CHAPTER

14

Concluding Remarks

We have given an overview of the Bayesian analysis of models for population analysis using WinBUGS. By population analysis, we mean the analysis of data from populations and communities, especially data on distribution and abundance, and the four vital rates governing their dynamics: survival, recruitment, immigration, and emigration probability. We almost always use hierarchical models, which are fitted very naturally in a Bayesian framework of inference using the simple and flexible BUGS language. In particular, hierarchical models enable direct modeling of the observation process, thereby accounting for false-negative observation errors. We have extensively used capture–recapture-type models, which achieve a partitioning of an observed response into one component describing the ecological process of interest and another representing its imperfect observation. In this concluding chapter, we first reflect on the power and beauty of hierarchical models (Section 14.1) and on the importance of accounting for the observation process in any inference about populations and communities from ecological field data (Section 14.2). We continue with remarks on possible future avenues for population analysis (Section 14.3) and finally emphasize some of the applications in which rigorous population analyses appear to be particularly important (Section 14.4).

14.1 THE POWER AND BEAUTY OF HIERARCHICAL MODELS

The concept of hierarchical models runs as a common thread throughout this book. In this respect, we owe a great debt to Royle and Dorazio (2008), who have laid much of the intellectual groundwork for us and from which many code examples are taken. As we have seen many times in our book, the use of hierarchical models, especially when fitted in WinBUGS, has many advantages; some of which we discuss in the following.

14.1.1 Hierarchical Models Make the Fitting of Complex Statistical Models Easier

Hierarchical models express the observed data as a result of a sequence of linked, simpler probabilistic systems, with each random variable being dependent on the outcome of the random variable preceding it in the hierarchy of a model. A neat example is that for the dynamic occupancy model (Section 13.5). It consists of three linked Bernoulli random variables, or logistic regressions, describing the initial occupancy state,

occupancy dynamics, and the observation process, respectively. Ignoring site indices, this model can be written as follows:

Random variable 1 (initial state): $z_1 \sim \text{Bernoulli}(\psi_1)$
Random variable 2 (state dynamics): $z_{t+1} \mid z_t \sim \text{Bernoulli}(z_t \phi_t + (1 - z_t)\gamma_t)$
Random variable 3 (observation process): $y_t \mid z_t \sim \text{Bernoulli}(z_t p_t)$

The hierarchical model decomposes a complicated stochastic system into a sequence of three dependent subprocesses. In this way, a complex model becomes much easier to understand and fit. The beauty of hierarchical models lies in the almost unbelievable simplicity when a complex model is decomposed into its individual component models. The entire model may be difficult to understand and fit for an ecologist, but each individual submodel is really simple. For example, the incorporation of additional complexity, such as covariate or random effects, is straightforward.

14.1.2 Hierarchical Models Foster a Synthetic Understanding of a Large Array of Models

A big advantage of the hierarchical specification of complex models in population analysis is that it fosters a whole new and synthetic under-standing of a vast array of models, which may often be thought of as being unrelated. For instance, in the capture–recapture literature a big divide is typically made between models for closed and models for open populations. However, when written as a hierarchical model, we cannot avoid recognizing the similarities rather than seeing the differences between them. For instance, Table 14.1a shows the hierarchical specifica-tion of a closed-population model for abundance estimation implemented by data augmentation (Chapter 6) and that for an open population (dynamic occupancy model, Section 13.5).

In both the closed- and the open-population model, the initial state is modeled as a Bernoulli trial with a success parameter (ψ_1). In the closed model, $z_1 = 1$ denotes a genuinely existing individual, whereas in the open model $z_1 = 1$ denotes an occupied site. The description of the state dynamics in the closed model is simply that there is none: the state at occa-sion $t + 1$ is identical to the state at occasion t. In contrast, in the open model, the state at occasion $t + 1$ is a function of the state at occasion t and para-meters for survival (ϕ) and colonization (γ). Finally, the observation process is again identical in both models: at time t, all existing individuals or occu-pied sites flip a coin to determine whether they are detected or not.

