

Foreword

In the early 1990s, Ullas Karanth asked my advice on estimating tiger density from camera trap data. Historic uses of camera traps had been restricted to wildlife photography and the documentation of species presence. Ullas had the innovative idea to extend these uses to inference about tiger population size, density, and even survival and movement by exploiting the individual markings of tigers. I had worked on development and application of capture-recapture models, so we began a collaboration that focused on population inferences based on detection histories of marked tigers. Early on in this work, we had to consider how to deal with two problems associated with the spatial distributions of both animals and traps.

The first problem was that of heterogeneous capture probabilities among animals resulting from the positions of their ranges relative to trap locations. Animals with ranges centered in the middle of a trapping array are much more likely to encounter traps and be captured than animals with range centers just outside the trapping array. Ad hoc abundance estimators were available to deal with such heterogeneity, and we resolved to rely primarily on such estimators for our work.

Ullas was more interested in tiger density (defined loosely as animals per unit area) than in abundance, and the second problem resulted from our need to translate abundance estimates into estimates of density. This translation required inference about the total area sampled, that is the area containing animals exposed to sampling efforts. In the case of fixed sampling devices such as traps and cameras, the area sampled is certainly greater than the area covered by the devices themselves (e.g., as defined by the area of the convex hull around the array of devices), but how do we estimate this area? This problem had been recognized and considered since the 1930s, and ad hoc approaches to solving it included nested grids, assessment lines, trapping webs, and use of movement information from either animal recaptures or radiotelemetry data. We selected an approach using distances between captures of animals.

We thus recognized these two problems caused by spatial distribution of animals and traps, and we selected approaches to deal with them as best we could. We were well aware of the ad hoc nature of our pragmatic solutions. In particular, we viewed the use of movement information based on recaptures to translate our abundance estimates into density estimates as the weak link in our approach to inference about density.

In the early 2000s, Murray Efford developed a novel approach to inference about animal density based on capture-recapture data. The manuscript on this work was rejected initially by a top ecological journal without review (an interesting comment on the response of our peer-review system to innovation), but was published in Oikos in 2004. The approach was anchored in a conceptual model of the trapping process in which an animal's probability of being captured in any particular trap was a decreasing function of the distance between the animal's home range center and the trap. This assumed relationship was very similar to the key relationship on which distance

sampling methods are based. Efford viewed the distribution of animal range centers as being governed by a spatial point process, and the target of estimation was the intensity of this process, equivalent to animal density in the study area. Efford (2004) initially used an ad hoc approach to inference based on inverse prediction. He later teamed with David Borchers to develop a formal likelihood approach to estimation (Borchers and Efford, 2008 and subsequent papers).

At about the same time that Efford was formalizing his approach, yet independently of that work, Andy Royle developed a similar approach for the related problem of density estimation based on locations of captures of animals obtained during active searches of prescribed areas (as opposed to captures in traps with fixed locations). Andy approached the inference problem using explicit hierarchical models with both a process component (the spatial distribution of animal range centers and a probability distribution reflecting movement about those centers) and an observation component (non-zero capture probability for locations within the surveyed area and zero outside this area). He used the data augmentation approach that he had just developed (Royle et al., 2007) to deal with animals in the population that are never captured, and he implemented the model using Markov chain Monte Carlo sampling (Royle and Young, 2008). Ullas and I asked Andy for help (Figure 1) with inference about tiger densities, and he extended his approach to deal with fixed trap locations by modeling detection probability as a function of the distance between range center and trap, thus solving our two fundamental problems emanating from spatial distributions of animals and traps (Royle et al., 2009a,b).



FIGURE 1

Jim Nichols (left) discussing capture-recapture with K. Ullas Karanth and Andy Royle at Patuxent Wildlife Research Center, October 15, 2007.

