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AU:1, page 529	Please note that Figure citation are not sequentially numbered.
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2012: A Spatial Capture-Recapture Odyssey

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p0005 You've finally made it to the last chapter and we realize it's been a long journey
 [AU:1] 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.

p0010 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 meth-
 ods 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 rel-
 evant 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~~
 (Figure 20.3), bears, mustelids such as fishers (*Martes pennanti*, Figure 20.1) or
 weasels (e.g., long-tailed weasel *Mustela frenata*, Figure 20.2), and many other
 species.

p0015 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.

p0020 We have seen a great increase in the number of papers that use or cite SCR models,
 and to articulate and quantify this growth, we did a Google Scholar search on March
 6, 2013 using the terms:

530 CHAPTER 20 2012: A Spatial Capture-Recapture Odyssey



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.



FIGURE 20.2

A long-tailed weasel taking bait on a hair snare, A. Fuller southern NY fisher study.

Photo credit: Marty DeLong.



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.

o0005 "spatial capture recapture" OR "spatially explicit capture recapture",

AU:2 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 analyses as related to capture-recapture models.

p0025 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 on our belief that SCR provides 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

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%.

sp020

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

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.

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20.1 Emerging topics

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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.

p0035

s0010 20.1.1 Modeling territoriality

p0040 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 improve population size estimates in terms of bias and precision relative to the usual independence model.

p0045 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.

s0015 20.1.2 Combining data from different surveys

p0050 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 Chapter 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.

p0055 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 .

p0060 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 Chapters 13 and 19 for examples), and possibly opportunistic observations, although to our knowledge this latter issue has not been tackled in the context of SCR, yet.

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 survey, 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 Chapter 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.

p0080 To our knowledge no attempts have been made to deal with misidentification in an SCR framework. While all of the mis-ID cases described above require distinct approaches, we believe that there is one unifying theme to all of them: the capture locations of the potentially misidentified 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.

s0025 20.1.4 Gregarious species

p0085 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.

p0090 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 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 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.

s0030 20.1.5 Single-catch traps

p0095 In Chapter 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 misspecifying the model would be low under certain conditions (i.e., when the proportion of occupied traps is low).

As discussed in Chapter 9, Section 9.1, 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 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 Chapter 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 Chapters 15 and Chapter 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 other forms of movement (e.g., Jonsen et al., 2005; Johnson et al., 2008a; 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, 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.

20.2 Final remarks

s0045

p0125 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.

p0130 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.

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Abstract: In this chapter, we briefly review the major themes that tie the book together, emphasizing the importance of space in both ecological and sampling processes. We ~~then speculate on~~ the future of spatial capture-recapture models in ecological research and suggest that they will increase in importance and largely replace non-spatial capture-recapture models. This prediction stems from the fact that, although we have demonstrated many potential uses for SCR models, many more await to be developed. For instance, we foresee models to describe and predict the consequences of individual interactions, such as competition and territoriality. Another exciting extension is to embed explicit movement models into SCR models for inference about movement behavior and to improve the description of the observation process. SCR models are also lagging behind non-spatial models in some important ways. For instance, at the time of this writing, no one has devised methods for accomodating misidentification, and very few methods exist for combining different sources of data. Other important extensions that we briefly cover include models for gregarious species and models for ~~the~~ single catch traps. Each of these extensions should be achievable, and headway has already been made in some cases. We hope this book will inspire more rapid progress, and motivate new ideas and perspectives that will ultimately increase the usefulness of SCR models for addressing important problems in ecology and conservation.

Keywords: Combining data, Gregarious species, Misidentification, Movement models, Single catch traps, Territoriality