

© Copyright 2023

Abby Bratt

PREVIEW

PREVIEW

From Mark-Resight to Management: Bayesian Hierarchical Models for
Endangered Bird Populations

Abby Bratt

A dissertation

submitted in partial fulfillment of the
requirements for the degree of

Doctor of Philosophy

University of Washington

2023

Reading Committee:

Sarah Converse, Chair

Beth Gardner

Scott Pearson

Program Authorized to Offer Degree:

Quantitative Ecology and Resource Management, College of the Environment

University of Washington

Abstract

From Mark-Resight to Management: Bayesian Hierarchical Models for Endangered Bird Populations

Abby Bratt

Chair of the Supervisory Committee:
Sarah Converse

School of Aquatic and Fishery Sciences, School of Environmental and Forest Sciences

Producing reliable estimates of demographic rates is critical to our understanding of wildlife population dynamics and can provide valuable information for prioritizing conservation and management efforts. Precise and unbiased estimates are challenging to obtain when monitoring data are sparse, knowledge gaps are pervasive, or model assumptions are violated. This is often the case for species of conservation concern, which may be poorly understood and difficult to monitor. Bayesian hierarchical models are particularly useful for estimating demographic rates because they separate imperfect observation processes from the underlying biological processes, especially when combined in an integrated framework that leverages multiple data sources for increased precision and parameter identifiability.

Here I present three case studies using Bayesian hierarchical models to better understand the demography of threatened birds, with particular contributions to mark-resight and integrated

population modeling. In Chapter 2, I addressed a common but poorly understood problem in mark-resight studies of open populations: partial mark loss and degradation. I present a novel approach to sampling latent states in a Markov Chain Monte Carlo framework using a backtracking algorithm, and I apply this approach in the context of a multi-event model to the Oregon Vesper Sparrow (*Pooecetes gramineus affinis*) in South Puget Sound, Washington, USA. The results from this model constitute some of the first estimates of age-specific survival and dispersal rates for this species of conservation concern. In Chapter 3, I developed a novel multi-site integrated population model (IPM) to better understand the population dynamics of Streaked Horned Larks (*Eremophila alpestris strigata*) in South Puget Sound, Washington. These estimates will inform future habitat management and a planned reintroduction effort, and the multi-site framework addresses a critical gap in modeling small populations monitored over fragmented landscapes. In Chapter 4, I developed an IPM to examine the impact of a cryptic threat, bycatch in commercial fisheries, on the population dynamics of Atlantic Yellow-nosed Albatross (*Thalassarche chlororhynchos*). Results from this model will motivate ongoing monitoring of Atlantic Yellow-nosed Albatross and seabird bycatch in the South Atlantic and inform fisheries regulation decisions. Broadly, the work I present here makes contributions to the development of complex demographic models with the goal of supporting conservation and management decisions by quantifying and reducing key uncertainties in the population dynamics of threatened species.

TABLE OF CONTENTS

List of Figures	iv
List of Tables	x
Chapter 1. Introduction	15
1.1 Background	15
1.2 Research Objectives	17
1.3 Broader Impacts	18
1.4 References	19
Chapter 2. An Unbiased Survival Estimator Based on Mark-resight Data in the Presence of Mark Degradation	22
2.1 Introduction	23
2.2 Materials and Methods	27
2.2.1 Overview	27
2.2.2 Example	27
2.2.3 Model Description	30
2.2.4 Generating the Mark Transition Matrix	31
2.2.5 Backtracking Algorithm	32
2.2.6 Initialization and Sampling	34
2.2.7 Confusion Index	35
2.2.8 Simulation Study	35
2.2.9 Case Study	37
2.2.10 Implementation	39

2.3	Results.....	39
2.3.1	Simulation Study.....	39
2.3.2	Case Study	42
2.4	Discussion.....	43
2.5	Acknowledgements.....	49
2.6	Figures & Tables.....	50
2.7	References.....	59

