

# 2012: A Spatial Capture-Recapture Odyssey

# 20

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 had been described 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 models for species that could not be studied efficiently even a few years ago, especially those that are difficult to capture or handle including bears, mustelids such as fishers (*Martes pennanti*, Figure 20.1) or weasels (e.g., long-tailed weasel *Mustela frenata*, Figure 20.2), most felids (Figure 20.3), and many other species.

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



**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, 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.*

“spatial capture recapture” OR “spatially explicit capture recapture”.

The results from this literature search are shown in Table 20.1. We see a rapid 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. 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. The results, we think, suggest a bright future for the development and application of spatial 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 on the fact 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 “ $\epsilon$ -improvement” of existing technology. But the relevance is much bigger and more profound because, once we have

**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

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, as well as 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.

## 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 that 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

While we discussed inhomogeneous point processes in Chapter 11, there is still a need for more general point process models to account for biological and behavioral processes such as territoriality and interactions among individuals. Very little work has been done on this topic and there are many useful models that could be borrowed from the point process literature to improve the biological reality of SCR models. In ongoing work, [Reich et al. \(in review\)](#) propose a model that accounts for spatial variation in density and potential interactions between individuals' territory centers. Under this model, the activity 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 regularly distributed 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.

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. \(in review\)](#) developed an approximation to the Strauss likelihood that 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 acquired 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.

[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 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.,  $\sigma$  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.

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 yet been tackled in the context of SCR.

### 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 Chapter 19, in the context of mark-resight models, we discussed the case where individuals can not definitely be identified as marked—a violation of a basic mark-resight assumption. Further, we 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. \(2001\)](#) addressed 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 \(2005\)](#) developed 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. \(2009\)](#) dealt 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. Recently, [McClintock et al. \(in press\)](#) developed a Bayesian approach to dealing with single flank photographs in camera trapping studies.

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 than 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.

#### 20.1.4 Gregarious species

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  $s_i$  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.

### 20.1.5 Single-catch traps

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 Section 9.3, we recognize that the *time*, or order, of capture of an individual in any trapping interval will affect the encounter probabilities 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 update the ordering based on the data. ~~We have found~~ in simulations that our updating process for the order of trap closures works well for estimating abundance, particularly when compared to models that allow multiple individuals to be captured in traps. We expect that this work will 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 of density estimates to misspecification of certain model components. Bayesian model selection remains an active area of research and development, with much work yet to be done to make existing methods accessible and practical to use ([Millar, 2009](#); [Tenan et al., 2013](#)).

### 20.1.7 Explicit movement models

We briefly discussed the topics of dispersal, transience, and migration in Chapter 16 and sketched out a few ideas that allow for dynamics related to movement or migration. Temporary emigration and transience 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; Chandler et al., 2011; Gilroy et al., 2012). 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 transience 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.

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## 20.2 Final remarks

Everything in ecology is spatial, and now so too are capture-recapture models, models that 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 focus from one of estimation to one of formalizing hypotheses about spatial and temporal variation in ecological processes. These processes include resource selection, landscape connectivity, movement, 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.

However, much work remains 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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## Non Print Items

**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 discuss 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 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