The preceding narrative about the solution of two inference problems faced by Ullas Karanth and me was presented to motivate interest in the models that are the subject of *Spatial Capture-Recapture*. SCR models provide a formal solution to the problem of heterogeneous capture probabilities associated with locations of animal ranges relative to trap locations. They also provide a formal and direct (as opposed to ad hoc and indirect) means of estimating density, naturally defined for SCR models as the number of range centers per unit area. This motivation is perhaps adequate, but it is certainly incomplete. As noted in this book's Introduction, SCR models should not be viewed simply as extensions of standard capture-recapture models designed to solve specific spatial problems. Rather, SCR models represent a much more profound development, dealing explicitly with ecological processes associated with animal locations and movement as well as with the spatial aspects of sampling natural populations. They provide improvements over standard capture-recapture models in our abilities to address questions about demographic state variables (density, abundance) and processes (survival, recruitment), and they provide new possibilities for addressing questions about spatial organization and space use by animals.

As the promise of SCR models has become recognized, work on them has proliferated over the last 5 years, with substantive new developments led in part by the authors of this book, Andy Royle, Richard Chandler, Rahel Sollmann, and Beth Gardner. Because of this explosive development, it is no longer possible to consult one or two key papers in order to learn about SCR. Royle and colleagues recognized the need for a synthetic treatment to integrate this work and place it within a common framework. They wrote *Spatial Capture-Recapture* in order to fill this need.

The history of methodological development in quantitative ecology contains numerous examples of synthetic books and monographs that have been extremely influential in advancing the use of improved inference procedures. *Spatial Capture-Recapture* will become a part of this history, serving as a catalyst for use and further development of SCR methods. The writing style is geared to a biological readership such that this book will provide a single source for biologists interested in learning about SCR models. The statistical development is sufficiently rigorous and complete that this synthesis of existing work should serve as a springboard for statisticians interested in extensions and new developments. I believe that Spatial Capture-Recapture will be an extremely important book.

Spatial Capture-Recapture is organized around four major sections (plus appendices). The first, "Background and Concepts," provides motivation for SCRs and a history of relevant concepts and modeling. Two chapters are devoted to statistical background, one including material introducing random variables, common probability distributions, and hierarchical models. The second chapter on statistical background develops the concept of SCRs as generalized linear mixed models, with some emphasis on Bayesian inference methods for such models. Also included in this section is a chapter on standard (non-spatial) capture-recapture models for closed populations. This chapter helps motivate SCRs and introduces the idea of data augmentation as an approach to dealing with zero-inflated models for inference about

abundance. The authors develop a primitive SCR model in this chapter by noting that location data for captured animals can be viewed as individual covariates.

The second major section, “Basic SCR Models,” begins with a complete development of SCRs as hierarchical models with observation and spatial point process components. Included is a clear discussion of space use by animals, important because any model of the detection process implies a model for space use. A chapter is devoted to likelihood analysis of SCR models including both model development and an introduction to software available for fitting models. Another chapter is devoted to various approaches to modeling variation in encounter probability. A variety of basic models are introduced, as well as approaches to modeling covariates associated with traps, time, individual capture history, and individual animals (e.g., sex, body mass, random effects models). The chapter on model selection and assessment does not provide an omnibus, one-size-fits-all statistic. Rather, it describes useful approaches including AIC for likelihood analyses and both DIC and the Kuo and Mallick (1998) indicator variable approach for Bayesian analyses. For assessing model adequacy, they use the Bayesian *p*-value approach (Gelman et al., 1996) applied to different components of model fit. Another chapter is devoted to the encounter process which requires attention to the nature of the detection device (e.g., can an animal be caught only once or multiple times during an occasion, do traps permit catches of multiple or only single individuals, can an individual be detected multiple times by the same device) and the kinds of data produced by these devices. The final chapter in this section deals with the important topic of study design. A fundamental design trade-off involves the competing needs to capture a good number of animals (sample size) and to attain a reasonably high average capture probability, and the authors emphasize the need for designs that represent a good compromise rather than those that emphasize one component to the exclusion of the other. General recommendations about trap spacing and clustering, and use of ancillary data (telemetry) are discussed as well. The material in this section is extremely important in conveying the basic principles underlying SCR modeling and, as such, will be the section of primary interest to many readers.