Chapter 3. Population Dynamics and Viability of an Endangered Grassland Bird on a

	Fragmented Landscape	65
3.1	Introduction.....	66
3.2	Methods.....	68
3.2.1	Study System and Species	68
3.2.2	Population Monitoring Data	69
3.2.3	Statistical Modeling	71
3.2.4	Population Projections	80
3.3	Results.....	80
3.3.1	Demographic Rates.....	80
3.3.2	Abundance	82
3.3.3	Population Sensitivity	82
3.4	Discussion.....	83
3.5	Acknowledgements.....	86
3.6	Figures & Tables.....	88
3.7	References.....	100

Chapter 4. Quantifying the Effect of Bycatch Mitigation Efforts On the Population Dynamics of A Long-Lived Seabird	106
4.1 Introduction.....	107
4.2 Methods.....	111
4.2.1 Study System and Species	111
4.2.2 Population Monitoring Data	112
4.2.3 Bycatch Mitigation Data.....	115
4.2.4 Statistical Modeling	115
4.2.5 Model Fitting	121
4.2.6 Population Sensitivity and Viability	122
4.3 Results.....	122
4.3.1 Demographic Rates.....	122
4.3.2 Abundance and Population Viability	123
4.4 Discussion.....	124
4.5 Acknowledgements.....	129
4.6 Figures & Tables.....	130
4.7 References.....	140
Appendix A.....	149

LIST OF FIGURES

Figure 2.1: Example spatial representation of marks observed in each year for three individual passerines, each marked with two colored auxiliary marks and one metal permanent band. Individuals were marked with auxiliary marks in colors Blue and Green (BG), Red and Green (RG), and Blue and Purple (BP). Marks were observed without error in Year 1 when individuals were captured at one of three sites. The same three sites were monitored for the remaining three years of study during which resight surveys were conducted. During this period, individuals could move throughout the study area and undergo partial loss of auxiliary marks, as demonstrated in years two and three. No marked individuals were observed in the study area in year four. 51

Figure 2.2: Visualization of how the backtracking algorithm assigns individuals to observed marks, using the described example. The algorithm is run separately on years 1-3 (top-bottom). Within each year, the algorithm begins with the set of observed marks, where observed marks are not yet assigned to any individuals. Each node of the search tree increments the previous partial solution by assigning one more observed mark to an individual (green check marks). Green boxes around nodes indicate that each observed mark has been successfully matched to an individual. Red boxes around nodes indicate that not all observed marks can be successfully matched to individuals and therefore this branch of the search tree has not resulted in a valid solution..... 52

Figure 2.3: Graph constructed using the valid terminal nodes constructed by the backtracking algorithm for each of Years 1-3 (Figure 2.2). Each terminal node from Year 1 is connected to each terminal node from Year 2, and each terminal node from Year 2 is connected to each terminal node from Year 3. No marks were observed in Year 4 so it is omitted from the graph. The path through this graph indicated by the darker arrows results in the true encounter history described within the in-text example. 53

Figure 2.4: Map of Oregon Vesper Sparrow monitoring sites in western Washington, USA, where the shaded blue area represents Joint Base Lewis-McChord. Sites A-D are native prairie sites, while site E is a municipal airport. Site A is Lower Weir prairie, B is Upper Weir prairie, C is Range 76, D is Tenalquot prairie, and E is Sanderson Airport. ... 54

Figure 2.5: Median (points) and 95% confidence intervals (line ranges) of log-scale confusion indices across all 100 simulated datasets relative to the probability of partial mark degradation, assuming sequential mark deployment (A), or random mark deployment (B). The color of the points and line ranges are scaled to the percent of models successfully run, with darker blues indicating more models run. Also shown are median RB (C, D) and RMSE (E, F) in survival estimates when observations of degraded marks are included in the analysis, using the model described here. RB and RMSE are presented with respect to survival probability, detection probability, and the probability of partial mark degradation when marks deployed either sequentially (A, C, E), or randomly (B, D, F). 55

