

Spatial Capture-Recapture

This page is intentionally left blank

Spatial Capture-Recapture

J. Andrew Royle

Richard B. Chandler

Rahel Sollmann

Beth Gardner

USGS Patuxent Wildlife Research Center
North Carolina State University



AMSTERDAM • BOSTON • HEIDELBERG • LONDON
NEW YORK • OXFORD • PARIS • SAN DIEGO
SAN FRANCISCO • SINGAPORE • SYDNEY • TOKYO

Academic Press is an Imprint of Elsevier



Academic Press is an imprint of Elsevier
225, Wyman Street, Waltham, MA 02451, USA
The Boulevard, Langford Lane, Kidlington, Oxford OX5 1GB, UK
Radarweg 29, PO Box 211, 1000 AE Amsterdam, The Netherlands

Copyright © 2014 Elsevier Inc. All rights reserved.

No part of this publication may be reproduced, stored in a retrieval system or transmitted in any form or by any means electronic, mechanical, photocopying, recording or otherwise without the prior written permission of the publisher.

Permissions may be sought directly from Elsevier's Science & Technology Rights Department in Oxford, UK: phone (+44) (0) 1865 843830; fax (+44) (0) 1865 853333; email: permissions@elsevier.com. Alternatively you can submit your request online by visiting the Elsevier web site at <http://elsevier.com/locate/permissions>, and selecting Obtaining permission to use Elsevier material.

Notice

No responsibility is assumed by the publisher for any injury and/or damage to persons or property as a matter of products liability, negligence or otherwise, or from any use or operation of any methods, products, instructions or ideas contained in the material herein. Because of rapid advances in the medical sciences, in particular, independent verification of diagnoses and drug dosages should be made.

Library of Congress Cataloging-in-Publication Data

A catalog record for this book is available from the Library of Congress

British Library Cataloguing-in-Publication Data

A catalogue record for this book is available from the British Library

ISBN: 978-0-12-405939-9

For information on all Academic Press publications
visit our website at <http://store.elsevier.com>

Printed in the United States of America
14 15 16 17 9 8 7 6 5 4 3 2 1



Working together
to grow libraries in
developing countries

www.elsevier.com • www.bookaid.org

Contents

Foreword	xvii
Preface	xxiii
Acknowledgments	xxix

PART I BACKGROUND AND CONCEPTS

CHAPTER 1 Introduction	2
1.1 The study of populations by capture-recapture	4
1.2 Lions and Tigers and Bears, oh my: Genesis of Spatial Capture-Recapture Data	5
1.2.1 Camera trapping	5
1.2.2 DNA sampling	6
1.2.3 Acoustic sampling	7
1.2.4 Search-encounter methods	7
1.3 Capture-Recapture for Modeling Encounter Probability	8
1.3.1 Example: Fort Drum bear study	8
1.3.2 Inadequacy of non-spatial capture-recapture	11
1.4 Historical Context: a Brief Synopsis	12
1.4.1 Buffering	12
1.4.2 Temporary emigration	13
1.5 Extension of Closed Population Models	14
1.5.1 Toward spatial explicitness: Efford's formulation	15
1.5.2 Abundance as the aggregation of a point process	15
1.5.3 The activity center concept	16
1.5.4 The state-space	16
1.5.5 Abundance and density	17
1.6 Characterization of SCR Models	17
1.7 Summary and Outlook	18
 CHAPTER 2 Statistical Models and SCR	 21
2.1 Random Variables and Probability Distributions	22
2.1.1 Stochasticity in ecology	22
2.1.2 Properties of probability distributions	24
2.2 Common Probability Distributions	22
2.2.1 The binomial distribution	27
2.2.2 The Bernoulli distribution	29
2.2.3 The multinomial and categorical distributions	30

