Very nice! Only minor suggestions to improve clarity

Foreword

(Nichols?) specify

In the early 1990's, 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.

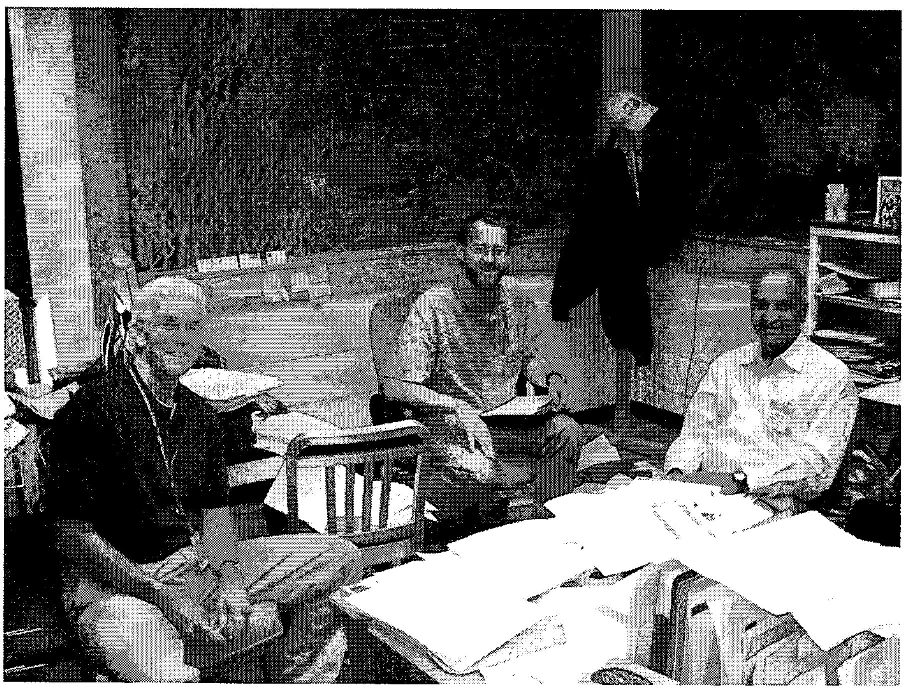

Figure 1. Jim Nichols (left) discussing capture-recapture with K. Ullas Karanth and Andy Royle at Patuxent Wildlife Research Center, Oct. 15, 2007.

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 initially

array. Ad hoc abundance estimators were available to deal with such heterogeneity, and we resolved to rely primarily on such estimators for our work.

1st name

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 1930's, 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.

issues? challenges for capture-recapture analyses

this is a bit awkward here - it's more of a discrepancy initially between analytic approach + reality

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 2000's, 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).

You use Efford here

independently

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

and Andy here

pick either 1st or last name.

the surveyed area and 0 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 (Fig. 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., 2009b,a).

again consider rewording to refer to discrepancy

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 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.

and consistently?

As the promise of SCR models has become recognized, work on them has proliferated over the last five 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 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 is 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 ~~as well~~). 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 enough 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
March 14, 2013

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~~s~~ 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.

in space

Is this really what you would like to say?

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 ~~which~~ that 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.

Many

?

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, 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 (Chapt. 12), use of telemetry information to model resource selection with SCR (Chapt. 13), and to accommodate unmarked individuals (Chapt. 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 on-line 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.

ubiquitous

(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 have 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).

omnipotent' means all powerful.

(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 `secr` (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 out 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 Chapt. 17)
a few of

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., Chapts. 12, 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.

ADD DISCLAIMER?

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 s 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.

Ideally, the reader...
Switched to will reader a candidate?

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 stand-alone product. Because we do likelihood analysis of many models, there is an introduction to the relevant elements of likelihood analysis in Chapt. 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 Chapt. 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 Chapt. 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 Chapt. 4.

Could either skip this stuff here or in Preface to shorten up

In the 2nd section of the book, we extend capture-recapture to SCR models (Chapt. 5), and discuss a number of different conceptual and technical topics including tools for likelihood inference (Chapt. 6), analysis of model fit and model selection (Chapt. 8), and sampling design (Chapt. 10). Along with Chapts. 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 3rd 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 (Chapt. 11, modeling landscape connectivity or "ecological distance" using SCR models (Chapt. 12), and modeling space usage or resource selection (Chapt 13), which includes material on integrating telemetry data into SCR models. After this there are ~~a series of~~ 3 chapters that involve some elements of modeling spatially or temporally stratified populations. We cover Bayesian multi-session models in Chapt. 14, what we call "search-encounter" models in Chapt. 15 and, finally, fully open models involving movement or population dynamics in Chapt. 16. The reason we view the search-encounter models chapter, Chapt. 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 models 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 individuals activity center.

