Foreword

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.

The first problem was that of heterogeneous capture probabilities among animals resulting from with 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 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.

We thus recognized these two problems caused by spatial distribution of animals and traps, and we selected ad hoc 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 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 or density of this process. 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 active 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 hierarchical modeling, 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 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 MCMC (Royle and Young 2008). Ullas and I asked Andy for help 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. 2009 *ab*).

The preceding narrative about the solution of two inference problems faced by Ullas Karanth and I 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 both statics and dynamics of spatial organization and space use by animals.

As the promise of SCR models has become recognized, work on them has proliferated over the last five years, with substantive new developments led by the authors of this book, Andy Royle, Richard Chandler, Rahel Sollman 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) 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 or 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 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 with 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 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.

Andy, Richard, Rahel and Beth, ya done good!

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