BAYESIAN METHODS FOR MARINE MAMMAL POPULATION ASSESSMENT

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"THE DELUSION OF CONTROL ARISES FROM OVERCONFIDENCE"

T. Homer-Dixon (2000, p.6)
The Ingenuity Gap
Vintage, Canada

CONTENTS

DECLARATION

I declare that I composed this thesis and that it has not been submitted in any previous application for a degree. All quotations have been distinguished by quotation marks and sources of information have been acknowledged. All of the work presented in this thesis is my own, except where collaborations with other workers are specifically acknowledged in the text and preface to each chapter.

John Durban

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ABSTRACT

Policy-makers increasingly need to use scientific data that are imprecise. This problem is particularly apparent for marine mammal management issues, where practical research constraints leave scientists and managers with the problem of drawing inference from sparse data. Effective use of such data therefore places great demands on our methods of data analysis and statistical inference. In this thesis I introduce novel Bayesian methods for the analysis of data on marine mammal abundance and trends.

Bayesian methods are applied to a suite of case studies to inform current management issues of importance both in the UK and overseas. These include estimating the probability of density dependence in the growth of a killer whale (*Orcinus orca*) population inhabiting the inshore waters of Washington State; estimating the size of a widespread population of bottlenose dolphins (*Tursiops truncatus*) in the Bahamas; and assessing the population status and abundance trends of bottlenose dolphins within a newly designated Special Area of Conservation in the Moray Firth, NE Scotland.

Each of these case studies uses model-based analysis of individual photo-identification data to make inference about unknown population parameters of interest. Specifically, Bayesian inference, based on "posterior" probability distributions and statements, is used to facilitate scientific reporting in the face of uncertainty about these unknowns. Additional issues addressed are the selection of alternative statistical models for inference based on posterior model probabilities; incorporating model selection uncertainty into inference through the estimation of model-averaged parameter estimates; and the use of random effects prior distributions to model the relatedness between unknown parameters and increase estimate precision. The application of these methods is accomplished through the use of Markov chain Monte Carlo sampling methods, which are implemented using the WinBUGS software.

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PREFACE

This thesis is presented as a series of four distinct papers (Chapters 3 to 6), linked by several common themes, outlined in a General Introduction (Chapter 1) and Discussion (Chapter 7). Some repetition between the chapters, particularly in the methods, is therefore unavoidable. However, to minimise this repetition, Chapter 2 provides an additional introduction to the Bayesian statistical methods that underlie the work presented in the subsequent data chapters.

These data chapters build upon existing long-term projects that have involved many people. Therefore, these chapters have multiple authors. Ken Balcomb provided the time series of killer whale population data for Chapter 3. Diane Claridge and Ken Balcomb contributed the dolphin photo-identification data from the Bahamas for use in Chapter 4. However, I participated in the majority of the data collection in the Bahamas, in collaboration with Kim Parsons, and performed most of the photographic analysis. Additional photographic data were analysed by David Ellifrit. Paul Thompson and Phillip Hammond provided photo-identification data of bottlenose dolphins from around NE Scotland (Chapters 5 and 6), and Ben Wilson provided additional data and background information on aspects of this work in which he was involved.

All collaborators contributed valuable comments on earlier drafts of the manuscripts for the data chapters. Additional comments were provided by Paul Thompson, Xavier Lambin and David Elston, who supervised the research that underlies this thesis. David Elston is a co-author on all data chapters, reflecting his valuable technical advice on the statistical methods that have been employed. However, the ideas behind the statistical analyses, and the conception of this project, are my own. I performed all the statistical analysis and wrote all the manuscripts.

CHAPTER 1

GENERAL INTRODUCTION

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CHAPTER ONE

General Introduction

Wildlife populations must be actively managed for a number of reasons (Shea, 1998). For example, concern for the future viability of endangered populations may necessitate conservation management to avoid extinctions (Mangel *et al.*, 1996), and when animals provide a key natural resource, harvesting must be managed to ensure the sustainability of the resource (Sutherland, 2001). Effective management in such situations depends on the existence of environmental policies, which must clearly be based on good science. However, it is rarely possible to conduct experiments to inform the management of natural resources. The scientific data relating to environmental issues are therefore often of an observational nature, and are generally sparse. As a result, there can be enormous uncertainty about scientific advice, which can constrain communication between scientists, policy makers and the public (Ludwig *et al.*, 2001). This thesis is concerned with facilitating the transfer and transparency of scientific advice through the analysis and communication of uncertainty in scientific data, specifically data on the status of marine mammal populations.