2.2.4 The Poisson distribution	31
2.2.5 The uniform distribution	32
2.2.6 Other distributions	33
2.3 Statistical Inference and Parameter Estimation	34
2.4 Joint, Marginal, and Conditional Distributions	37
2.5 Hierarchical Models and Inference.....	40
2.6 Characterization of SCR Models	41
2.7 Summary and Outlook.....	45

CHAPTER 3 GLMs and Bayesian Analysis

3.1 GLMs and GLMMs	48
3.2 Bayesian Analysis.....	50
3.2.1 Bayes' rule	50
3.2.2 Principles of Bayesian inference	52
3.2.3 Prior distributions	53
3.2.4 Posterior inference	54
3.2.5 Small sample inference.....	55
3.3 Characterizing Posterior Distributions by MCMC	
Simulation.....	56
3.3.1 What goes on under the MCMC hood	57
3.3.2 Rules for constructing full conditional distributions.....	59
3.3.3 Metropolis-Hastings algorithm.....	59
3.4 Bayesian Analysis Using the BUGS Language	60
3.4.1 Linear regression in WinBUGS	61
3.5 Practical Bayesian Analysis and MCMC.....	63
3.5.1 Choice of prior distributions	63
3.5.2 Convergence and so forth	65
3.5.3 Bayesian confidence intervals.....	68
3.5.4 Estimating functions of parameters	68
3.6 Poisson GLMs	69
3.6.1 North American breeding bird survey data.....	69
3.6.2 Poisson GLM in WinBUGS.....	71
3.6.3 Constructing your own MCMC algorithm.....	72
3.7 Poisson GLM with Random Effects	75
3.8 Binomial GLMs	77
3.8.1 Binomial regression	78
3.8.2 North American waterfowl banding data.....	79
3.9 Bayesian Model Checking and Selection	80
3.9.1 Goodness-of-fit	82
3.9.2 Model selection.....	83
3.10 Summary and Outlook.....	84

CHAPTER 4	Closed Population Models	87
4.1	The Simplest Closed Population Model: Model M_0	88
4.1.1	The core capture-recapture assumptions	90
4.1.2	Conditional likelihood	91
4.2	Data Augmentation	92
4.2.1	DA links occupancy models and closed population models	93
4.2.2	Model M_0 in BUGS	95
4.2.3	Formal development of data augmentation (DA)	97
4.2.4	Remarks on data augmentation	97
4.2.5	Example: Black bear study on Fort Drum	98
4.3	Temporally Varying and Behavioral Effects	102
4.4	Models with Individual Heterogeneity	103
4.4.1	Analysis of model M_h	105
4.4.2	Analysis of the Fort Drum data with model M_h	106
4.4.3	Comparison with MLE	108
4.5	Individual Covariate Models: Toward Spatial Capture-Recapture	109
4.5.1	Example: location of capture as a covariate	110
4.5.2	Fort Drum bear study	111
4.5.3	Extension of the model	114
4.5.4	Invariance of density to B	116
4.5.5	Toward fully spatial capture-recapture models	117
4.6	Distance Sampling: a Primitive SCR Model	117
4.6.1	Example: Sonoran desert tortoise study	120
4.7	Summary and Outlook	121

PART II BASIC SCR MODELS

CHAPTER 5	Fully Spatial Capture-Recapture Models	125
5.1	Sampling design and data structure	126
5.2	The Binomial Observation Model	127
5.2.1	Definition of home range center	128
5.2.2	Distance as a latent variable	129
5.3	The Binomial Point Process Model	130
5.3.1	The state-space of the point process	131
5.3.2	Connection to model M_h and distance sampling	133
5.4	The Implied Model of Space Usage	135
5.4.1	Bivariate normal case	136
5.4.2	Calculating space usage	137