Figure 2.6: Median relative bias (RB; A, B) and root mean square error (RMSE; C, D) in survival estimates when observations of degraded marks are omitted from the analysis, and when marks are deployed either sequentially (A, C), or randomly (B, D). RB and RMSE are presented with respect to survival probability, detection probability, and the probability of partial mark degradation. 56

Figure 2.7: Age-specific survival estimates for western Washington Oregon Vesper Sparrows from model omitting observations of partially degraded marks (blue) compared to estimates from model including degraded marks (yellow). Posterior distributions are shown, as well as medians (points), and 95% credible intervals (line ranges). Inclusion of degraded marks leads to slightly higher and more precise estimates of survival across all age-classes.57

Figure 2.8: Median site- and age-specific probabilities of site fidelity for Oregon Vesper Sparrow in western Washington, USA (A, B) from model omitting observations of degraded marks (A) compared to model including observations of degraded marks (B). Also shown are site- and age-specific dispersal probabilities (C, D) from model omitting observations of degraded marks (C) compared to model including observations of degraded marks (D). L and HY birds are shown on the left, compared to AHY birds on the right. Omitting degraded marks results in slightly higher estimates of site fidelity and lower estimates of dispersal. 58

Figure 3.1: Map of study sites in the South Puget Sound region of Washington State, USA. Blue sites are native prairies and red sites are airfields. The purple shaded area represents Joint Base Lewis-McChord. 88

Figure 3.2: Life-cycle diagram for Streaked Horned Larks. Age-classes represented are near one-year-olds ($N1$) and older adults (Nad). Both age-classes survive with rate ϕ_{ad} . Both age-classes produce chicks with rate f , who then survive to become near one-year-olds with rate ϕ_1 89

Figure 3.3: Site-specific nest survival probabilities by nest state. Site labels correspond to the site labels in Figure 1. Shown are age-specific medians (points), and 95% credible intervals (line ranges). The vertical lines represent the stage-specific means. 90

Figure 3.4: Annual nest survival probabilities by nest stage. Posterior distributions are shown along with medians (points), and 95% credible intervals (line ranges). The horizontal lines represent the stage-specific means..... 91

Figure 3.5: Apparent and true survival probabilities by age. Shown are age-specific medians (points), and 95% credible intervals (line ranges). 92

Figure 3.6: Site-specific survival probabilities by age. Site labels correspond to the site labels in Figure 1. Shown are age-specific medians (points), and 95% credible intervals (line ranges). The vertical lines represent the age-specific means..... 93

Figure 3.7: Annual nest survival probabilities by age. Posterior distributions are shown along with medians (points), and 95% credible intervals (line ranges). The horizontal lines represent the age-specific means..... 94

Figure 3.8: Median site- and age-specific probabilities of site fidelity (top) and site- and age specific dispersal probabilities (right) for Streaked Horned Larks in South Puget Sound. Fledglings (L) are shown on the left, compared to adult (AHY) birds on the right. Site labels correspond to the site labels in Figure 1. Post-fledglings (HY) are assumed to disperse at the same rate as fledglings and are therefore omitted from this figure. 95

Figure 3.9: Estimated region-wide (left) and site-specific (right) abundance of Streaked Horned Larks at occupied sites in South Puget Sound over the data period, using non-informative priors for site-specific initial abundances. Medians are represented by the bold lines, while 95% credible intervals are represented by the shaded areas. Site labels correspond to the site labels in Figure 1. There is substantial variation in trend between years, and limited synchrony between sites. The resulting trend is substantially different than in Figure 3.10,

revealing model sensitivity to initial population size at infrequently monitored sites (i.e., C, F, I)..... 96