The next section, “Advanced SCR Models,” will be of great interest to ecologists, not just because of the advanced model structures presented, but because of the ecological questions that become accessible using these methods. For example, the authors show how spatial variation in density can be modeled as a function of spatial covariates associated with all locations in the state space. Similarly, the authors relax the assumption of basic SCR models that encounter probability is a function of Euclidean distance between range center and trap, and focus instead on the “least cost path” between the range center and trap. The least cost path concept is modeled by including resistance parameters related to habitat covariates, and is relevant to the ecological concepts of connectivity and variable space use. The authors note ecological interest in resource selection functions, which focus on animal use of space as a function of specific resource or habitat covariates and which are typically informed by radiotelemetry data. They present a framework for development of joint models that combine SCR and resource selection function telemetry data. In some

situations, sampling is done via a search encounter process rather than using detection devices with fixed locations, and SCR models are extended to deal with these. Models are developed for combining data from sampling at multiple sites or across multiple occasions. The extension of the SCR framework to models for open populations permits inference about the processes of survival, recruitment, and movement. Inference about time-specific changes in space use is also directly accessible using this approach, and I anticipate a great many advances in the development and application of open population SCR models.

The final section, “Super-Advanced SCR Models,” includes a technical chapter on development of MCMC samplers for the primary purpose of providing increased flexibility in SCR modeling. A chapter of huge potential importance introduces SCR models for unmarked populations, relying on the spatial correlation structure of resulting count data to draw inferences about animal distribution and density. These models will see widespread use in studies employing remote detection devices (camera traps, acoustic detectors) to sample animals that do not happen to have individually recognizable visual patterns or acoustic signatures. In many sampling situations, some animals will be individually identifiable and many will not, and the authors develop mark-resight models to combine detection data from these two classes of animals. The final chapter provides a glimpse of the future by pointing to a sample of neat developments that should be possible using the conceptual framework provided by SCR models.

I very much like the writing style of the authors and found the book relatively easy to read (there were exceptions), with clear presentations of important ideas. Most models are illustrated nicely with actual examples and corresponding sample computer code (frequently WinBUGS).

In summary, I repeat my claim that *Spatial Capture-Recapture* is an extremely important and useful book. A thorough read of the section on basic SCR models provides a good understanding of exactly how these models are constructed and how they “work” in terms of underlying rationale. The two sections on advanced SCR models present a thorough account of the current state of the art written by those who have largely defined this state. As an ecologist, I found myself thinking of one potential application of these models after another. These methods will free ecologists to begin to think more clearly about interesting questions concerning the statics and dynamics of space use by animals. The ability to draw inferences about distribution and density of animals based on counts of unmarked individuals using remote detection devices has the potential to revolutionize conservation monitoring programs.

So does *Spatial Capture-Recapture* solve the inference problems encountered by Ullas Karanth and me two decades ago? You bet. But it does so much more than that. Andy, Richard, Rahel, and Beth, thanks for an exceptional contribution.

James D. Nichols
Patuxent Wildlife Research Center

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Preface

Capture-recapture (CR) models have been around for well over a century, and in that time they have served as the primary means of estimating population size and demographic parameters in ecological research. The development of these methods has never ceased, and each year new and useful extensions are presented in ecological and statistical journals. The seemingly steady clip of development was recently punctuated with the introduction of spatial capture-recapture (SCR; a.k.a. spatially explicit capture-recapture ~~models~~, or SECR) models, which in our view stand to revolutionize the study of animal populations. The importance of this new class of models is rooted in the fact that they acknowledge that both ecological processes and observation processes are inherently spatial. The purpose of this book is to explain this statement, and to bring together all of the developments over the last few years while offering researchers practical options for analyzing their own data using the large and growing class of SCR models.