5.4.3	Relevance of understanding space usage.....	139
5.4.4	Contamination due to behavioral response.....	139
5.5	Simulating SCR Data.....	140
5.5.1	Formatting and manipulating data sets.....	141
5.6	Fitting Model SCR_{θ} in BUGS.....	142
5.7	Unknown N.....	144
5.7.1	Analysis using data augmentation in WinBUGS.....	146
5.7.2	Implied home range area.....	149
5.7.3	Realized and expected density.....	149
5.8	The Core SCR Assumptions.....	151
5.9	Wolverine Camera Trapping Study.....	153
5.9.1	Practical data organization.....	153
5.9.2	Fitting the model in WinBUGS.....	156
5.9.3	Summary of the wolverine analysis.....	158
5.9.4	Wolverine space usage.....	159
5.10	Using a Discrete Habitat Mask.....	160
5.10.1	Evaluation of coarseness of habitat mask.....	161
5.10.2	Analysis of the wolverine camera trapping data.....	162
5.11	Summarizing Density and Activity Center Locations.....	163
5.11.1	Constructing density maps.....	163
5.11.2	Example: Wolverine density map.....	166
5.11.3	Predicting where an individual lives.....	169
5.12	Effective Sample Area.....	169
5.13	Summary and Outlook.....	171

CHAPTER 6	Likelihood Analysis of Spatial Capture-Recapture Models.....	173
6.1	MLE with Known N.....	173
6.1.1	Implementation (simulated data).....	175
6.2	MLE When N is Unknown.....	179
6.2.1	Integrated likelihood under data augmentation.....	183
6.2.2	Extensions.....	183
6.3	Classical model selection and assessment.....	184
6.4	Likelihood Analysis of the Wolverine Camera Trapping Data.....	184
6.4.1	Sensitivity to integration grid and state-space buffer.....	186
6.4.2	Using a habitat mask (restricted state-space).....	187
6.5	DENSITY and the R Package <i>secr</i>.....	189
6.5.1	Encounter device types and detection models.....	191
6.5.2	Analysis using the <i>secr</i> package.....	192
6.5.3	Likelihood analysis in the <i>secr</i> package.....	195

6.5.4 Multi-session models in <code>secr</code>	196
6.5.5 Some additional capabilities of <code>secr</code>	197
6.6 Summary and outlook	200
CHAPTER 7 Modeling Variation in Encounter Probability	201
7.1 Encounter Probability Models	202
7.1.1 Bayesian analysis with <code>bear</code> - JAGS	204
7.1.2 Bayesian analysis of encounter probability models	204
7.2 Modeling Covariate Effects	207
7.2.1 Date and time	208
7.2.2 Trap-specific covariates	210
7.2.3 Behavior or trap response by individual	211
7.2.4 Individual covariates	213
7.3 Individual Heterogeneity	216
7.3.1 Models of heterogeneity	216
7.3.2 Heterogeneity induced by variation in home range size	216
7.4 Likelihood Analysis in <code>secr</code>	218
7.4.1 Notes for fitting standard models	219
7.4.2 Sex effects	220
7.4.3 Individual heterogeneity	220
7.4.4 Model selection in <code>secr</code> using AIC	220
7.5 Summary and Outlook	221
CHAPTER 8 Model Selection and Assessment	223
8.1 Model Selection by AIC	224
8.1.1 AIC analysis of the wolverine data	224
8.2 Bayesian Model Selection	228
8.2.1 Model selection by DIC	229
8.2.2 DIC analysis of the wolverine data	229
8.2.3 Bayesian model-averaging with indicator variables	231
8.2.4 Choosing among detection functions	235
8.3 Evaluating Goodness-of-Fit	236
8.4 The Two Components of Model Fit	237
8.4.1 Testing uniformity or spatial randomness	238
8.4.2 Assessing fit of the observation model	241
8.4.3 Does the SCR model fit the wolverine data?	243
8.5 Quantifying Lack-of-Fit and Remediation	245
8.6 Summary and Outlook	246