Figure 3.10: Estimated region-wide (left) and site-specific (right) abundance of Streaked Horned Larks at occupied sites in South Puget Sound over the data period, using informative priors for site-specific initial abundances. Medians are represented by the bold lines, while 95% credible intervals are represented by the shaded areas. Site labels correspond to the site labels in Figure 1. There is substantial variation in trend between years, and limited synchrony between sites. The resulting trend is substantially different than in Figure 3.9, revealing model sensitivity to initial population size at infrequently monitored sites (i.e., C, F, I)..... 97

Figure 3.11: Estimated annual population growth rates relative to estimated demographic rates over the data period. Posterior medians are shown (points), with 95% credible intervals (line ranges) for stage-specific nest survival probabilities (top row) and age-specific survival probabilities (bottom row). All parameters show strong correlation with population growth rate, though the correlation is stronger for survival probabilities. There is no substantial difference in correlation between classes for stage-specific or age-specific survival probabilities..... 98

Figure 4.1: Location of Gough Island which is centrally located in the South Atlantic Ocean, surrounded by the red box. Atlantic Yellow-nosed Albatross (AYNA) foraging ranges span the Southern Atlantic between South America and Africa. On Gough, the AYNA study area is located on the southern tip of the island, which is a lowland plateau. 130

Figure 4.2: Life-cycle diagram for Atlantic Yellow-nosed Albatross as described by the population model. For adults, represented states are 1) breeding; 2) loafing within the breeding colony; and 3) at sea. Conditional on surviving, adults may cycle between these three states according to the transition probabilities described in the text. If breeding, adults produce juveniles, which may then survive to become immature individuals of age 1. Conditional on surviving, immature birds may recruit into the breeding population with an age-specific transition probability. Note that this is a female-based model and thus fecundity is halved, assuming an equal sex-ratio at fledging..... 131

Figure 4.3: Proportion of international (International Commission for the Conservation of Atlantic Tuna; ICCAT) and national (Namibia, South Africa, and Uruguay) longline and demersal trawl fishing fleets that have implemented seabird bycatch mitigation measures by year, as elicited from experts from the Albatross Task Force. The large discontinuities amongst the national fleets reflect changes to mitigation mandates, whereas mitigation is still “opt-in” for the ICCAT fleet. 132

Figure 4.4: Annual survival probability for juvenile (yellow) and adult (blue) Atlantic Yellow-nosed Albatross, where any bird over 1 year old is assumed to survive at the adult rate. Posterior distributions are shown along with medians (points), and 95% credible intervals (line ranges). Horizontal lines represent age-specific means, noting that y-axis begins at 0.6. 133

Figure 4.5: Annual fecundity estimates. Fecundity represents the probability of successfully fledging a chick of either sex. Posterior distributions are shown along with medians (points), and 95% credible intervals (line ranges). The horizontal line represents the inter-annual mean. 134

Figure 4.6: Estimated age-at-recruitment curve. The curve takes a sigmoidal shape, where average age at recruitment is around 9. Recruitment probability is low prior to this, and increases steeply as individuals age, with an asymptote of 1. Shown are age-specific medians (points), and 95% credible intervals (line ranges). 135

Figure 4.7: Estimated abundance of breeding (yellow) and all (blue) females associated with the Gough Island study area over the data period. Posterior distributions are shown along with medians (points), and 95% credible intervals (line ranges). Despite some interannual variation, both groups appear relatively stable over this period. There is more variability present amongst all females, which includes loafers, adults at sea, and immature birds in addition to breeding individuals. There is some asynchrony between breeding and total abundance. 136

Figure 4.8: Estimated annual population growth rates relative to estimated demographic rates over the data period. Posterior medians are shown (points), with 95% credible intervals (line ranges) for fecundity, adult survival, and juvenile survival. 137

Figure 4.9: Projected total abundance of females within the Gough Island study area. Medians are represented by the bold lines, while 95% credible intervals are represented by the shaded areas. Projections are 50 years long, with blue representing the data period prior to 2020 and the “status quo” projection. 138

PREVIEW

LIST OF TABLES

Table 2.1: Model parameters, latent states, and data for described multi-state model including observations of degraded marks.....	50
Table 3.1: Model parameters and their priors, with references when informative priors were used.	99
Table 4.1: Model parameters and their priors, with references when informative priors were used.	139

PREVIEW

ACKNOWLEDGEMENTS

Writing this dissertation has been hard, but writing the acknowledgments section has been easy.