CR and SCR have been thought of mostly as ways to “estimate density” with not so much of a direct link to understanding ecological processes. So one of the things that motivated us in writing this book was to elaborate on, and develop, some ideas related to modeling ecological processes (movement, space usage, landscape connectivity) in the context of SCR models. The incorporation of spatial ecological processes is where SCR models present an important improvement over traditional, non-spatial CR models. SCR models explicitly describe exposure of individuals to sampling that results from the juxtaposition of sampling devices or traps with individuals, as well as the ecologically intuitive link between abundance and area, both of which are unaccounted for by traditional CR models. By including spatial processes, these models can be adapted and expanded to directly address many questions related to animal population and landscape ecology, wildlife management and conservation. As such, SCR models stand to revolutionize how researchers study animal populations. With such advanced tools at hand, we believe that, but for some specific situations, traditional closed population models are largely obsolete, except as a conceptual device.

So, while we do have a lot of material on density estimation in this book—this is problem #1 in applied ecology—we worked hard to cover a lot more of the spatial aspect of population analysis as relevant to SCR. There are a lot of books out there that cover spatial analysis of population structure ~~that~~ which are more theoretical or mathematical, and there are a lot of books out there that cover sampling and estimation, but that are *not* spatial. Our book bridges these two major ideas as much as is possible as of, roughly mid-late 2012.

Themes of this book

In this book, we try to achieve a broad conceptual and methodological scope from basic closed population models for inference about population density, movement,

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AQ1 space usage, and resource selection, on up to open population models for inference about vital rates such as survival and recruitment. Much of the material is a synthesis of recent research but we also expand SCR models in a number of useful directions, including to the development of explicit models of landscape connectivity based on ecological or least-cost distance (Chapter 12), use of telemetry information to model resource selection with SCR (Chapter 13), and to accommodate unmarked individuals (Chapter 18), and many other new topics that have only recently, or not yet at all, appeared in the literature. Our intent is to provide a comprehensive resource for ecologists interested in understanding and applying SCR models to solve common problems faced in the study of populations. To do so, we make use of hierarchical models (Royle and Dorazio, 2008), which allow great flexibility in accommodating many types of capture-recapture data. We present many example analyses, of real and simulated data using likelihood-based and Bayesian methods—examples that readers can replicate using the code presented in the text and the resources made available online and in our accompanying R package `scrbook`.

The conceptual and methodological themes of this book can be summarized as follows:

1. *Spatial ecology*: Much of ecology is about spatial variation in processes (e.g., density) and the mechanisms (e.g., habitat selection, movement) that determine this variation. Temporal variation is also commonly of interest and we cover this as well, but in less depth.
2. *Spatial observation error*: Observation error is omnipotent in ecology, especially in the study of free-ranging vertebrates, and in fact the entire 100+ year history of capture-recapture studies has been devoted to estimating key demographic parameters in the presence of observation error because we simply cannot observe all the individuals that are present, and we can't know their fates even if we mark them all. What has been missing in most of the capture-recapture methods is an acknowledgment of the spatial context of sampling and the fact that capture (or detection) probability will virtually always be a function of the distance between traps and animals (or their home ranges).
3. *Hierarchical modeling*: Hierarchical models (HM) are the perfect tool for modeling spatial processes, especially those of the type covered in this book, where one process (the ecological process) is conditionally related to another (the observation process). We make use of HMs throughout this book, and we do so using both Bayesian and classical (frequentist, likelihood-based) modes of inference. These tools allow us to mold our hypotheses into probability models, which can be used for description, testing, and prediction.
4. *Model implementation*: We consider proper implementation of the models to be very important throughout the book. We explore likelihood methods using existing software such as the R package `sect` (Efford, 2011a), as well as development of custom solutions along the way. In Bayesian analyses of SCR models, we emphasize the use of the BUGS language for describing models. We also show readers how to devise their own MCMC algorithms for Bayesian analysis of SCR models, which can be convenient (even necessary) in some practical situations.