CHAPTER 9	Alternative Observation Models	249
9.1	Poisson Observation Model	250
9.1.1	Poisson model of space usage	251
9.1.2	Poisson relationship to the Bernoulli model	252
9.1.3	A cautionary note on modeling encounter frequencies	254
9.1.4	Analysis of the Poisson SCR model in BUGS	254
9.1.5	Simulating data and fitting the model	255
9.1.6	Analysis of the wolverine study data	257
9.1.7	Count detector models in the <i>secr</i> package	258
9.2	Independent Multinomial Observations	258
9.2.1	Multinomial resource selection models	260
9.2.2	Simulating data and analysis using JAGS	261
9.2.3	Multinomial relationship to the Poisson	263
9.2.4	Avian mist-netting example	264
9.3	Single-Catch Traps	270
9.3.1	Inference for single-catch systems	271
9.3.2	Analysis of Efford's possum trapping data	272
9.4	Acoustic Sampling	275
9.4.1	The signal strength model	276
9.4.2	Implementation in <i>secr</i>	278
9.4.3	Implementation in BUGS	278
9.4.4	Other types of acoustic data	279
9.5	Summary and Outlook	279
CHAPTER 10	Sampling Design	281
10.1	General Considerations	282
10.1.1	Model-based not design-based	282
10.1.2	Sampling space or sampling individuals?	283
10.1.3	Focal population vs. state-space	284
10.2	Study Design for (Spatial) Capture-Recapture	285
10.3	Trap Spacing and Array Size Relative to Animal Movement	287
10.3.1	Black bears from Pictured Rocks National Lakeshore	290
10.4	Sampling Over Large Areas	291
10.5	Model-Based Spatial Design	293
10.5.1	Statement of the design problem	294
10.5.2	Model-based Design for SCR	296
10.5.3	An optimal design criterion for SCR	297
10.5.4	Too much math for a Sunday afternoon	298
10.5.5	Optimization of the criterion	300
10.5.6	Illustration	302
10.5.7	Density covariate models	303

10.6	Temporal Aspects of Study Design.....	303
10.6.1	Total sampling duration and population closure.....	304
10.6.2	Diagnosing and dealing with lack of closure.....	305
10.7	Summary and Outlook.....	306

PART III ADVANCED SCR MODELS

CHAPTER 11	Modeling Spatial Variation in Density.....	311
11.1	Homogeneous Point Process Revisited.....	312
11.2	Inhomogeneous Point Processes.....	315
11.3	Observed Point Processes.....	318
11.4	Fitting Inhomogeneous Point Process SCR Models.....	322
11.4.1	Continuous space.....	322
11.4.2	Discrete space.....	324
11.5	Argentina Jaguar Study.....	326
11.6	Summary and Outlook.....	330
CHAPTER 12	Modeling Landscape Connectivity.....	333
12.1	Shortcomings of Euclidean Distance Models.....	334
12.2	Least-Cost Path Distance.....	335
12.2.1	Example of computing cost-weighted distance.....	337
12.3	Simulating SCR Data Using Ecological Distance.....	339
12.4	Likelihood Analysis of Ecological Distance Models.....	342
12.4.1	Example of SCR with least-cost path.....	342
12.5	Bayesian Analysis.....	343
12.6	Simulation Evaluation of the MLE.....	343
12.7	Distance in an Irregular Patch.....	345
12.7.1	Basic geographic analysis in R.....	345
12.8	Ecological Distance and Density Covariates.....	349
12.9	Summary and Outlook.....	350
CHAPTER 13	Integrating Resource Selection with Spatial Capture-Recapture Models.....	353
13.1	A Model of Space Usage.....	354
13.1.1	A simulated example.....	356
13.1.2	Poisson model of space use.....	358
13.2	Integrating Capture-Recapture Data.....	359
13.3	SW New York Black Bear Study.....	360
13.4	Simulation study.....	364
13.5	Relevance and Relaxation of Assumptions.....	365
13.6	Summary and Outlook.....	366