In fact, throughout the last six months of my dissertation, I came back to it many times.

Whenever I had writer's block, I would look to the acknowledgments I had drafted, and the words would start to flow. This is a small, but I hope meaningful, example of how the people listed below have supported me both directly and indirectly during my education. I could not have done it without them.

I have received financial support over the years from the University of Washington's Quantitative Ecology & Resource Management Program, the College of the Environment, the Washington Cooperative Fish & Wildlife Research Unit, the Northwest Climate Adaptation Science Center, and the Royal Society for the Protection of Birds.

I am so grateful to my coauthors of these chapters. In particular, I'd like to thank Steffen Oppel and Nathan Hostetter. To Steffen Oppel, who has been pushing Chapter 4 forward for over a decade. Thank you for trusting that I could contribute meaningfully to this project, and for your continued support and expertise. And to Nathan Hostetter, you're my hero. Thank you for your generosity, your brilliance, and your graciousness.

I'd also like to thank my colleagues in the Quantitative Conservation Lab and the co-op unit. To Staci Amburgey, Lisanne Petracca, Matt Farr, Hannah Sipe, Mark Sorel, Amanda Warlick, Amelia DuVall, Brielle Thompson, Liam Pendleton, Eve Hallock, Nate Redon, Kelly Mistry, Verna Blackhurst, and Sarah Romero. I have learned so much from each of you. Thanks for looking at code and drafts, and for being the sounding boards for all my best (and worst) ideas.

To my fellow QERMies, thanks for all the soup! To my cohort in particular, Martin Endress, Maria Kuruvilla, Yian Lin, and Megan Ferguson. You guys helped shoulder the challenges of that first year and even made it fun. To Tim Essington, Beth Gardner, Trevor Branch, and Erica Owens. Thanks for all you do to keep QERM the supportive professional and personal community that it is.

Thank you to my committee members, Sarah Converse, Beth Gardner, Gary Slater, Scott Pearson, and Ryan Kelly, for their mentorship. Ryan, thank you for going above and beyond as a member of my committee, for asking great questions, and for broadening my perspective on the world. Scott, thank you for your ever-thoughtful feedback and for pointing me in the right directions when I got lost. Gary, thank you for getting me out from behind the desk and trusting that a young statistician could turn into a young ecologist. Beth, you've worn several hats as a member of this committee and as the director of QERM and your contributions as both have been invaluable. Thank you for challenging me and reminding me to laugh at the same time. And to Sarah. I cannot begin to describe the impact you've had on my life as a scientist and a human being. Working with you has been an honor and a privilege.

I am grateful also for the unwavering support and understanding I have received from friends and family as near as the bedroom across the hall and as far as Norway. To my parents, Beth and Nick. Thank you for giving me space to dream. Thank you for teaching me to find joy in hard things. Thank you for making sure I know I always have a safe place to land. To Jesse, Miriam, Jens, and Maud. Time zones are generally a curse, but for me, they have been a blessing. What a joy it's been to wake up to messages from you nearly every day. I was also fortunate enough to gain some new family members over the course of this ride. To Halinka,

Dalton, Izzy, and George. Thank you for keeping me company during the darkest and lightest times of the past few years. Becoming a member of your family has been the honor of a lifetime.

And to Henry. 99% of people (real statistic) think statistics is the most boring subject on the planet. I feel so fortunate to have found a partner who is so curious about the world and who asks the most insightful questions. Thank you for seeing me. Thank you for knowing when I need a hug, a laugh, a break, or a meal. You are my best distraction. I love you so much.

PREVIEW

DEDICATION

To my grandfathers:

Charles Christopher Bratt and Lloyd William Eichhorn

Champions of conservation, lovers of poetry, advocates for a good breakfast.