The final conceptual 4th 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 (Chapt. 18) or partially marked populations (Chapt. 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.

and inspiration for future developments?

20

2012: A SPATIAL CAPTURE-RECAPTURE ODYSSEY

You've finally made it to the last chapter and we realize it's been a long journey to get here. Congratulations! (and thank you!) We hope this book has provided you with many ideas on how to conduct ecological studies and address specific questions that were previously thought difficult or impossible to answer, and given you a solid foundation for carrying out SCR analyses using either Bayesian or classical methods of statistical inference. However, we believe this journey is only just beginning, and we leave you now with a few thoughts on what we see as the future of SCR methods.

Let us first briefly consider how we got here. Over a century ago, around 1786 in France, Pierre-Simon Laplace and others first developed capture-recapture methods and introduced the study of populations. This was of course regarding human population demography, but still, the foundation of how we would go on to study animal populations was being laid out then and there. The Lincoln-Petersen method was articulated by the 1930s and development of capture-recapture models began to grow rapidly starting in the 1950s. Soon, capture-recapture methods had become a cornerstone of ecological and wildlife modeling and analysis. Today, spurred on by the advent and rapid development of non-invasive technologies like DNA sampling, camera trapping, acoustic sampling, and other methods, capture-recapture is more relevant and widely used than ever before. These new survey methods allow researchers to use capture-recapture for species that could not be studied efficiently even a few years ago, especially those that are difficult to capture or handle including most felids (Fig. 20.3), bears, mustelids such as fishers (*Martes pennanti*, Fig. 20.1) or weasels (e.g., long-tailed weasel *Mustela frenata*, Fig. 20.2), and many other species.

models

order of Fig. entries list

With these new sampling techniques, like many commonly used capture-recapture sampling methods, spatial information about location of capture is collected. Classical capture-recapture models ignore this information, and in doing so fail to provide a formal method for modeling spatial variation in density and encounter probability. It was these deficiencies that motivated the development of SCR models, starting around 2003 - 2004.

We have seen a great increase in the number of papers that use or cite SCR models,

or inconsistencies

Figure 20.1. Fisher assaulting tree # 8-12, outfitted with a baited hair snare. *Photo credit: NYSDEC (New York State Department of Environmental Conservation), A Fuller/NYSDEC camera trap and hair snare study of fishers in southern NY*

and to articulate and quantify this growth, we did a Google Scholar search on March 6, 2013 using the terms:

```
''spatial capture recapture'' OR ''spatially explicit capture recapture''
```

The results from this literature search are shown in Table 20.1. We see the number of citations involving SCR rapidly increasing, with growth in citation counts after 2004 fueled by publication of Efford (2004) and the release of the software DENSITY (Efford et al., 2004). In 2012 there were 84 articles published and 27 through the first 9 weeks of 2013. The results, we think, suggest a bright future for the development and application of spatial capture-recapture models. Most (but not all) of these papers are about the type of SCR models discussed in this book, although a handful had to do with other types of spatial analysis as related to capture-recapture models.

We believe that use and growth of SCR modeling in conservation biology, management, wildlife, fisheries, and many other disciplines that we place under the general umbrella of ecology will only continue. This prediction is based our belief that SCR provides

Figure 20.2. A long-tailed weasel taking bait on a hair snare, A. Fuller southern NY fisher study *Photo credit: Marty DeLong.*

a flexible framework for studying spatial and temporal variation in ecological processes while acknowledging the fact that these processes are almost always observed imperfectly. The "big idea" of SCR, if you could distill the whole thing into one idea, is based on extending closed population models by augmenting them with a point process model that describes the distribution of individuals (Efford, 2004) in space. In a sense, that is really all there is to it. It seems like a little thing, a minor addition to a model, some incremental advance or "ϵ-improvement" of existing technology. But the relevance is much bigger and more profound because, once we have made space explicit in the model, we can think about building population models that embody explicit spatial processes and using those models to improve our understanding of population biology and ecology, and to test explicit hypotheses about mechanisms that govern populations.