CHAPTER 14 Stratified Populations: Multi-Session and Multi-Site Data	369
14.1 Stratified Data Structure	370
14.2 Multinomial Abundance Models	371
14.2.1 Implementation in BUGS	373
14.2.2 Groups with no individuals observed	373
14.2.3 The group-means model	374
14.2.4 Simulating stratified capture-recapture data	375
14.3 Other Approaches to Multi-Session Models	376
14.4 Application to Spatial Capture-Recapture	376
14.4.1 Multinomial (“multi-catch”) observations	377
14.4.2 Reanalysis of the ovenbird data	378
14.5 Spatial or Temporal Dependence	379
14.6 Summary and Outlook	381
CHAPTER 15 Models for Search-Encounter Data	383
15.1 Search-encounter designs	384
15.1.1 Design 1: fixed search path	384
15.1.2 Design 2: Uniform Search Intensity	385
15.2 A Model for Fixed Search Path Data	385
15.2.1 Modeling total hazard to encounter	386
15.2.2 Modeling movement outcomes	388
15.2.3 Simulation and analysis in JAGS	388
15.2.4 Hard plot boundaries	390
15.2.5 Analysis of other protocols	392
15.3 Unstructured Spatial Surveys	392
15.3.1 Mountain lions in montana	393
15.3.2 Sierra national forest fisher study	394
15.4 Design 2: Uniform Search Intensity	395
15.4.1 Alternative movement models	396
15.4.2 Simulating and fitting uniform search models	397
15.4.3 Movement and dispersal in open populations	399
15.5 Partial Information Designs	399
15.6 Summary and Outlook	400
CHAPTER 16 Open Population Models	403
16.1 Introduction	403
16.1.1 Brief overview of population dynamics	404
16.1.2 Animal movement related to population demography	405
16.2 Jolly-Seber Models	406

16.2.1 Traditional Jolly-Seber models	406
16.2.2 Data augmentation for the Jolly-Seber model	409
16.2.3 Spatial Jolly-Seber models	413
16.3 Cormack-Jolly-Seber Models	418
16.3.1 Traditional CJS models.....	418
16.3.2 Multi-state CJS models.....	421
16.3.3 Spatial CJS models	425
16.4 Modeling Movement and Dispersal Dynamics	428
16.4.1 Thoughts on movement of American shad	430
16.4.2 Modeling dispersal.....	430
16.5 Summary and Outlook.....	431

PART IV SUPER-ADVANCED SCR MODELS

CHAPTER 17 Developing Markov Chain Monte Carlo

Samplers	435
17.1 Why build your own MCMC algorithm?.....	435
17.2 MCMC and Posterior Distributions	436
17.3 Types of MCMC Sampling.....	438
17.3.1 Gibbs sampling	438
17.3.2 Metropolis-Hastings sampling.....	443
17.3.3 Metropolis-within-Gibbs	446
17.3.4 Rejection sampling and slice sampling.....	450
17.4 MCMC for Closed Capture-recapture Model M_h.....	451
17.5 MCMC Algorithm for Model SCRO.....	454
17.5.1 SCR model with binomial encounter process.....	457
17.6 Looking at Model Output	458
17.6.1 Markov chain time series plots	459
17.6.2 Posterior density plots.....	459
17.6.3 Serial autocorrelation and effective sample size.....	460
17.6.4 Summary results	462
17.6.5 Other useful commands	463
17.7 Manipulating the State-space.....	463
17.8 Increasing Computational Speed	467
17.8.1 Parallel computing	467
17.8.2 Using C++	470
17.9 Summary and Outlook.....	473