Uncertainty is fundamental to all scientific activities (Pielke, 2001), and therefore its inclusion in decision making processes is not only desirable, but is essential. Ignoring ecological uncertainty has repeatedly led to environmental catastrophes (Ludwig *et al.*, 1993), and can result in a lack of public trust in science (Haerlin and Parr, 1999). Nonetheless, the inability to make precise predictions has often resulted in ecological advice being overlooked during the development of environmental policies (Ludwig *et al.*, 2001), precluding the development of a sound scientific basis to sustainable resource management (e.g. Hilborn *et al.*, 1993). This points to an urgent need to develop more effective frameworks for incorporating uncertain ecological data into decision making processes (Lubchenco, 1998; Norton, 1998).

The application of Bayesian statistical inference can provide ecologists with a powerful and formal tool for presenting the kind of complex and uncertain advice that underlies environmental conservation and management decisions (Ellison, 1996; Wade, 2000). Bayesian analysis is well suited for this purpose because it directly analyses and conveys the *probability* of a scientific hypothesis, providing decision-makers with advice in probabilistic rather than categorical fashion. This is in direct contrast to the strict dichotomy of the conventional statistical approach, where inference is based on either accepting or rejecting a chosen null hypothesis (Shrader-Frechette and McCoy, 1992). Furthermore, Bayesian analysis can be applied either to discrete hypotheses or to a continuum of hypotheses, enabling decisions to be based on a full probability distribution of possible outcomes (Chapter 2). These statistical statements of probability can be logically translated into common language, to describe the *chance*, *plausibility* or *confidence* associated with each hypothesis under consideration (Andersen, 1998). Bayesian inference can therefore be used to communicate uncertainty in a language that is intuitively understood by scientists, decision-makers and resource users, with different levels of technical appreciation. This should lead to greater understanding of environmental problems across all interest groups, and facilitate the successful transformation of scientific advice into environmental policy and practices (Meffe and Viederman, 1995; Weeks and Packard, 1997)

Bayesian inference is increasingly being used to incorporate sparse data into model-based assessments of complex issues such as fisheries (Punt and Hilborn, 1997; McAllister and Kirkwood, 1998), where intense political and international scrutiny requires that rigorous statistical inference be used to communicate uncertainty to managers. Similar requirements have led to the use of Bayesian inference in both the scientific study and management of marine mammal populations (e.g. Raftery *et al.*, 1995). In this thesis, I further develop Bayesian methods for making inference about marine mammal population size and abundance trends.

In the past, marine mammal populations have primarily been managed for the purpose of sustainable exploitation, for example under the auspices of the International Whaling Commission (Knauss, 1997). However, increasing concerns for the future viability of many populations have now resulted in marine mammals being managed through conservation-oriented environmental policies. Marine mammal populations are now protected under the EU Habitats Directive within the European Union (Council of the European Communities, 1992), and by the Marine Mammal Protection Act for species occurring in U.S. waters (Read and Wade, 2000). Under these policies, information on the status of marine mammal populations is required to determine the need for conservation or management action, and to assess the subsequent success of such action. Knowledge of population size and trends in abundance are clearly key components of these status assessments. For example, the U.S. Marine Mammal Protection Act requires stock assessments for every stock of marine mammal that occurs in U.S. waters. Estimates of population size and rates of change are central to these assessments, allowing calculations of the potential biological removal level (PBR) used to manage human-caused mortality such as fisheries by-catch (Wade 1998; Read and Wade, 2000; Taylor *et al.*, 2000). Similarly, where populations are protected under the EU Habitats Directive, status assessments will form a key part of the monitoring programs established for Special Areas of Conservation (SAC). These results must be incorporated into a formal report that member states will make to the EU every six years, categorising the condition of the population of interest as either favourable or unfavourable and, if unfavourable, determining whether it is declining, recovering or showing no change.

However, due to the inherent difficulties of studying highly mobile animals in the marine environment, population size and trends are generally not directly observable for marine mammals. As an alternative, these population parameters must be estimated from sample data using statistical models. The past two decades have seen major breakthroughs in the collection and analysis of such sample data. For example, for cetaceans (whales, dolphins and porpoises) this has often involved the application of mark-recapture models to photo-identification data to produce estimates of population size (e.g. Hammond *et al.*, 1990) and trends (e.g. Whitehead *et al.*, 1997), or the use of distance sampling methods (e.g. Buckland *et al.*, 1993) to estimate abundance in a given area. Even where populations can be assessed during predictable annual migrations, counts must be corrected for missed animals using statistical procedures (e.g. Zeh, 1999). For pinnipeds (seals, sea-lions and walruses) that spend at least some time hauled-out on shore, population assessment has generally used counts at haul-outs to estimate population size (e.g. Thompson *et al.*, 1997) or to provide an index of population size for assessing trends (e.g. Calkins *et al.*, 1999; Frost *et al.*, 1999). Similarly, for sirenians (dugongs and manatees) population assessment has been based on the statistical analysis of counts of individuals at aggregation sites (e.g. Craig *et al.*, 1997).