We covered many ecological processes that can be studied using SCR, such as landscape connectivity, resource selection, and spatial variation in density. These are all by themselves profound extensions of the basic capture-recapture method, and they broaden and expand the relevance and utility of capture-recapture for studying animal populations. Although we filled almost 600 book pages (mostly) with SCR methods, there remains much to be done in the continued development of SCR models. In the following section, we highlight some emerging topics that show promise or might be in need of further development. Finally, we end with a few remaining thoughts on the use of SCR models in the future.

Figure 20.3. Canada Lynx, ear-tagged and radio collared, producing high quality data in the name of science. *Photo credit: A Fuller, Cornell University*

20.1 EMERGING TOPICS

In this book, we provided an overview and synthesis of capture-recapture methods as known to us around the end of 2012. There are many emerging topics which we have not covered either because of lack of technical knowledge, lack of time for satisfactory development, or lack of a good framework for implementation. Here we present some of those topics. This is not a complete list by any means, just a subset of topics that we or our colleagues are currently working on, or that we think might make good PhD, Masters or other research projects.

20.1.1 Modeling territoriality

In currently developing work, Reich et al. (2012) propose a model that accounts for spatial variation in density and potential interactions between individuals' territory centers. Under this model, the territory centers follow an inhomogeneous Strauss process (Strauss, 1975), which includes a parameter that determines the strength of repulsion between territory centers. The idea is based on the notion that territorial species would have well defined (and defended) territories and thus activity centers may be more regular on the landscape than predicted by a homogeneous point process. A simulation study demonstrated that properly accounting for interactions between individuals can substantially

Table 20.1. Google Scholar citations by year based on a search of ``spatial capture recapture'' OR ``spatially explicit capture recapture'' conducted on March 6, 2013. The estimated growth rate of this population of papers was 33.4%.

Time period	Cumulative cites	Cites in year previous
since 2002	274 cites	
since 2003	274 cites	0 articles published in 2002
since 2004	271 cites	3 articles published in 2003
since 2005	269 cites	2 articles published in 2004
since 2006	264 cites	5 articles published in 2005
since 2007	261 cites	3 articles published in 2006
since 2008	253 cites	8 articles published in 2007
since 2009	242 cites	11 articles published in 2008
since 2010	222 cites	20 articles published in 2009
since 2011	176 cites	46 articles published in 2010
since 2012	111 cites	65 articles published in 2011
since 2013	27 cites	84 articles published in 2012
		27 published so far in 2013, since March 6

Move to p. 523?

graph?

improve population size estimates in terms of bias and precision relative to the usual independence model.

While the Strauss model is intuitive and shows great potential, it presents computational challenges. The first challenge is that the likelihood includes a high-dimensional integral that has no closed form. To address this issue, Reich et al. (2012) developed an approximation to the Strauss likelihood which allows for posterior sampling, extending related work for categorical Markov random fields (Green and Richardson, 2002; Smith and Smith, 2006). The second challenge is that N is treated as an unknown parameter to be updated and hence N varies and so does the dimension of the posterior distribution. In this case, the dimension-changing problem can be overcome by using data augmentation, as we have done in many situations in this book.

20.1.2 Combining data from different surveys

In some instances, researchers apply different survey techniques to the population of interest, because they yield complementary information. For example, camera trapping is the prime tool for estimating population size/density and other demographic parameters for uniquely marked species, while genetic surveys can yield additional information on the genetic diversity and health of a population that cannot be studied using camera traps. At the same time, genetic surveys, when samples are analyzed to the individual level, also yield spatial capture recapture data (see Chapt. 15). In this situation, we have two data sets at hand that carry information on animal density, and we should be able to get more precise estimates of density if we combine these two data sets into a single SCR model.

Gopalaswamy et al. (2012a) developed two approaches to combining data from different survey types. In the first case, both surveys are carried out at the same time, so that we can assume that they both sample the same – closed – animal population, i.e., there are no possible changes in population density between the two surveys. For camera trapping and genetic surveys, we cannot match records of individuals between the two data sets.

However, models for the distinct sample methods may share some parameters (e.g., σ of the encounter probability model) and, if the studies were conducted simultaneously, they share a common population size N.

A second approach of using information from one survey in the analysis of a second survey (that maybe does not yield quite as much data as the primary survey) is by analyzing the primary data set alone, then taking the posterior distribution of a parameter both surveys share and using it as an informative prior distribution in the analysis of the second data set. Gopalaswamy et al. (2012a) refer to this as the stepwise approach, and they implemented this approach by equating the mean and variance of the posterior distribution of ψ and σ from the photographic survey to the mean and variance of a beta and a gamma prior for these parameters, respectively, for the genetic survey. The authors found that this approach produced almost identical density estimates compared to the combined model approach described above.