As another example, Table 14.1b shows the relationships between two superficially very different models, one an implicit and the other an explicit hierarchical model (Royle and Dorazio 2008). The first is a

TABLE 14.1 Two examples of The Power of Hierarchical Models to Clarify the Relationships among Model Classes

(a) Conceptual Similarity between a Closed-Population Model (see Chapter 6) and an Open-Population Model (dynamic occupancy model; see Chapter 13)*

Submodel	Closed-Population Model	Open-Population Model
Initial State	$z_1 \sim \text{Bernoulli}(\psi_1)$	$z_1 \sim \text{Bernoulli}(\psi_1)$
State Dynamics	$z_{t+1} \mid z_t = z_t$	$z_{t+1} \mid z_t \sim \text{Bernoulli}(z_t\phi_t + (1-z_t)\gamma_t)$
Observation Process	$y_t \mid z_t \sim \text{Bernoulli}(z_t p_t)$	$y_t \mid z_t \sim \text{Bernoulli}(z_t p_t)$

(b) Conceptual Similarity between a State-Space Model (see Chapter 5) and the Cormack–Jolly–Seber Model (see Chapter 7)**

Submodel	State-Space Model	CJS Model
Initial State	$N_1 \sim f(\theta_1)$	$z_1 = 1$
State Dynamics	$N_{t+1} \mid N_t \sim g(N_t, \theta_2)$	$z_{t+1} \mid z_t \sim g(z_t, \theta_2)$
Observation Process	$y_t \mid N_t \sim h(N_t, \theta_3)$	$y_t \mid z_t \sim h(z_t, \theta_3)$

*t indexes occasions in the closed-population model and primary occasions in the open-population model. To make all parameters in the latter identifiable, data are required from secondary occasions during a period of closure.
**To clarify the difference between states in the two models, the relative abundance state at time t in the state-space model is denoted as N_t, whereas the "alive" state in the CJS model is denoted as z_t.

state-space model for a single time series of population counts (Chapter 5) and the second is the Cormack–Jolly–Seber (CJS) model for multiple time series of survival events (Chapter 7). The initial state is modeled using a distribution f with parameter θ_1 in the state-space model. In contrast, the initial state is not modeled in the CJS model but is 1 by definition because the CJS model conditions on initial capture. In both models, for all later time steps, the state at time $t + 1$ is a random variable that depends on the state at time t and on parameter θ_2 via a distribution g. For g, we use a normal distribution with a mean and a variance parameter for the state-space model and a Bernoulli distribution with a parameter representing the success probability for the CJS model. Finally, as a description of the observation error at time t, we use a distribution h, which depends on the true state at time t and on parameter θ_3. The statistical description of the observation process is another normal for the state space and a Bernoulli distribution for the CJS model. Similar schemes can be devised for all hierarchical models.

Hence, a hierarchical specification of models for population analysis emphasizes the similarities among models that appear to be very different at a first glance. We believe that the unified perspective on a large number of models provided by their hierarchical description will be very beneficial for your population modeling. Moreover, we have seen at many places how the specification of a model in the BUGS language is almost a direct

translation of a hierarchical model described in algebra, as in Table 14.1. Thus, we believe that statistical modeling in BUGS will foster in you a more synthetic understanding of large classes of models: they may *appear* quite different, but in fact they share many commonalities!

Throughout this book, we have emphasized the algebraic description of hierarchical models. There is another, very general way to describe hierarchical models: by directed acyclic graphs (DAGs; Spiegelhalter, 1998). We have not used DAGs in this book, except for Fig. 11.3, but if you have experience in reading and drawing DAGs, it can be very enlightening to draw them for the models in this book (R. A. Hutchinson, pers. comm.). This will also allow you to see the surprising similarities among these models.

14.1.3 Hierarchical Models Lead to Cleaner Thinking

We believe that hierarchical models foster a unified way of thinking about statistical modeling. For instance, for ecological field data, it becomes completely natural to think in terms of a hierarchical model that separates the ecological and the observation processes. Indeed, after a while of being in that mode of thinking, it becomes hard *not* to partition in your mind any kind of field data into the result of an ecological process and that of an observation process. So, indirectly, working with WinBUGS can be an act of intellectual hygiene that leads to a more mechanistic thinking about the systems we study.