Altogether, these elements provide for a formulation of SCR models that will allow the reader to learn the fundamentals of standard modeling concepts and ultimately implement complex hierarchical models. We also believe that while the focus of the book is spatial capture-recapture (that is, in fact, the title), the reader will be able to apply the general principles that we cover in the introductory material (e.g., principles of Bayesian analysis) and even the advanced material (e.g., building your own MCMC algorithm) to a broad array of topics in general ecology and wildlife science. Although we aim to reach a broad audience, at times we go into details that may only be of interest to advanced practitioners who need to extend capture-recapture models to unique situations. We hope that these advanced topics will not discourage those new to these methods, but instead will allow readers to advance their own understanding and become less reliant on restrictive tools and software.

Computing

We rely heavily on data processing and analysis in the **R** programming language, which by now is something that many ecologists not only know about, but use frequently. We adopt **R** because it is free, has a large community that constantly develops code for new applications, and it gives the user flexibility in data processing and analyses. There are some great books there, including Venables and Ripley (2002), Bolker (2008), and Zuur et al. (2009), and we encourage those new to **R** to read through the manuals that come with the software. We use a number of **R** packages in our analyses, which are described in Appendix 1, and moreover, we provide an **R** package containing the scripts and functions for all of our analyses (see below).

We also rely on the various implementations of the **BUGS** language including **WinBUGS** (Lunn et al., 2000) and **JAGS** (Plummer, 2003). Because **WinBUGS** is not in active development any more, we are transitioning to mainly using **JAGS**. Sometimes models run better or mix better in one or the other. As a side note, we don't have much experience with **OpenBUGS** (Thomas et al., 2006), but our code for **WinBUGS** should run just the same in **OpenBUGS**. The **BUGS** language provides not only a computational device for fitting models but it also emphasizes understanding of what the model is and fosters understanding of how to construct models. As our good colleague Marc Kéry wrote (Kéry, 2010, p. 30) "**BUGS** frees the modeler in you." While we mostly use **BUGS** implementations, we do a limited amount of developing our own custom MCMC algorithms (see Chapter 17) which we find very helpful for certain problems where **BUGS/JAGS** fail or prove to be inefficient.

You will find a fair amount of likelihood analysis throughout the book, and we have a chapter that provides the conceptual and technical background for how to do this, and several chapters use likelihood methods exclusively. We use the **R** package **secr** (Efford et al., 2009a) for many analyses, and we think people should use this tool because it is polished, easy to use, fairly general, has the usual **R** summary methods, and has considerable capability for doing analysis from start to finish. In some chapters we discuss models that we have to use likelihood methods for, but which are not implemented (at the time when we wrote this book) in **secr** (e.g., Chapters 12 and 13).

These provide good examples of why it is useful to understand the principles and to be able to implement these methods yourself.

The R package `scrbook`

As we were developing content for the book it became clear that it would be useful if the tools and data were available for readers to reproduce the analyses and also to modify so that they can do their own analysis. Almost every analysis we did is included as an **R** script in the `scrbook` package. The **R** package will be very dynamic, as we plan to continue to update and expand it.

The package is not meant to be general-purpose, flexible software for doing SCR models but, rather, a set of examples and templates illustrating how specific things are done. Code can be used by the reader to develop methods tailored to his/her situation, or possibly even more general methods. Because we use so many different software packages and computing platforms, we think it's impossible to put all of what is covered in this book into a single integrated package. The `scrbook` package is for educational purposes and not for production or consulting work.