PREVIEW

Chapter 1. INTRODUCTION

1.1 BACKGROUND

Understanding population dynamics and drivers of population trends can support the conservation of threatened species. However, estimating demographic rates and their variation over space and time is challenging for small, declining, fragmented, or otherwise difficult-to-monitor populations. Knowledge gaps may impede decision making when data are sparse. Population modelers aim to leverage available data to close these knowledge gaps and identify key uncertainties for future study.

One approach to population modeling is integrated population modeling, where multiple data sources with shared underlying parameters are combined in a joint analysis. Integrated population models (IPMs; Besbeas et al., 2002; Brooks et al., 2004; Schaub & Abadi, 2011; Zipkin & Saunders, 2018) have become popular in part because they leverage all available data to provide information about both demographic states (i.e., abundance) and rates (e.g., survival, productivity). Crucially, IPMs can improve precision (Abadi et al., 2010a; Schaub et al., 2007) and produce estimates of demographic rates that are unobservable (e.g., Opperl et al., 2022) or may otherwise be unidentifiable (Abadi et al., 2010b). Though much of the preliminary work demonstrating the utility of IPMs focused on taxa with simple life histories (e.g., herons; Besbeas et al., 2002), as available computing power increases, IPMs for species with complex life histories (e.g., apex predators; Regehr et al., 2018) are becoming more common. Like other hierarchical model types, IPMs can facilitate estimation of the effects of environmental conditions or anthropogenic stressors on demographic rates (e.g., Opperl et al., 2014), which is of useful when trying to identify causes of decline for threatened or indicator species.

To be a true integrated model, IPMs need to include a dataset relevant to the estimation of abundance and at least one additional dataset that allows for the estimation of one or more demographic parameters; commonly this is a mark-recapture or mark-resight dataset. Studies of marked populations can lend insights about a number of demographic parameters, including survival (e.g., Lebreton et al., 1992), recruitment (e.g., Tucker et al., 2023), movement (e.g., Sollmann et al., 2013), and productivity (e.g., Lahoz-Monfort et al., 2013). Often these parameters are strongly correlated with population trend and therefore it is valuable to estimate these parameters precisely and to identify their drivers to inform conservation decision-making. Mark-resight models vary widely in complexity, from Cormack-Jolly-Seber models (Cormack, 1964; Jolly, 1965; Seber, 1965), to multi-state models (Nichols & Kendall, 1995), to multi-event models (Pradel, 2005) and can therefore accommodate many sampling situations, provided that model assumptions are met.

While the development of complex models and integrated models can help resolve some uncertainty in our understanding of demography, there is no substitute for a well-designed monitoring program. Underpinning all models are assumptions about the underlying observation and biological processes and when those assumptions are violated it may render results invalid. Some assumptions may matter relatively little (e.g., independence of datasets in integrated population models; Abadi et al., 2010a), where others can matter more (e.g., mark loss in mark-resight models; Chapter 2). Given that we rely on long-term monitoring programs to inform conservation decisions for endangered wildlife (Nichols & Williams, 2006), great care should be taken at the outset to design a monitoring program that has the power to produce accurate and precise estimates of demographic rates, and that are more likely to detect changes in population

trends. Similarly, monitoring programs should be regularly reevaluated to ensure they are being implemented correctly and functioning as intended (Lindenmayer & Likens, 2009).

1.2 RESEARCH OBJECTIVES

The objectives of my research were twofold, including (1) advancing Bayesian hierarchical modeling of mark-resight data in the context of integrated population models, and (2) estimating vital rates for three poorly understood species of conservation concern. To this end, I developed a novel multi-state model for mark-resight data in the presence of mark loss for Oregon Vesper Sparrow (*Pooecetes gramineus affinis*) in Washington State, and IPMs for Streaked Horned Larks (*Eremophila alpestris strigata*) and Atlantic Yellow-nosed Albatross (*Thalassarche chlororhynchos*) in Washington State and on Gough Island in the South Atlantic.