14.1.4 Hierarchical Models Lead to a Step-Up Approach in Tackling a Problem

Although conceptually easy, fitting hierarchical models using WinBUGS can be complicated in practice and many things can go wrong. Hence, we always favor a modeling strategy where we start from a simple model and increasingly add in complexity until we are at the desired model (see Appendix 1, tip 28). This step-up approach may force on us a whole new way of thinking, where we start thinking about a problem in a very simplified way. Once we have understood the problem in that setting, we incrementally add in more complexity until we (hopefully) understand the model we wanted to fit to start with. We believe that this is exactly the way in which successful science should work: we must first understand a simple version of a problem before we can go on to try and understand the more complex ones. Often, we see people who immediately want to attack a very complex version of a problem, without first even trying to understand its simpler versions. We believe that this is a recipe for failure. Thus, modeling in WinBUGS trains us to think in a more disciplined way about doing science in general.

14.1.5 What Kind of Hierarchical Model? Primary Model Selection in WinBUGS

One of the aims of this book is to provide an accessible entry point to the literature on a large number of models that are useful for population analysis and to illustrate their implementation in WinBUGS. So which one in this bewildering multitude of models should we choose to answer our ecological questions? Obviously, the best choice among these models will depend on many things, including modeling objectives, data, sampling design and the assumptions one is willing to make.

The first criterion for primary model choice should always be our scientific or management questions, that is, the *objectives of the model*. This cannot be stressed enough: we ought to be very clear about the objective behind every modeling exercise. For example, prediction may require quite a different model than explanation. Further, model choice may depend on how similar the inferences (for instance, the estimate of the effect of a management intervention) under different models are and whether these differences are of practical importance given the modeling objectives. It may be reasonable to choose a second-best model when the inferences are practically identical to those under the best model and when the second-best model has other advantages (e.g., runs much faster).

Second, model choice depends on the data at hand. For instance, if data are available to estimate detection probability in a time series of counts, we would not use the rather simplistic description of the observation process of the models in Chapter 5. Rather, we might use a binomial or other suitable distribution to explicitly model false-negative detection errors (see Section 1.3). If no such information on detection probability is available, the implicit hierarchical models in Chapters 4 and 5 may be the best that can be done. Similarly, occurrence data such as territory occupancy or species distribution could be modeled using a variant of a binomial GLM (Chapters 3 and 4). Such an approach balls up in a single parameter the probabilities of occupancy and detection (Kéry et al. 2010a, Kéry 2011b). However, often we *do* have extra information on the observation process, for example, replicated detection or nondetection observations within a short time period. If this is the case, we find it hard to understand how one would choose *not* to jointly model the ecological process and the observation process in an explicit hierarchical model (i.e., a site-occupancy model, Chapter 13).

Sampling design is intimately linked to the previous point as are the assumptions that we may want or have to make. Often, we must make assumptions to compensate for deficiencies in the design and the data. For instance, absent data that are directly informative about the observation process, we must make strong assumptions about detection probability, for example, that it is constant on average or even that it is equal to 1.

Such primary decisions in the selection among broad classes of models require a great flexibility in our modeling and indeed an "organic" approach to statistical modeling, where the model can be tailored exactly to one's needs. Fitting hierarchical models in WinBUGS typically gives one this flexibility.

14.1.6 Secondary Model Selection: Hierarchical Models and Variable Selection

Once we have made the primary decision about the general class of model for population analysis, there are additional decisions to take, for instance about the types or the form of covariates to incorporate. These secondary modeling decisions are often called model selection. Over the last decades, Burnham and Anderson (e.g., 2002) have been very influential in population ecology and management with their ideas about model building by a certain form of model selection. In a way, they advocate the opposite approach from the one that we are almost forced to adopt when using WinBUGS. Burnham and Anderson argue that, first, one must think hard about a problem and come up with a set of models that each represent a distinct biological hypothesis that we want to compare and test. Second, one must fit exactly these models to the data and use the Akaike's information criterion (AIC) as a referee as to which model explains the observed data best.

We endorse this general strategy of doing science and like the emphasis on a priori thinking, instead of rushing into the data and doing data dredging. However, it appears to us that a strict adherence to the recipe of Burnham and Anderson is difficult with complicated models regardless of whether they are fitted in a frequentist or Bayesian way. As described in Section 14.1.4, there is much heuristic value in an incremental model building strategy. Thus, with WinBUGS, we are almost forced to do something that *resembles* data dredging, in which our fitting of a desired ultimate model often means that we have to fit several similar neighboring models as well. We believe that the ideal of Burnham and Anderson could still be upheld when a set of different a priori hypotheses are formulated before the start of the modeling exercise.

