

Contents

Preface	xv
Acknowledgments	xxi

Part I Background and Concepts

1. Introduction	
1.1 Operational Definitions	4
1.2 Sampling Animal Populations and Communities: General Principles	5
1.2.1 Why?	5
1.2.2 What?	8
1.2.3 How?	10
1.3 Inference About Dynamics and Causation	14
1.3.1 Generation of System Dynamics	15
1.3.2 Statics and Process vs. Pattern	20
1.4 Discussion	23
2. Occupancy Applications	
2.1 Geographic Range	29
2.2 Habitat Relationships and Resource Selection	38
2.3 Metapopulation Dynamics	42
2.3.1 Inference Based on Single-Season Data	43
2.3.2 Inference Based on Multiple-Season Data	46
2.4 Large-Scale Monitoring	49
2.5 Multi-Species Occupancy Data	51
2.5.1 Inference Based on Static Occupancy Patterns	51
2.5.2 Inference Based on Occupancy Dynamics	55
2.6 Paleobiology	58
2.7 Disease Dynamics	59
2.8 Non-Ecological Applications	64
2.9 Discussion	69

3. Fundamental Principles of Statistical Inference

3.1 Definitions and Key Concepts	73
3.1.1 Random Variables, Probability Distributions, and the Likelihood Function	74
3.1.2 Expected Values and Variance	77
3.1.3 Introduction to Methods of Estimation	79
3.1.4 Properties of Point Estimators	80
3.1.5 Computer Intensive Methods	82
3.2 Maximum Likelihood Estimation Methods	82
3.2.1 Maximum Likelihood Estimators	83
3.2.2 Properties of Maximum Likelihood Estimators	84
3.2.3 Variance, Covariance (and Standard Error) Estimation	84
3.2.4 Confidence Interval Estimators	85
3.2.5 Multiple Maxima	86
3.2.6 Observed and Complete Data Likelihood	87
3.3 Bayesian Estimation	87
3.3.1 Theory	88
3.3.2 Computing Methods	90
3.4 Modeling Predictor Variables	93
3.4.1 The Logit Link Function	93
3.4.2 Interpretation	95
3.4.3 Estimation	97
3.5 Hypothesis Testing	99
3.5.1 Background and Definitions	99
3.5.2 Likelihood Ratio Tests	100
3.5.3 Goodness of Fit Tests	101
3.6 Model Selection	101
3.6.1 Akaike's Information Criterion (AIC)	102
3.6.2 Goodness of Fit and Overdispersion	105
3.6.3 Quasi-AIC	105
3.6.4 Model Averaging and Model Selection Uncertainty	106
3.6.5 Bayesian Assessment of Model Fit	107
3.6.6 Bayesian Model Selection	108
3.7 Discussion	110

Part II

Single-Species, Single-Season Occupancy Models

4. Basic Presence/Absence Situation

4.1 The Sampling Situation	115
4.2 Estimation of Occupancy if Probability of Detection Is 1 or Known Without Error	117
4.3 Two-Step <i>Ad Hoc</i> Approaches	119
4.3.1 Geissler-Fuller Method	119
4.3.2 Azuma-Baldwin-Noon Method	121
4.3.3 Nichols-Karanth Method	122

4.4 Model-Based Approach	123
4.4.1 Building a Model	123
4.4.2 Estimation	130
4.4.3 Constant Detection Probability Model	131
4.4.4 Survey-Specific Detection Probability Model	132
4.4.5 Probability of Occupancy Given Species Not Detected at a Unit	133
4.4.6 Example: Blue-Ridge Two-Lined Salamanders	135
4.4.7 Missing Observations	141
4.4.8 Covariate Modeling	144
4.4.9 Violations of Model Assumptions	146
4.4.10 Assessing Model Fit	155
4.4.11 Diagnostic Plots	162
4.4.12 Examples	170
4.5 Case Study: Troll Distribution in Middle Earth	202
4.6 Discussion	214
 5. Beyond Two Occupancy States	
5.1 The Sampling Situation	219
5.2 Model Based Approach	221
5.2.1 Observed Data Likelihood	223
5.2.2 Matrix Formulation	225
5.3 Alternative Parameterizations	226
5.4 Missing Observations	229
5.5 Covariates and Predictor Variables	230
5.6 Model Assumptions	230
5.7 Examples	231
5.7.1 California Spotted Owl Reproduction	231
5.7.2 Breeding Success of Grizzly Bears	234
5.8 Discussion	240
 6. Extensions to Basic Approaches	
6.1 Estimating Occupancy for a Finite Population or Small Area	243
6.1.1 Prediction of Unobserved Occupancy State	244
6.1.2 Example: Blue Ridge Two-Lined Salamanders Revisited	249
6.1.3 Consequences of a Finite Population	252
6.1.4 A Related Issue	252
6.2 Accounting for False Positive Detections	254
6.2.1 Modeling Misclassification for a Single Season	255
6.2.2 Discussion	273
6.3 Multi-Scale Occupancy	274
6.3.1 Model Definition	277
6.3.2 Example: Striped Skunks	281
6.3.3 Discussion	285
6.4 Autocorrelated Surveys	288

