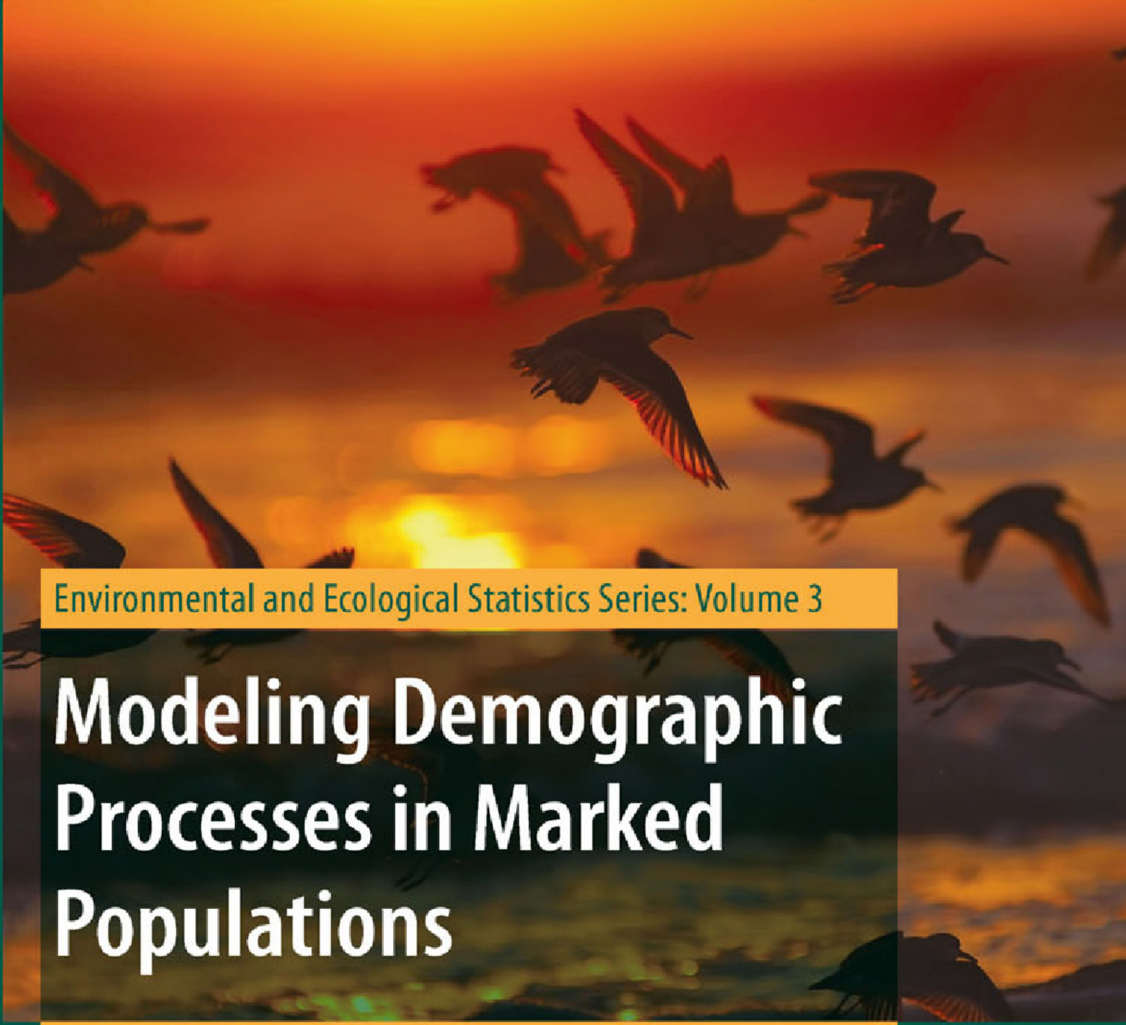

Environmental and Ecological Statistics Series: Volume 3

Modeling Demographic Processes in Marked Populations

David L. Thomson, Evan G. Cooch and Michael J. Conroy

Springer

Modeling Demographic Processes In Marked Populations

Environmental and Ecological Statistics

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David L. Thomson • Evan G. Cooch
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Editors

Modeling Demographic Processes In Marked Populations

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Foreword

Demography can be considered the key to understanding much of biology. It is the demographic processes of birth and death which govern the spread of populations through environments and the spread of genes through populations. An understanding of demography can yield not only an understanding of population size and population change, it can help us to understand the form and function of life histories; when organisms mature, when they breed, and when they die. Demographic insights allow us to see how populations function, how they interact with their changing environment, and how they adapt.