When teaching WinBUGS workshops to ecologists, one of the biggest disappointments we see is always the lack of an automated variable selection strategy that can be as easily implemented as AIC in maximum likelihood analyses. In hierarchical models, use of the standard DIC (Spiegelhalter et al., 2002) is controversial (Celeux et al., 2006) or downright wrong for at least some hierarchical models (Millar, 2009)—and most interesting models in this book are hierarchical. Furthermore, Bayesian variable selection is more involved and computationally demanding (O'Hara and Sillanpää, 2009).

The lack of an automated variable selection procedure can be seen as a good or as a bad thing. Of course, we would like to be able to filter through a large number of hierarchical models and have an easily computed criterion to help us pick the most useful one. On the other hand, we believe that the very ease with which AIC does variable selection has defeated part of the intentions of its advocates, Burnham and Anderson: since model comparison is made so easy, AIC may often lead to more rather than less data dredging. So, it may be that only when variable selection is difficult, do we actually think hard about which models we want to fit!

14.1.7 Hierarchical Models and MARK, unmarked, E-SURGE, and PRESENCE

Hierarchical models can be fitted using frequentist and Bayesian methods. We believe that the choice between a frequentist and a Bayesian analysis of a model should in a large part be made on the basis of how practical it is and how well each one meets the objectives of the modeling. In this sense, we argue for a pragmatic choice between frequentist and Bayesian approaches (Little, 2006; Gelman and Hill, 2007; Gelman, 2008). Our own preference for Bayesian modeling using WinBUGS is, first and foremost, due to the fact that the BUGS language and the automated generation of MCMC algorithms in WinBUGS (and OpenBUGS or JAGS) have given us such a remarkable modeling freedom, one we have never experienced with any other software.

So, what about other frequentist software to fit population models as illustrated in this book? Examples of such software include MARK (White and Burnham, 1999), the new R package unmarked (Fiske and Chandler, 2011), E-SURGE (Choquet et al., 2009b), and PRESENCE (Hines, 2006). These useful software programs allow you to fit a very large number of models, many of them hierarchical, at least in concept (see Section 2.8). For instance, somebody commented to us that software MARK, along with its free and constantly evolving, excellent online manual of E. Cooch and G. White (www.phidot.org/software/mark/docs/book), is a competitor with our book or the way we do population modeling. We are not convinced that this is true. MARK, as well as unmarked, E-SURGE, and PRESENCE, represent tremendous endeavors that have done and continue to do an immeasurable service to the community of population ecologists to enhance the level of analyses that are possible and are conducted. For instance, MARK has about 100 different kinds of models that can be fitted by click and point techniques, and it has a reasonably unified layout of data entry and model building.

We think that MARK, unmarked, E-SURGE and PRESENCE and the modeling advocated in our book serve different audiences and targets:

for first-timers in population modeling or for someone who wants to fit some sort of standard model (which may be very sophisticated!), MARK or one of these other packages surely represent an ideal tool. By contrast, for users who want to fit nonstandard models, combine different models (integration of information) or use prior information, WinBUGS is the appropriate choice.

Finally, WinBUGS gives you a new way of thinking about statistical modeling in population analysis that comes with the model specification in the BUGS language. WinBUGS frees the modeler in you and allows for a fully "organic way" of model building. In WinBUGS, quick and easy jumps can often be made to totally different model classes by simply adding a line of code or two. In contrast, in software such as MARK, the same modification to a model might require one to start the whole modeling project anew, right from reading in the data into the software. Thereby, it is easy to lose sight of the underlying similarities of many of the models (as illustrated, for instance, in Table 14.1).

14.1.8 Hierarchical Models and Study Design

Study design is an important topic that we have not covered in this book. We heard the comment that we ought to include in our book a chapter on study design. We first agreed, but in the end did not do this. The reason was simply that we thought the topic would be too daunting. We thought that the kinds of designs underlying the data featured in this book are too diverse and that we could not have said anything useful within a single book chapter. Instead, we refer to useful (non-Bayesian) books by Borchers et al. (2001), Buckland et al. (2001), Thompson (2002), and Williams et al (2002).

We would never want to downplay the importance of design in population ecology and wildlife management—actually, design is very important, and important first principles of good study design are almost always violated in ecological field studies, for example, random sampling. Nevertheless, with the great modeling freedom given by modern software such as WinBUGS, study design is perhaps a *little* less important nowadays than it was for the older, more rigid ways of analyzing data, for example, using ANOVA for designed experiments. The new modeling freedom brings with it a certain design freedom because even quite nonstandard designs can still be rigorously accommodated in a nonstandard analysis. Modeling in WinBUGS is perfect for nonstandard analyses (see also the Foreword by J. D. Nichols in Kéry, 2010).