Organization of this book

We expect that readers have a basic understanding of statistical models and classical inference (What is frequentist inference? What is a likelihood? Generalized linear model? Generalized linear mixed model?), Bayesian analysis (what is a prior distribution? and a posterior distribution?), and have used the **R** programming environment and maybe even the **BUGS** language. The ideal candidate for reading this book has basic knowledge of these topics; however, we do provide introductory chapters on the necessary components which we hope can serve as a brief and cursory tutorial for those who might have only limited technical knowledge, e.g., many biologists who implement field sampling programs but do not have extensive experience analyzing data.

To that extent, we introduce Bayesian inference in some detail because we think readers are less likely to have had a class in that and we also wanted to produce a standalone product. Because we do likelihood analysis of many models, there is an introduction to the relevant elements of likelihood analysis in Chapter 6, and the implementation of SCR models in the package `secr` (Efford, 2011a). Our intent was to provide all of the material you need in one place, but naturally this led to one of the deficiencies with the book: it's a little bit long-winded, especially in the first, introductory part. This should not discourage you, and if you already have extensive background in the basics of statistical inference, you can skip straight ahead to the specifics of SCR modeling, starting with Chapter 5.

In the following chapters we develop a comprehensive synthesis and extension of spatial capture-recapture models. Roughly the first third of the book is introductory material. In Chapter 3 we provide the basic analysis tools to understand and analyze SCR models, namely generalized linear models (GLMs) with random effects, and

demonstrate their analysis in **R** and **WinBUGS**. Because SCR models represent extensions of basic CR models, we cover ordinary closed population models in Chapter 4.

In the second section of the book, we extend capture-recapture to SCR models (Chapter 5), and discuss a number of different conceptual and technical topics including tools for likelihood inference (Chapter 6), analysis of model fit and model selection (Chapter 8), and sampling design (Chapter 10). Along with Chapters 7 and 9, this part of the book provides the basic introduction to spatial capture-recapture models and their analysis using Bayesian and likelihood methods.

The third section of the book covers more advanced SCR models. We have a number of chapters on spatial modeling aspects related to SCR, including modeling spatial variation in density (Chapter 11), modeling landscape connectivity or “ecological distance” using SCR models (Chapter 12), and modeling space usage or resource selection (Chapter 13), which includes material on integrating telemetry data into SCR models. After this there are a series of three chapters that involve some elements of modeling spatially or temporally stratified populations. We cover Bayesian multi-session models in Chapter 14, what we call “search-encounter” model in Chapter 15 and, finally, fully open models involving movement or population dynamics in Chapter 16. The reason we view the search-encounter models chapter, Chapter 15, as a prelude to fully open models is that these models apply to situations where we observe the animal locations “unbiased by fixed sampling locations”—so we get to observe clean measurements of movement outcomes. When this is possible, we can resolve parameters of explicit movement models free of those that involve encounter probability. For example, one such model has two “scale” parameters: σ that determines the rate of decay in encounter probability from a sampling point or line, and τ which is the standard deviation of movements about an individual’s activity center.

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The final conceptual fourth section of this book is what we call “Super-advanced SCR Models.” We include a chapter on developing your own MCMC algorithms for SCR models because many advanced models require you to do this, or can be run more efficiently than in the **BUGS** language, and we thought some readers would appreciate a practical introduction to MCMC for ecologists. Following the MCMC chapter, we have a number of topics related to unmarked individuals (Chapter 18) or partially marked populations (Chapter 19). This last section of the book contains some research areas that we are currently developing but lays the foundation for further development of novel extensions and applications.

When this project was begun in 2008, the idea of producing a 550 page book would have been unimaginable—there wasn’t that much material to work with. Optimistically, there was maybe a 250 page monograph that could have been squeezed out of the literature. But, during the project, great and new things appeared in the literature, and we developed new models and concepts ourselves, in the process of writing the book. This includes models of resource selection, landscape connectivity, and methods for dealing with unmarked individuals. There are at least 10 chapters in the book that we couldn’t have thought about 5 years ago. We hope that the result is a timely summary and a lasting resource.

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