This page is intentionally left blank

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**

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

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 SCR0 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

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

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 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 `secr` 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 `secr` 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

6.5.4 Multi-session models in secr 196
6.5.5 Some additional capabilities of secr 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 bear . 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 secr 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 secr 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

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 real data sets 141
5.6 Fitting Model SCRO 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 `secr` 189
6.5.1 Encounter device types and detection models 191
6.5.2 Analysis using the `secr` package 192
6.5.3 Likelihood analysis in the `secr` package 195

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 bear 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 Empirical analysis 137

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 47
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 Example: breeding bird survey data 69
3.6.2 Doing it 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 Example: 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

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

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.

British Library Cataloguing-in-Publication Data
A catalogue record for this book is available from the British Library

Library of Congress Cataloging-in-Publication Data
A catalog record for this book is available from the Library of Congress

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

Spatial Capture-Recapture

J. Andrew Royle

Richard B. Chandler

Rahel Sollmann

Beth Gardner

USGS Patuxent Wildlife Research Center
North Carolina State University

ELSEVIER

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

Academic Press is an Imprint of Elsevier

This page is intentionally left blank

Spatial Capture-Recapture