The methodological advancements made here were motivated by challenges presented in the available data. For Oregon Vesper Sparrow and Streaked Horned Larks, partial mark loss is pervasive and has hindered our understanding of survival and dispersal rates for these species. Thus, in Chapter 2 I developed a novel model and approach for sampling latent states for multi-state models of mark-resight data in the presence of partial mark loss and degradation. Streaked Horned Larks are intensively monitored at numerous sites, but the region-wide population dynamics are not well understood. Thus, in Chapter 3 I built a multi-site IPM, using mark-resight data to inform movement and survival across a fragmented landscape. Atlantic Yellow-nosed Albatross are vulnerable to cryptic threats but are difficult to monitor and only observable during some life history stages. Therefore, in Chapter 4 I built an IPM around a multi-event model of mark-resight data with several unobservable states. Each challenge that I have addressed here is not unique to the case-study species. Consequently, the methodology I present is applicable to

many endangered species which are monitored with through marking and resighting, over fragmented landscapes, or only during portions of their life-history.

1.3 BROADER IMPACTS

Collectively, the developed in these studies contribute new approaches for developing models of complex ecological processes and the specific case studies make contributions that will inform species conservation decisions. Ecologically, the Oregon Vesper Sparrow is a species of great conservation interest throughout the Pacific Northwest, including in Washington State, where it is listed as endangered. I present some of the first robust estimates of age-specific survival and dispersal probabilities for this subspecies, which will inform future population modeling efforts and influence conservation action. The Streaked Horned Lark is state and federally listed and is intensively monitored throughout South Puget Sound, where the model and demographic estimates I produced will be used to inform a reintroduction effort. Atlantic Yellow-nosed Albatross is endangered per the IUCN and is vulnerable to cryptic threats such as environmental change and anthropogenic stressors in the South Atlantic. Bycatch in commercial fisheries is a known threat to seabirds but the degree to which it impacts population dynamics of this species is not well understood. My work on this species identifies knowledge gaps for future study. Methodologically, I present novel model frameworks that facilitate robust estimation of vital rates in the face of common challenges with the integration of mark-resight data: mark loss or degradation, dispersal over fragmented landscapes, and multiple unobservable states.

1.4 REFERENCES

- Abadi, F., Gimenez, O., Arlettaz, R., & Schaub, M. (2010). An assessment of integrated population models: Bias, accuracy, and violation of the assumption of independence. *Ecology*, *91*(1), 7–14. JSTOR.
- Abadi, F., Gimenez, O., Ullrich, B., Arlettaz, R., & Schaub, M. (2010). Estimation of immigration rate using integrated population models. *Journal of Applied Ecology*, *47*(2), 393–400.
- Besbeas, P., Freeman, S. N., Morgan, B. J. T., & Catchpole, E. A. (2002). Integrating mark-recapture-recovery and census data to estimate animal abundance and demographic parameters. *Biometrics*, *58*(3), 540–547. <https://doi.org/10.1111/j.0006-341X.2002.00540.x>
- Brooks, S. P., King, R., & Morgan, B. J. T. (2004). A Bayesian approach to combining animal abundance and demographic data. *Animal Biodiversity and Conservation*, *16*.
- Cormack, R. M. (1964). Estimates of survival from the sighting of marked animals. *Biometrika*, *51*(3/4), 429–438. <https://doi.org/10.2307/2334149>
- Jolly, G. M. (1965). Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika*, *52*(1/2), 225–247. <https://doi.org/10.2307/2333826>
- Lahoz-Monfort, J. J., Harris, M. P., Morgan, B. J. T., Freeman, S. N., & Wanless, S. (2013). Exploring the consequences of reducing survey effort for detecting individual and temporal variability in survival. *Journal of Applied Ecology*, *51*(2), 534–543. <https://doi.org/10.1111/1365-2664.12214>