One important design that we have only touched upon very superficially (see Section 10.8) is the robust design of sampling capture–recapture data (Pollock, 1982; Kendall et al., 1997; Williams et al., 2002). Except for

demographic analyses of abundance and occurrence data from metapopulation designs (Chapters 12 and 13), we have not illustrated this powerful design in this book. The robust design can be used also for demographic analyses of single populations to get improved estimates of population size and population dynamics (e.g., Karanth et al., 2006; Link and Barker, 2010). Often, data can be collected in the robust design with little added costs in the field. The robust design should be adopted whenever possible to improve inference in population analysis.

14.2 THE IMPORTANCE OF THE OBSERVATION PROCESS

We have emphasized a hierarchical perspective on models for population analysis. This is a reflection of the hierarchical processes that generate the observed data: an ecological process, which is usually of primary interest, and a dependent observation process, which often is a mere nuisance, but must be modeled to avoid spurious inferences about the ecological process. We have also emphasized what we believe is an important conceptual distinction between explicit and implicit hierarchical models (Royle and Dorazio, 2008); the former have parameters with an explicit ecological meaning and the latter do not. Typically, the distinction between explicit and implicit hierarchical models boils down to the question of whether our model contains an explicit description of the observation process, often in the form of a binomial distribution for a response representing a count or a Bernoulli for a response representing an event.

The direct interpretation of observed data, without accounting for the observation process, can be seriously misleading, even with constant detection probability. For instance, in Section 1.3, we saw that the average count seriously underestimated the true population size of sparrows in our yard. Moreover, repeated counts suggested that population size varies, whereas in reality, the variation in the counts was merely a consequence of the chance element inherent in any count based on an observation process characterized by imperfect detection. As another example, in Section 13.2, we saw how inferences from species distribution models can be quite wrong when imperfect detection is not accounted for. These difficulties may be aggravated severely when detectability is not constant but varies in response to environmental variables (see Sections 12.2.2 and 13.3.2).

But do we really always need to model the observation process in population analyses? After all, this usually requires additional data and more complex models. For instance, we need replicated counts for inference about abundance under an binomial mixture model (Chapter 12), whereas unreplicated counts suffice to model relative abundance under a simple Poisson regression (Chapter 3) or state-space model (Chapter 5).

We believe that explicit modeling of the observation process may not always be required or even possible. Most importantly, whether our models need a component for the observation process or not depends on the goals of our modeling exercise as well as on the available data. If we are satisfied with detecting *patterns* in abundance, occurrence, or survival, for instance, and courageous enough to assume that detection probability is constant over the desired dimensions of comparison (e.g., time), then we may well forego modeling of detection probability. Alternatively, we may have measured covariates that explain some or much of the variation in detection probability, and their inclusion in the model may standardize detection probability analytically (Link and Sauer, 2002; Sauer and Link, 2002). This may often be satisfactory. However, as soon as we want to interpret our data as true distribution, abundance, or survival, as opposed to relative distribution, relative abundance, and return rates, we must model detection probability explicitly and then also need the required data to do this (Kéry et al., 2010a). There is no escaping that. Treating a response in a model as relative abundance (i.e., not estimating detection probability as part of the model) and then reporting the results as "abundance" or "population size" is misleading and can be downright dishonest. When the required data to model detection explicitly are lacking (e.g., there are no replicated counts or no individual identification), then the model chosen should be as realistic as possible, but it must always be kept in mind that the model parameters confound the ecological and the observation process. The results of such an analysis must then be reported with due caution.

Perhaps, one ought to take a model-selection view of detection probability. Its inclusion in a model is associated with a cost as we need more and different data and a more complex model, so we ought to include it in the model only when its inclusion is warranted or practically feasible from a design standpoint. However, at the start, any rigorous population analysis ought to consider inclusion of detection probability as an essential model component. Only when we have reasons to exclude it should this be done. In other words, we believe that the choice of whether or not to include in a model a component for detection probability should be an active and conscious one and must be described and justified.