In summary, no matter which approach is chosen, combining data across surveys can help researchers obtain more precise population size or density estimates, which is especially valuable when dealing with rare and elusive species like big cats that almost always will produce sparse individual data sets. The paper by Gopalaswamy et al. (2012a) considers the situation where we have two SCR data sets, but we can imagine combining SCR data with other sources of information, such as telemetry data (see Chapt. 19 and Chapt. 13 for examples), and possibly opportunistic observations, although to our knowledge this latter issue has not been tackled in the context of SCR, yet.

potentially cite PLoS ONE article or see other paper if there that combines datasets?

20.1.3 Misidentification

Imperfect identification of individuals can happen in a variety of ways. In genetic surveys there is usually some probability of misidentification due to genotyping error (e.g. Lukacs and Burnham (2005)). In camera trap surveys a different type of imperfect identification can occur when only the only one flank of an animal is recorded in a detection event and cannot be matched to any of the individuals identified by both flanks. In that case, we can match single-flank pictures with the same side flank pictures, but not with opposite side flank pictures and thus cannot construct definite encounter histories for these single-flank individuals (a right flank and a left flank picture could be the same individual, or could be from two distinct individuals). Finally, in Chapt. 19, in the context of mark-resight models, we discussed the case where individuals can either not definitely be identified as marked or not – a violation of a basic mark-resight assumption, and developed an approach to dealing with the situation where we can always tell if an animal is marked or not, but we are not always able to ascertain its individual identity.

In non-spatial capture recapture some efforts have been made to formally deal with misidentification. Stevick et al. (2001) address this problem by double-sampling to derive an error rate for genetic identification, and then including this error rate as a known constant into a Lincoln-Petersen estimator of abundance. Lukacs and Burnham (2005) develop an approach that includes an additional parameter in the model – the probability of a genotype being identified correctly, which is estimated as part of the model likelihood. Link et al. (2010) developed an approach toward solving the same problem implemented in a Bayesian framework that relaxes some of the assumptions of the initial approach. Yoshizaki et al. (2009) deal with misidentification from camera trap pictures due to evolving marks (i.e., natural marks that change over time, such as scars). This situation is different from the genotyping error one. Here, a change in marks creates a supposedly 'new' individual that can be recaptured several times, while the original individual is never captured again (its mark is no longer in the population). In contrast, in genotyping error it is assumed that misidentification creates a 'new' individual that is never observed again, because each error leads to a new unique genotype. Yoshizaki et al. (2009) approach this situation similarly, by including a parameter describing the probability of correctly identifying an individual upon recapture (the parameter can also be interpreted as the probability that a mark does not change between capture occasions). Because of the dependencies between true and false detection histories (when a 'new' individual is created, the 'real' one can no longer be recaptured), the standard multinomial approach to coming up with a model likelihood does not work and implementing the model in a maximum likelihood framework is difficult. The authors instead demonstrate an implementation of the model based on minimizing a function of the squared differences between the observed and expected frequencies of the observed capture histories.

To our knowledge no attempts have been made to deal with misidentification in an SCR framework. While all of the misID cases described above require distinct approaches, we believe that there is one unifying theme to all of them: the capture locations of the potentially mis-identified records should be informative about identity. For example, a right flank and a left flank camera trap picture that are taken at two neighboring camera traps should be more likely to belong to the same individual that a right and a left flank picture taken at cameras located at opposing ends of the trap array, especially if animal movement is smaller than the extent of the trap array. SCR models provide a natural way of using this additional information to reduce the uncertainty arising from misidentification.

Excellent point.

20.1.4 Gregarious species (individual heterogeneity?)

One of the key assumptions of the SCR models that we described throughout this book is that the activity centers are independent of one another, but this assumption will be violated for species that associate in pairs, family groups, or any other type of aggregation. However, we believe that general models can be developed for use in studies of gregarious species.

The two issues that must be addressed are that (1) detections are not independent – a trap that catches one individual of given group is likely to capture others in the same group, and (2) the activity centers $\mathbf{s}_i$ should appear clustered or, in fact, completely redundant in some cases. A possible way to account for this is to change our definition of $\mathbf{s}_i$ from the location of an individual's activity center, to the location of a group's activity center (Russell et al., 2012). Ideally, to accommodate unknown group size, the SCR model would be expanded to include a model component for group size, so that formal estimation of both group density and group size would be possible.