6.4.1	Model Description	291
6.4.2	Example: Tigers on Trails	294
6.4.3	Discussion	295
6.5	Staggered Entry-Departure Model	296
6.5.1	Model Description	297
6.5.2	Example: Maryland Amphibians	300
6.5.3	Discussion	302
6.6	Spatial Autocorrelation in Occurrence	303
6.6.1	Covariates	305
6.6.2	Conditional Auto-Regressive Model	305
6.6.3	Autologistic Model	307
6.6.4	Kriging	308
6.6.5	Restricted Spatial Regression	309
6.7	Discussion	311
7.	Modeling Heterogeneous Detection Probabilities	
7.1	Occupancy Models with Heterogeneous Detection	315
7.1.1	General Formulation	315
7.1.2	Finite Mixtures	317
7.1.3	Continuous Mixtures	321
7.1.4	Abundance-Induced Heterogeneity Models	322
7.1.5	Evaluation of Model Fit	325
7.2	Example: Breeding Bird Point Count Data	326
7.3	Modeling Covariate Effects on Detection	329
7.4	Example: Anuran Calling Survey Data	331
7.5	On the Identifiability of ψ	331
7.6	Discussion	337
Part III		
Single-Species, Multiple-Season Occupancy Models		
8.	Basic Presence/Absence Situation	
8.1	Basic Sampling Scheme	342
8.2	An Implicit Dynamics Model	343
8.3	Modeling Dynamic Changes Explicitly	345
8.3.1	Modeling Dynamic Processes when Detection Probability is 1	347
8.3.2	Conditional Modeling of Dynamic Processes	348
8.3.3	Unconditional Modeling of Dynamic Processes	350
8.3.4	Missing Observations	356
8.3.5	Including Covariate Information	357
8.3.6	Alternative Parameterizations	359
8.3.7	Example: House Finch Expansion in North America	363
8.4	Violations of Model Assumptions	371

8.5 Discussion	374
9. More than Two Occupancy States	
9.1 Basic Sampling Scheme	378
9.2 Defining an Explicit Dynamics Model	380
9.3 Modeling Data and Parameter Estimation	383
9.4 Covariates and 'Missing' Observations	385
9.5 Model Assumptions	386
9.6 Examples	386
9.6.1 Maryland Green Frogs	387
9.6.2 California Spotted Owls	391
9.7 Discussion	395
10. Further Topics	
10.1 False Positive Detections	399
10.1.1 Confirmation Designs	400
10.1.2 More Observation and Occupancy States: General Approach	407
10.1.3 Discussion	410
10.2 Autocorrelated Within-Season Detections	411
10.3 Spatial Correlation in Dynamics	413
10.4 Investigating Occupancy Dynamics	416
10.4.1 Markovian, Random, and No Changes in Occupancy	416
10.4.2 Equilibrium	420
10.4.3 Example: Northern Spotted Owl	422
10.4.4 Further Insights	427
10.4.5 Chronological Order of Surveys	429
10.4.6 Discussion	429
10.5 Sensitivity of Occupancy to Dynamic Processes	430
10.5.1 Two-State Situation	430
10.5.2 General Situation	432
10.6 Modeling Heterogeneous Detection Probabilities	432
10.7 Discussion	435

Part IV

Study Design

11. Design of Single-Season Occupancy Studies

11.1 Defining the Population of Interest	441
11.2 Defining a Sampling Unit	442
11.3 Unit Selection	448
11.4 Defining a 'Season'	451
11.5 Conducting Repeat Surveys	452
11.5.1 General Considerations	452

11.5.2	Special Note on Using Spatial Replication	456
11.6	Allocation of Effort, Number of Sites vs. Number of Surveys	458
11.6.1	Standard Design	461
11.6.2	Double Sampling Design	466
11.6.3	Removal Sampling Design	469
11.6.4	More Units vs. More Surveys	473
11.6.5	Finite Population	473
11.7	Discussion	474
12.	Multiple-Season Study Design	
12.1	Time Interval Between Seasons	478
12.2	Same vs. Different Units Each Season	480
12.3	More Units vs. More Seasons	482
12.4	More on Unit Selection	484
12.5	Discussion	486
Part V		
Advanced Topics		
13.	Integrated Modeling of Habitat and Occupancy Dynamics	
13.1	Introduction	489
13.2	Basic Sampling Situation	490
13.3	Model Development and Estimation	491
13.3.1	Missing Observations	494
13.3.2	Covariates	495
13.4	Biological Questions of Interest	495
13.4.1	Effect of Habitat Change on Occupancy Dynamics	496
13.4.2	Effect of Species Presence on Habitat Dynamics	497
13.5	System Summaries	497
13.6	Model Extensions	498
13.7	Example	501
13.7.1	Patuxent Spotted Salamanders	501
13.8	Discussion	506
14.	Species Co-Occurrence	
14.1	Detection Probability and Inferences About Species Co-Occurrence	510
14.2	A Single-Season Model	517
14.2.1	General Sampling Situation	517
14.2.2	Statistical Model	518
14.2.3	Derived Parameters and Alternative Parameterizations	527
14.2.4	Covariates	531
14.2.5	Missing Observations	535

14.3 Addressing Biological Hypotheses	537
14.4 Example: Terrestrial Salamanders in Great Smoky Mountains National Park	539
14.5 Extension to Multiple Seasons	543
14.6 Example: Barred and Northern Spotted Owls	547
14.7 Study Design Issues	553
14.8 Generalizing to More than Two Species	554
14.9 Discussion	556
 15. Occupancy in Community-Level Studies	
15.1 Investigating the Community at a Single Unit	558
15.1.1 Fraction of Species Present in a Single Season	560
15.1.2 Changes in the Fraction of Species Present over Time or Space	561
15.2 Investigating the Community at Multiple Units	562
15.2.1 Single-Season Studies: Modeling Occupancy and Detection	563
15.2.2 Single-Season Studies: Multi-Species Occupancy Models (MSOMs)	566
15.2.3 Example of the Dorazio–Royle Multi-Species Occupancy Model	570
15.3 The Yamaura Extensions: Multi-Species Abundance Models	575
15.4 Multiple-Season Multi-Species Occupancy Models	577
15.5 Discussion	580
 16. Final Comments	
 Appendix	589
Bibliography	597
Index	631