These considerations are also important at the design state of a study. We think that it should become much more natural to choose a design that includes collection of data informative on the observation process. To the extent possible, each ecological field study should be as follows:

1. Try to maximize detection probability and make it stable (eliminate as much variation in detection probability as possible, for instance, among observers, sites, and over time). Responses will still be variable (see Section 1.3), but at least some noise is eliminated.

2. Record the values of covariates that could be informative about the observation process, for instance, the experience and age of an observer, wind speed, and other measures of the conditions during a survey, and adjust your response variable for the effects of these nuisance variables.
3. Choose a design that enables explicit hierarchical models to be fitted, that is, collect data that allow detection probability to be estimated.

14.3 WHERE WILL WE GO?

In our book, we have presented a broad array of models useful for population analysis, but obviously, it was not possible to include everything. Population analysis is an extremely active field at the interface of ecology and statistics, so many new developments are foreseeable in the near future. Here, we highlight some new developments which we think are particularly relevant.

14.3.1 Combination of Information

The issue of combining different kinds of information in a single model is very general and includes the combined analysis of capture–recapture and mark-recovery data (Section 9.5) and integrated population models (Chapter 11). Such combinations represent the most efficient use of all available data from a study system and result in improved precision and increased number of parameters that can be estimated. This is especially important for rare and elusive species, where the increase from an effectively very small to a moderate amount of information may yield great benefits (Schaub et al., 2007; Kéry et al., 2011). Bayesian modeling is ideally suited for making such integrated modeling available to ecologists. We are likely to see increasing numbers of studies that combine all available data into a single model.

14.3.2 Population and Community Models for Metapopulation Designs

The development of site-occupancy models (MacKenzie et al. 2002; Tyre et al., 2003; Chapter 13) has started a rush in the development of models for the analysis of population and community data from metapopulation designs—collections of sites that are surveyed repeatedly. Models have been described for different kinds of responses (e.g., detection or nondetection data, counts), diverse ecological states (e.g., distribution, abundance, species richness), and static and dynamic systems. Metapopulation designs are extremely common especially in biodiversity

monitoring, but are frequently adopted also in ecological studies, and many new developments are likely for this kind of models in the near future. One example of a novel idea that combines metapopulation designs and the issue of combining information is an integrated metapopulation model (Conroy et al., 2008). Their model merges in a single analysis expensive data that directly inform on abundance (capture–recapture data), with cheaper data (detection/nondetection data), which can be collected over large areas for cheaper money.

14.3.3 Spatial Models

Spatial models describe the spatial dependence in a response or parameters due to neighborhood relations. Recent developments in statistics and computing increasingly allow modeling spatial relationships explicitly, rather than assuming them away or perhaps trying to eliminate them by careful study design. One example is occupancy modeling, where Royle and Dorazio (2008), Hines et al. (2010), and Bled et al. (2011) have described models where the occurrence of a species in one pixel, and possibly the associated colonization and extinction probabilities, depends on the state of neighboring pixels. This appears like an important and very obvious way of taking occupancy modeling to the next level of realism and ecological relevance. The same can also be undertaken for other types of spatially indexed data, for instance, for modeling abundance (Royle et al., 2007; Webster et al., 2008; Post van der Burg et al., 2011) and survival (Royle and Dubovsky, 2001; Saracco et al., 2010). We are certain to see a great increase of this type of models in the future.

One special case of spatial models is spatially explicit capture–recapture models (Efford, 2004; Borchers and Efford, 2008; Royle and Young, 2008; see also Section 6.5). Essentially, all individual capture–recapture data are spatially indexed. Explicitly taking into account this spatial information allows to obtain less-biased estimators for quantities such as density or survival (Gardner et al., 2010) and to directly estimate other interesting quantities, such as the radius of a home-range or a dispersal kernel. This is a very active field of research with much to hope for in the near future.

14.3.4 Relaxing the Closure Assumption

Many ecological models of the capture–recapture type rely on the closure assumption: they assume that replicated observations can be made over some short time interval, when the system state is approximately constant. Obviously, no population in the field is ever entirely constant, so this assumption can only ever hold approximately. Violation of the closure assumption must be common and has various biasing effects on estimators of models that assume closure (Kendall, 1999; Rota et al., 2009).