CHAPTER 18 Unmarked Populations..... 475

18.1 Existing Models for Inference about Density in unmarked populations.....	476
--	------------

18.2	Spatial Correlation in Count Data.....	478
18.2.1	Spatial correlation as information.....	478
18.2.2	Types of spatial correlation.....	479
18.3	Spatial Count Model.....	480
18.3.1	Data.....	480
18.3.2	Model.....	480
18.3.3	On N being unknown.....	482
18.3.4	Inference.....	483
18.4	How Much Correlation is Enough?.....	483
18.5	Applications.....	484
18.5.1	Simulation example.....	484
18.5.2	Northern parula in Maryland.....	489
18.6	Extensions of the Spatial Count Model.....	491
18.6.1	Improving precision.....	491
18.6.2	Dusky salamanders in Maryland.....	493
18.7	Summary and Outlook.....	496
CHAPTER 19	Spatial Mark-Resight Models.....	499
19.1	Background.....	500
19.1.1	Resighting techniques.....	501
19.1.2	Types of mark-resighting data.....	501
19.1.3	A short history of mark-resight models.....	502
19.1.4	The random sample assumption.....	504
19.2	Known Number of Marked Individuals.....	506
19.2.1	Implementing spatial mark-resight models.....	507
19.3	Unknown Number of Marked Individuals.....	510
19.3.1	Canada geese in North Carolina.....	511
19.4	Imperfect Identification of Marked Individuals.....	514
19.5	How Much Information Do Marked and Unmarked Individuals Contribute?.....	516
19.6	Incorporating Telemetry Data.....	518
19.6.1	Raccoons on the outer banks of North Carolina.....	521
19.7	Point Process Models for Marked Individuals.....	523
19.7.1	Homogeneous point process in a subset of S	523
19.7.2	Inhomogeneous point processes.....	525
19.8	Summary and Outlook.....	526
CHAPTER 20	2012: A Spatial Capture-Recapture Odyssey.....	529
20.1	Emerging Topics.....	532
20.1.1	Modeling territoriality.....	533
20.1.2	Combining data from different surveys.....	533

20.1.3 Misidentification	534
20.1.4 Gregarious species	535
20.1.5 Single-catch traps	535
20.1.6 Model fit and selection	536
20.1.7 Explicit movement models	536
20.2 Final Remarks	537

PART V APPENDICES

20.3 WinBUGS	541
20.3.1 WinBUGS through R	542
20.4 OpenBUGS	541
20.4.1 OpenBUGS through R	542
20.5 JAGS	543
20.5.1 JAGS through R	543
20.6 R	544
20.6.1 R Packages	544
Bibliography	547
Index	571