20.1.5 Single Catch Traps

In Chapt. 9 we covered multinomial models in which an individual's probability of being captured in a trap is independent of all other individuals. This is the multi-catch type of device in which traps never fill-up, but an individual can only be caught in one trap in any given occasion. We suggested (following Efford et al. (2009a)) that the multi-catch independent multinomial model could be used for "single catch" traps (traps that hold a single individual or "fill up") and that bias associated with mis-specifying the model would be low under certain conditions (i.e., when the proportion of occupied traps is low).

As discussed in Chapt. 9, Sec. , we recognize that the *time*, or order, of capture of an individual in any trapping interval will affect the encounter probability of subsequently captured individuals. Thus if the order of capture was known, then this information could be used to write the likelihood of the detection model exactly. In practice, the order of capture is almost never known, but it should be possible to regard capture order as a latent variable and consider all possible orderings. This would be computationally intense and so we are working on a solution that selects an arbitrary ordering of the captures as a practical approximation to the single-catch process. This will hopefully lead to a formal model for the the single catch trap problem.

20.1.6 Model Fit and Selection

Evaluation of model adequacy or "fit" is an important part of any applied analysis. In Chapt. 8, we offered up a number of ideas based on standard considerations and adapted and applied them to SCR models. However, these ideas have not been widely applied, or evaluated, and much work needs to be done. In particular, some basic analysis of their power under meaningful alternatives would increase their relevance and possibly lead to insights for devising better methods. This applies to both Bayesian and likelihood-based methods, for which there are even fewer published applications of goodness-of-fit assessment.

Similarly, we discussed model selection strategies using more-or-less conventional ideas based on AIC/DIC, and model indicator variables using the Kuo and Mallick (1998) method. Calibration of these methods under alternatives is needed, along with some analysis of sensitivity to density estimates to misspecification of certain model components.

20.1.7 Explicit movement models

We briefly discussed the topics of dispersal, transience, and migration in Chapts. ?? and 16 and sketched out a few ideas that allow for dynamics related to movement or migration. Temporary emigration and transiency are two topics where a significant amount of work has been accomplished in non-spatial closed and open capture-recapture models (Kendall et al., 1997; Pradel et al., 1997; Hines et al., 2003; Clavel et al., 2008; Gilroy et al., 2012; Chandler et al., 2011). Additionally, models for dispersal (e.g., Clobert et al. (2001); Ovaskainen (2004); Ovaskainen et al. (2008) and and other forms of movement (e.g., Jonsen et al. (2005); ?; McClintock et al. (2012)) have received quite a bit of attention and development in ecology.

With the recent development of SCR models, the framework is in place to provide a formal integration of the movement dynamics governing the processes of dispersal, emigration, and transiency. Further, the availability of SCR models that allow for explicit population dynamics (survival, recruitment) (Gardner et al., 2010a) now sets the stage to integrate models of movement dynamics directly with models of population demography,

(perhaps ?)

Recently Graves et al (in prep I guess) developed a technique to ~~expand~~ ~~distance~~ extend ~~models~~ dispersal kernels ~~...~~ to incorporate least cost di[...] Similarly ar[...] Movement in[...]

and parameterize interactions among population processes. What remains as an area of fruitful research is the development of realistic models of movement dynamics, dispersal, temporary emigration, and transiency that can be effectively fitted given typical sparse individual encounter history data generated from capture-recapture studies. Dispersal and emigration can also be related to the life stage of an individual in a certain population. Ultimately, combining multi-state models, where the states are age classes or breeding status categories, with open population SCR models and explicitly modeling patterns of movement and dispersal as a function of state (e.g., age or size class) seems like an important area of development.

MORE ON OPTIMAL DESIGN?

20.2 FINAL REMARKS

Everything in ecology is spatial, and now so too are capture-recapture models, models which have been the cornerstone of ecological research on populations for decades. Historically, the main use of capture-recapture was to obtain population size estimates, but SCR models move the problem from one of estimation to one of formalizing hypotheses about spatial and temporal variation in ecological processes. These processes include resource selection, landscape connectivity, and how individuals organize themselves in space. SCR models allow for this formalization by borrowing methods from spatial statistics, but unlike many spatial models, SCR models include key demographic parameters such as density and survival and thus allow for mechanistic rather than just phenomenological descriptions of natural variation. For these reasons, we believe SCR models will continue to be developed and extended, and their use will continue to grow.

However, much work still needs to be done to improve computational feasibility, to address many technical or methodological holes in the literature, and to make these methods more accessible to practitioners. We look forward to these developments and hope that this book will help catalyze further exploration on this nascent odyssey.