The analysis of demographic processes in free-living organisms is however no simple task and involves considerable challenges in observation and analysis. Some 20 years ago, there was a concerted effort to promote inter-disciplinary collaboration between biologists and statisticians to address these challenges and thereby to further our understanding of demographic processes in natural populations. Although many diverse organisms can be studied in the wild, birds have proved particularly amenable with large numbers being marked and followed by large networks of observers. It was no coincidence then that the European Union for Bird Ringing (EURING) played a leading role in these initiatives, teaming up in the mid-1980s with the Mathematical Ecology Group of the Biometric Society, and the British Ecological Society, to bring together experts from diverse fields to address the challenges in hand. Twenty years on, progress has been considerable and we now have significant insights into demographic processes thanks to the wide range of quantitative tools and systematically collected datasets which have been built up over this period.

The biological questions and the methodological challenges are however by no means settled, indeed the field continues to progress at an ever accelerating pace. In 2003, a group of just under 100 scientists met to discuss and identify the key areas of development in which ongoing research effort should be focused. As listed in the Contents section, the group identified five areas defined by biological applications and five areas defined by statistical approaches including the issue of software with which to implement state-of-the-art analyses. Experts in each of these areas then took the lead in assembling authoritative contributions, with one or two overview- or perspectives- papers prepared by leading figures, and three to five primary research papers which reported the most significant new findings. A further open-forum was created for notable contributions which lay outside the ten targeted areas. Authors came together to discuss their contributions at a meeting hosted by the University of Otago at the beginning of 2007.

This field continues to move rapidly, but we hope this resulting volume will stand as a definitive compilation on the state-of-the-field at the present time, and that it will steer the further development of the field over the years ahead. As reflected in this volume, we anticipate increasing emphasis on integrated approaches which combine multiple sources of information and an increasing emphasis on Bayesian approaches. In terms of biological applications, it has traditionally been the field of wildlife management which has provided the impetus for developing modern approaches, but increasingly we see the activities of evolutionary biologists and biodemographers as a driver of growth in this field. Modeling demographic processes in marked populations is a truly interdisciplinary endeavour, and we look forward to continued fruitful dialogue not just between biologists and statisticians but between these different fields of biology which are conceptually similar and which share the same need for sound quantitative approaches to demographic analysis.

This volume has been a team effort, and as well as crediting all the work of the authors themselves and the associate editors listed in the Contents section, we would like to acknowledge Prof. Richard Barker and his team for their hard work and kind hospitality in hosting a successful meeting of contributors in Dunedin. All contributions have benefited from the expert input of at least two referees, and we would of course like to thank Prof. G.P. Patil, Manjula Jude (Project Manager at Integra Software Services), Lindy Paul and the team at Springer for facilitating the publication of this volume.

David L. Thomson
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Section I

Population Dynamics – Growth, Density-Dependence and Decomposing λ

Paul Doherty and David Fletcher

Bayesian Hierarchical Models for Inference About Population Growth

Richard J. Barker, Matthew R. Schofield, Doug P. Armstrong, and R. Scott Davidson

Abstract Mark recapture models have long been used for estimating wildlife population parameters. Typically, the data are summarized in terms of parameters that are interpreted in the context of an implicit demographic model for describing population dynamics. Usually, this demographic model plays little or no role in the mark-recapture model. Bayesian hierarchical models (BHM) offer a way to explicitly include demographic models in an analysis. We argue that such an approach should have wide appeal to ecologists as it allows inference to focus on ecological models of interest rather than obtaining a parsimonious depiction of the sampling process. We discuss the use of BHM's for modeling mark-recapture data with a focus on models describing density-dependent growth.

1 Introduction

Ecologists interested in population dynamics of wildlife populations typically work with two kinds of models: demographic models, in which predicted population trajectories are obtained conditional on parameter values and statistical models in which parameter estimates are obtained using data sampled from the study population.

Demographic models may be matrix- or individual-based and can be deterministic or stochastic (Williams et al. 2002). Whether population models are deterministic or stochastic they depend on parameters. Formally, we can write our model as $\mathcal{F}(Z;\lambda)$ where Z represents the output and λ represents demographic parameters. In using demographic models our interest lies in predicting future population behavior, usually in terms of summaries of Z such as extinction rate or equilibrium population size.

Statistical models are used to summarize data. We can formalize a statistical model as $\mathcal{F}(Y;\pi)$ where Y represents data and π parameters involved in describing

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the sampling process. Note that π might include some or all of the demographic parameters in λ. Once the data have been collected they are fixed; we use the statistical model to describe the mechanism by which we imagine our data were generated. We use our data and the model to obtain information about the parameters. In the model, Y is regarded as random outcome sampled from $\mathcal{F}(Y;\pi)$ with the parameters π fixed at (usually) unknown values.