This page is intentionally left blank

Foreword

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

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

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

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

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

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

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

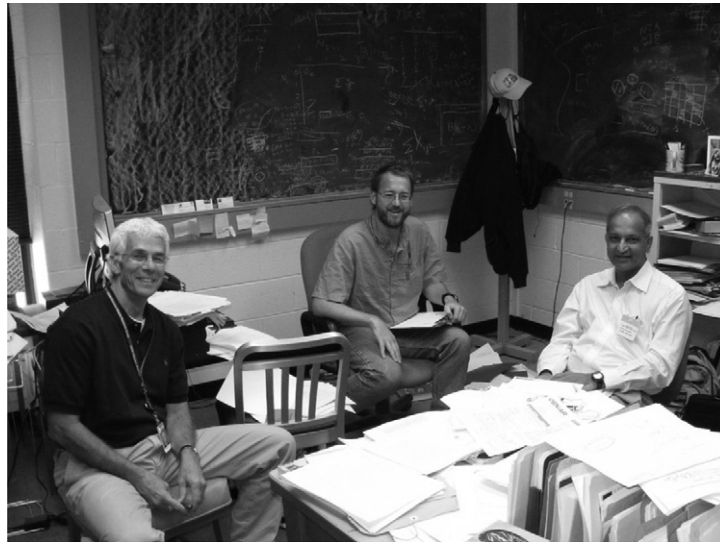


FIGURE 1

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

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

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

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

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

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

The second major section, “Basic SCR Models,” begins with a complete development of SCRs as hierarchical models with observation and spatial point process components. Included is a clear discussion of space use by animals, important because any model of the detection process implies a model for space use. A chapter is devoted to likelihood analysis of SCR models including both model development and an introduction to software available for fitting models. Another chapter is devoted to various approaches to modeling variation in encounter probability. A variety of basic models are introduced, as well as approaches to modeling covariates associated with traps, time, individual capture history, and individual animals (e.g., sex, body mass, random effects models). The chapter on model selection and assessment does not provide an omnibus, one-size-fits-all statistic. Rather, it describes useful approaches including AIC for likelihood analyses and both DIC and the Kuo and Mallick (1998) indicator variable approach for Bayesian analyses. For assessing model adequacy, they use the Bayesian p -value approach (Gelman et al., 1996) applied to different components of model fit. Another chapter is devoted to the encounter process which requires attention to the nature of the detection device (e.g., can an animal be caught only once or multiple times during an occasion, do traps permit catches of multiple or only single individuals, can an individual be detected multiple times by the same device) and the kinds of data produced by these devices. The final chapter in this section deals with the important topic of study design. A fundamental design trade-off involves the competing needs to capture enough 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

This page is intentionally left blank

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, or SECR) models, which in our view stand to revolutionize the study of animal populations. The importance of this new class of models is rooted in the fact that they acknowledge that both ecological processes and observation processes are inherently spatial. The purpose of this book is to explain this statement, and to bring together all of the developments over the last few years while offering researchers practical options for analyzing their own data using the large and growing class of SCR models.

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

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

Themes of this book

In this book, we try to achieve a broad conceptual and methodological scope from basic closed population models for inference about population density, movement, space usage, and resource selection, and 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 the development of explicit models of landscape connectivity based on ecological or least-cost distance (Chapter 12), use of telemetry information to model resource selection with SCR (Chapter 13), and to accommodate unmarked individuals (Chapter 18), and many other new topics that have only recently, or not yet at all, appeared in the literature. Our intent is to provide a comprehensive resource for ecologists interested in understanding and applying SCR models to solve common problems faced in the study of populations. To do so, we make use of hierarchical models (Royle and Dorazio, 2008), which allow great flexibility in accommodating many types of capture-recapture data. We present many example analyses of real and simulated data using likelihood-based and Bayesian methods—examples that readers can replicate using the code presented in the text and the resources made available online and in our accompanying **R** package `scrbook`.

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

1. *Spatial ecology*: Much of ecology is about spatial variation in processes (e.g., density) and the mechanisms (e.g., habitat selection, movement) that determine this variation. Temporal variation is also commonly of interest and we cover this as well, but in less depth.
2. *Spatial observation error*: Observation error is ubiquitous in ecology, especially in the study of free-ranging vertebrates, and in fact the entire 100+ year history of capture-recapture studies has been devoted to estimating key demographic parameters in the presence of observation error because we simply cannot observe all the individuals that are present, and we can't know their fates even if we mark them all. What has been missing in most of the capture-recapture methods is an acknowledgment of the spatial context of sampling and the fact that capture (or detection) probability will virtually always be a function of the distance between traps and animals (or their home ranges).
3. *Hierarchical modeling*: Hierarchical models (HM) are the perfect tool for modeling spatial processes, especially those of the type covered in this book, where one process (the observation process) is conditionally related to another (the ecological 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, 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.

Computing¹

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 on **R** 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 Chapter 17) which we find very helpful for certain problems where **BUGS/JAGS** fail or prove to be inefficient.

You will find a fair amount of likelihood analysis throughout the book, and we have a chapter that provides the conceptual and technical background for how to do this, and several chapters use likelihood methods exclusively. We use the **R** package

¹Use of product names does not imply endorsement by the federal government.

`secr` (Efford et al., 2009a) for many analyses, and we think people should use this tool because it is polished, easy to use, fairly general, has the usual **R** summary methods, and has considerable capability for doing analysis from start to finish. In some chapters we discuss models that we have to use likelihood methods for, but which are not implemented (at the time when we wrote this book) in `secr` (e.g., Chapters 12 and 13). These provide good examples of why it is useful to understand the principles and to be able to implement these methods yourself.

The **R** package `scrbook`

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

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

Organization of this book

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

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

background in the basics of statistical inference, you can skip straight ahead to the specifics of SCR modeling, starting with Chapter 5.

