  
5 R, for a large set of ecological problems that range from very simple to  
6 moderately complex;
- p0200 7 2. enhance your understanding of the *core of modern applied statistics*:  
8 linear, generalized linear, linear mixed, and generalized linear mixed  
9 models and features common to all of them, such as statistical  
10 distributions and the design matrix;
- p0205 11 3. demonstrate the *great value of simulation*; and
- p0210 12 4. thereby building a solid grounding of the use of WinBUGS (and R) for  
13 relatively simple models, so you can tackle more complex ones, and to  
14 help *free the modeler in you*.