In the context of the EURING technical meetings, the mark-recapture model is an important class of statistical model. A strong tradition of the EURING technical meetings has been the stimulation of the development of mark-recapture analysis, to the extent that one of the main aims of these meetings has been to establish mark-recapture as one of the standard methodologies in ecology and conservation biology (Senar et al. 2004b). The past 20 years have seen the development of models appropriate for analyzing almost every conceivable type of mark-recapture data, and the development of powerful software such as MARK (White and Burnham 1999), MSURGE (Choquet et al. 2004) and POPAN (Arnason and Schwarz 2002). Obviously, the development of mark-recapture modeling is not an end in itself. The value of mark-recapture models lies in their application. “I note that although EURING conferences have focused on estimation issues, it is important to recall that estimation is not a ‘stand-alone’ activity or an inherently useful endeavor and attains value primarily in the context of larger processes, such as science or management” (Nichols 2004).

Applications of mark-recapture models have tended to focus on estimation as a means for summarizing status of populations, for example the MAPS program in North America (Tautin et al. 1999), or the interpretation of vital rates and factors influencing these e.g. (Catchpole et al. 1999; Conroy et al. 2002; Reed 2004).

Implicit to a mark-recapture model is a demographic model that describes the population dynamics of the study population, at least in part. For example, in the Cormack–Jolly–Seber model (Cormack 1964; Jolly 1965; Seber 1965), the number of marked survivors alive at occasion $i + 1$ is a binomial random variable with index being the number of marked animals in the population immediately after sample i and probability the survival rate for interval $[i, i + 1)$. The implied demographic model has tended to play little part in subsequent analysis, although the most recent EURING conference (Senar et al. 2004a) saw the appearance of a number of papers that focused on assessment of population dynamics based on mark-recapture data (e.g., Caswell and Fujiwara 2004; Francies and Saurola 2004; Gauthier and Lebreton 2004; Brooks et al. 2004).

Caswell and Fujiwara (2004) stressed the potential benefits of explicitly incorporating demographic models into a mark-recapture analysis by “... making the estimation of demographic models a goal at the outset of a mark-recapture study”. A key advantage to integrating demographic and statistical models, of which mark-recapture models are an example, is that it allows full expression of uncertainties.

Typically, demographic modelers have used fixed values for parameters in their models. For example, Francis and Saurola (2004) used a deterministic model based on mean parameter values to construct a deterministic predator-prey model to make predictions about tawny owl *Strix aluco* demographics. While this approach allows general predictions to be made, it does not provide any measure of prediction uncertainty associated with the fact that parameters must be estimated. Conditioning on a set of parameter estimates allows one to consider the implications of this particular set of parameter values (Caswell and Fujiwara 2004). To assess the influence of parameter uncertainty Caswell and Fujiwara (2004) discusses use of "perturbation analysis" based on derivatives of population summaries, or functions of these, such as sensitivities and elasticities.

An alternative to expression of parameter uncertainty using calculus and sensitivities is to use probability distributions. The use of probability distributions to describe uncertainty is a defining feature of Bayesian inference. In Bayesian inference prior probability distributions for parameters are combined with models for data to construct posterior distributions for parameters and posterior predictive distributions for predicted values. These posterior distributions express the uncertainty that we have about parameters and associated predictions after the data have been collected. Instead of focusing on the implications of a particular set of parameter estimates for projected population growth, the Bayesian approach allows us to consider a range of plausible parameter values with the contribution of any particular combination weighted by its posterior density.

The use of posterior distributions to summarize knowledge about parameters is convenient if interest is in exploring the demographic consequences of certain choices of parameter values in demographic simulations. Predictions under the demographic model can be made by sampling plausible values for parameters from the posterior distributions generated by the statistical model. Alternatively, we can combine the demographic and sampling models to obtain a fully integrated analysis.

A specific advantage of Bayesian inference procedures is that Bayesian models are naturally hierarchical. Hierarchical models have several levels of variability. In a Bayesian model we have data which depends on parameters that are themselves drawn from a distribution that also has parameters. The term hyperparameters is often used to describe parameters for distributions of parameters. Bayesian hierarchical models offer a way to formally integrate statistical models for estimating parameters with simulation models for predicting the likely future behavior of populations based on sample data. Mark-recapture models are also naturally hierarchical in that parameters such as survival probability and abundance are often modeled as random variables by demographers. Moreover, ecologists are often interested in relationships among parameters, such as density-dependent survival or recruitment, that have major implications for predicted population trajectories. Hierarchical mark-recapture models offer a way to model all sources of data as well as to model relationships among parameters (Link and Barker 2004) in a way that allows all posterior uncertainty, including uncertainty about predictions, to be expressed using probability distributions.

In this paper we use a case study of North Island saddlebacks (*Philesturnus rufusater*) to illustrate the use of Bayesian hierarchical modeling to predict population trajectories based on a density-dependent population model. Our emphasis is on accounting for parameter uncertainty conditional on the model. Methodology for multi-model inference in a Bayesian setting has been well covered elsewhere (Brooks et al. 2004).