In the following chapters we develop a comprehensive synthesis and extension of spatial capture-recapture models. Roughly the first third of the book is introductory material. In Chapter 3 we provide the basic analysis tools to understand and analyze SCR models, namely generalized linear models (GLMs) with random effects, and demonstrate their analysis in **R** and **WinBUGS**. Because SCR models represent extensions of basic CR models, we cover ordinary closed population models in Chapter 4.

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

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

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

When this project was begun in 2008, the idea of producing a 550 page book would have been unimaginable—there wasn’t that much material to work with.

Optimistically, there was maybe a 250 page monograph that could have been squeezed out of the literature. But, during the project, great and new things appeared in the literature, and we developed new models and concepts ourselves, in the process of writing the book. 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.

Acknowledgments

The project owes a great intellectual debt to Jim Nichols, who has been an extraordinary mentor and colleague, and who generously shared his astounding insight into animal sampling and modeling problems, his knowledge of the literature and history of abundance and density estimation and, most importantly, his extremely valuable time. He has been an extremely helpful guy on all fronts. We are honored that Jim agreed to write the Foreword to introduce the book. We thank Marc Kéry for being a great friend and colleague, and for his creativity, energy, and enthusiasm in developing new ideas and presenting workshops on hierarchical modeling in ecology.

Special thanks to the following people: (1) Kimberly Gazenski whose support was invaluable. She worked on administrative, technical, and editorial aspects of the whole project. She maintained the `BIBTEX` database, worked on the GitHub repository that housed the `LATEX` and `R` package source trees, edited `LATEX` files, tested `R` scripts, did GIS and `R` programming, analysis, debugging, and graphics; (2) Our WCS Tiger program colleagues K. Ullas Karanth and Arjun Gopalaswamy for continued support and collaboration on SCR problems; (3) Sarah Converse, our PWRC colleague, for her interest in SCR models and developing a number of methodological and application papers related to multi-session models, providing feedback on draft material, and friendship; (4) Murray Efford whose seminal 2004 *Oikos* paper first introduced spatial capture-recapture models. His `R` package `secr` is a powerful tool for analyzing spatial capture-recapture data used throughout the book. Murray also answered many questions regarding `secr` that were helpful in developing our applications and examples.

We thank the following people for providing data, photographs, or figures: Agustín Paviolo (jaguar data in Chapter 11, and the cover image). Michael Wegan, Paul Curtis, and Raymond Rainbolt (black bear data from Fort Drum, NY); Audrey Magoun (wolverine data and photographs); Cat Sun and Angela Fuller (black bear data in Chapter 13; and Chapter 20 photos); Joshua Raabe and Joseph Hightower (American shad photo and data in Chapter 16); Erin Zylstra (tortoise data in Chapter 4); Martha (Liz) Rutledge (Canada geese data and picture in Chapter 19); Craig Thompson (fisher data in Chapter 15 and photographs in Chapter 1); Jerrold Belant (black bear data in Chapter 10); Kevin and April Young (FTHL photograph, Chapter 15); Theodore Simons, Allan O'Connell, Arielle Parsons and Jessica Stocking (raccoon data in Chapter 19) Mary DeLong (weasel photograph, Chapter 20), and Bob Wiesner (mountain lion photograph, Chapter 15).

We thank the following people for reviewing one or more draft chapters and giving feedback along the way: David Borchers, Sarah Converse, Bob Dorazio, Tim Ginnett, Evan Grant, Tabitha Graves, Marc Kéry, Brett McClintock, Leslie New, Allan O'Connell, Krishna Pacifici, Agustín Paviolo, Brian Reich, Robin Russell, Sabrina Servanty, Cat Sun, Yifang Li, Earvin Balderama, and Chris Sutherland.

Additionally, many colleagues and friends, as well as our families, provided us with encouragement and feedback throughout this project and we thank them for their continued support.

This page is intentionally left blank