Development of study designs and of models that do not need the closure assumption is therefore interesting. For counts from metapopulation designs, Dail and Madsen (2011) have developed a Jolly–Seber kind of binomial mixture model. Their model yields estimates of the population dynamics (abundance, survival, and recruitment) from temporally and spatially replicated counts that do not conform to the robust design (i.e., there is no replication for a site and year combination, say). This model is a great conceptual advantage and similar extensions may be possible in other situations.

14.3.5 More Flexible Covariate Modeling

Modeling of nonlinear covariate relationships by using polynomials (e.g., Section 4.2) often gives sufficient flexibility. However, in many cases, more flexible covariate modeling is desirable, for instance, in the exploratory phase of an analysis, where one would like to "let the data speak for themselves". Splines, general additive modeling and boosted regression trees have recently been developed within models illustrated in this book (Gimenez et al., 2006a,b; Collier et al., 2011; R. A. Hutchinson, personal communication). This is likely to become an ongoing development. Similarly, simpler parametric assumptions like the Poisson for the state in the binomial mixture models may be replaced with more flexible "nonparametric" assumptions (Dorazio et al., 2008).

14.3.6 Accounting for Misclassification Error

A final topic we would like to highlight is the explicit modeling of misclassification. This had long had to be assumed away in capture–recapture models because simultaneous modeling of false-negative and false-positive errors proved too challenging. However, in recent years, there has been a surge of papers that deal with false-positive errors in addition to false-negative errors, for instance, in multistate models (Kendall et al., 2003; Pradel, 2005), for data from genetic analyses (Wright et al., 2009; Yoshizaki et al., 2009; Link et al., 2010) and in site-occupancy models (Royle and Link, 2006; Miller et al., 2011).

14.4 THE IMPORTANCE OF POPULATION ANALYSIS FOR CONSERVATION AND MANAGEMENT

In Chapter 1, we have claimed, perhaps with a little wink of our eyes, that for us the following equation is valid to a good approximation:

$$\text{Ecology} = \text{Population ecology} = \text{Population analysis}$$

The reason for this belief of ours is the central conceptual and practical importance of the population for all of ecology. In addition, population analysis is a pillar in many applied branches of ecology, such as wildlife and fisheries management and especially conservation biology. A rigorous scientific approach to conservation must be based on quantitative evidence and rely on the best available assessments of quantities such as distribution, abundance, species richness, population trend, and extinction probability or sustainability of a given harvest level (Caughley, 1994; Norris, 2004). These and other demographic quantities must be estimated, as well as possible, along with a full assessment in their uncertainty.

Unfortunately, the scientific standards of decision making in the arena of wildlife management and conservation in many countries are still extremely poor. Rather than basing decisions on hard evidence and rigorous science, unquantified claims and beliefs of stakeholders may be the sole basis for decisions. As an example, in 2011, the Swiss parliament approved of a change in the law that governs the control of predators of ungulates, such as wolf, bear, and lynx. It is now planned that complaints by one party of stakeholders, recreational hunters, about a decline in ungulate stocks be enough to trigger culling of these predators. The implementation details of the new law have yet to be worked out, but it is very likely that the decision to take action against these large predators will not be based on scientific standards of evidence, such as any scientifically defensible population analysis. In most Swiss cantons, there is not even a rigorous population monitoring of ungulates in place of the kind that is now commonplace for many taxa across Europe, including birds, plants, butterflies, and snails in Switzerland (Weber et al., 2004). Thus, even in countries such as Switzerland we still have a far way to go in making wildlife management evidence-based, rigorous, and scientifically defensible.

Recurring themes in population analyses for conservation biology are small sample sizes, data sets collected under nonstandard sampling designs or with no specified design at all, disparate data types, multiple levels of uncertainty, and stochasticity. As seen throughout this book, Bayesian population analysis using WinBUGS is extremely well suited for these challenges. Bayesian inference is exact for any sample size (Little, 2006). The remarkable modeling freedom given to the ecologist when using WinBUGS lets him or her adapt a model very flexibly to many idiosyncrasies of such data sets. The integration of information from disparate data types occurs very naturally (Chapter 11). Furthermore, multiple levels of uncertainty can be modeled flexibly using random effects. Thereby, all known components of uncertainty can be incorporated into an analysis and the combined uncertainty is propagated into all estimates and forecasts. Thus, we sincerely hope that Bayesian population analysis using WinBUGS not only makes you enjoy population modeling even more but also that it leads to better conclusions in science and to better decisions in wildlife management and conservation.