2 North Island Saddlebacks of Mokoia Island

The North Island saddleback is a member of the wattlebird family (Callaeidae), a family of birds endemic to New Zealand. The Callaeidae comprise two or three (depending on taxonomic fashion) extant species. By the end of the nineteenth century saddlebacks had become locally extinct from the mainland of New Zealand: a single remnant population survived on one island off the coast of the North Island (Armstrong et al. 2005) and a single remnant population survived on one island off the coast of the South Island. Since the early 1960 s translocations have been used to re-establish populations including some mainland populations.

Armstrong et al. (2005) used mark-resighting analysis and counts of fledged and unmarked birds to monitor the outcome of a translocation to Mokoia Island in Lake Rotorua. Thirty six adult birds were released on the 135-ha island in 1992 following rat eradication. Mokoia Island is 2.1 km from the nearest shore, a distance believed to be beyond the flying range of saddlebacks. The translocated population is thus believed to be closed to emigration.

Armstrong et al. (2005) were interested in predicting future population growth of the Mokoia Island saddleback population to assess future population viability and to devise strategies for translocating birds from re-established populations to places elsewhere. In particular, they were interested in evidence for density-dependent population dynamics as the presence of density dependence can have a major stabilizing influence on dynamics. Re-introductions are useful for studying density dependent growth because founding populations are usually established at low population densities and with a relatively high level of resource availability.

In their analysis, Armstrong et al. (2005) used a stochastic matrix model to project the likely future trajectory of the Mokia Island saddleback population. Their model tracked the number of males and females in the population at the start of each breeding season and used estimates of survival and fledging rates from analyses of their banding data and from fledgling surveys. Because Armstrong et al. (2005) conditioned on these parameter estimates, their projection model does not account for all the uncertainties in the analysis. Also, Armstrong et al. (2005) treated abundance estimates obtained in their analysis as fixed, using these to assess density-dependent effects on survival and juvenile production rates. In addition to unmodeled uncertainty there is also some sampling correlation unaccounted for between the abundance and survival probability estimates.

With multiple sources of data and with interest in modeling parameters such as survival and production rate as a function of population size, this problem is ideally suited to an approach based on fitting a hierarchical model using Bayesian model fitting procedures.

3 Data and Models

3.1 Mark-Resighting Data

The 36 founder birds were color-marked before release. Mark-resighting data were obtained from 24 surveys carried out between June 1992 and December 1997 at approximately 3-month intervals: in March, June, September, and December. The marked population comprised the 36 founding birds and 245 nestlings that were banded during the five breeding seasons that took place during the study. Nestlings were banded either in December or March according to when they were born. In October 1996 an aerial poison drop was used to try and eradicate mice from the island. An additional mark-resighting survey was carried out in November 1996 to assess the effect of the poison drop on the saddlebacks. During the mark-resighting surveys counts of all unmarked birds were also recorded.

To analyze the mark-recapture data we followed Armstrong et al. (2005) and fitted a simple 2-age model in which juveniles became adults after 9 months. The logit of the 3-month survival probabilities were modeled as a linear function of effects due to the age of the bird (juvenile/adult), poison drop, and the number of breeding pairs. We did not consider a sex-specific model as the analysis of the mark-resighting data by Armstrong et al. (2005) found negligible support for sex-specific survival.

To account for unexplained variation in three month survival probabilities over time we included a normal $N(0, \sigma^2)$ random effect. Because the intervals were not exactly 3-months, interval-specific survival probabilities were adjusted for the length of the interval.

Let y_j denote the length of time between survey j and survey $j + 1$ (3 months = 1.0), β_0 the overall mean 3-month survival probability on the logit scale, $Z_{1i} = 1$ for if individual i is juvenile and 0 if it is adult, $Z_{2j} = 1$ if there was a poison drop in the 3-month interval starting at the time of survey j and zero otherwise, and N_j denotes the number of breeding pairs in the breeding season associated with survey j, then:

$$\phi_{ij} = S_{ij}^{y_j}$$

and

$$\text{logit}(S_{ij}) \sim N(\beta_0 + \beta_1 Z_{1i} + \beta_2 Z_{2j} + \beta_3 Z_{1i} Z_{2j} + \beta_4 \ln(N_j), \sigma^2).$$

where ϕ_{ij} is the interval specific survival probability and S_{ij} the 3-month survival probability. Detection probabilities $(p_{ij}; i = 2 \ldots 25, j = 1$ for juveniles, $j = 2$ for adults) we modeled as age- and time-specific fixed effects.

For model fitting we used the complete data likelihood (Schofield and Barker 2008) which is proportional to:

$$[X|d, p, R][d|S, R][S|\beta, Z\sigma^2]$$