Despite the development of successful field-based sampling techniques, the expense and practical research constraints of studying marine mammals often leave biologists and managers with the problem of drawing inference from sparse data. In the majority of cases, quantitative information on abundance trends is simply not available (Read and Wade, 2000). Where data do exist, sample sizes are often small, and estimates are extremely uncertain. For example, small sample sizes of photo-identification data often result in high uncertainty in cetacean abundance estimates (Hammond, 1987), and there is consequently limited power for detecting significant trends in population estimates using conventional statistical methods (Gerrodette, 1987; Thompson *et al.*, 2000). Therefore, it is increasingly recognised that the conventional methods for abundance estimation and comparison of a series of abundance estimates are less than adequate.

In recent years, Bayesian methods have emerged as an alternative approach for statistical inference in such applications. Notably, Wade (1997) used Bayesian methods in an assessment of the population dynamics of gray whales (*Eschrictius robustus*), and Wade (1999) demonstrated the general utility of Bayesian methods for fitting population models to abundance data, using data for spotted dolphins (*Stenella attenuata*). These analyses demonstrated how the Bayesian approach of modelling uncertainty through probability distributions can facilitate practical population assessment. Specifically, an assessment of abundance trends can be based on analysis of Bayesian full probability distributions, and inference can be made in the form of direct probability statements that are not constrained by conventional notions of statistical significance. The graphical and easy-to-interpret probabilistic displays of parameter uncertainty that these studies present provide a persuasive argument for the use of Bayesian methods for population assessment. This thesis builds upon these principles.

Thesis synopsis

This thesis presents modern Bayesian approaches for making inference about marine mammal population size and abundance trends. I specifically focus on making inferences from photographic identification studies of cetaceans, particularly whales and dolphins, using mark-recapture techniques. The thesis is written as four distinct, but related, papers (Chapters 3 to 6), presenting case studies that build upon existing long-term projects. These papers are related by the common theme that many aspects of the underlying data are uncertain. I develop and apply Bayesian methods for an explicit and robust treatment of this uncertainty, with each paper treating different aspects of uncertainty.

By means of an introduction to the Bayesian methods applied in these papers, Chapter 2 introduces the Bayesian statistical paradigm as a suitable framework for model-based data analysis in the face of unavoidable uncertainty. This introduction begins by contrasting the Bayesian philosophy with the more widely used frequentist statistical approach, proceeds by elaborating on the fundamental advantages offered by Bayesian methods, and finally describes the recent computational advances that have made the these methods more accessible to ecologists.

Chapter 3 demonstrates how these modern Bayesian methods can be implemented using the freely available WinBUGS software. This chapter presents a general Bayesian framework for testing hypotheses about population dynamics, with application to assessing the evidence for density dependence in the growth of a killer whale (*Orcinus orca*) population using a 25-year time series of population size data.

This killer whale data set is highly unusual (and probably unique) for cetaceans, in that the population can be fully enumerated on an annual basis, therefore precluding the need for statistical estimation of population size. It is therefore a useful data set for this demonstration, because population models can be fitted to data with no observation error. However, this is not generally the case, and the rest of the thesis focuses on the more typical situation where abundance, and uncertainty about abundance, must be inferred from sample data using statistical models.

Chapters 4 and 5 present two different Bayesian modelling approaches for estimating dolphin population size from photo-identification sample data. These analyses address two common issues in photographic mark-recapture studies of cetaceans: first, the difficulty of adequately sampling across the full extent of mobile populations; and second, the need to model variability in individual detectability. Two different Bayesian solutions are presented for these problems, both using model-averaging methods to estimate a full distribution for population size that incorporates uncertainty from both sparse data and model selection choices. These methods provide general frameworks that may facilitate other studies, and also result in useful inference in the specific case studies presented. Specifically, in Chapter 4, I provide a full Bayesian probability distribution for the population size of bottlenose dolphins (*Tursiops truncatus*) inhabiting Little Bahama Bank in the NE Bahamas. This estimate provides a most likely value and bounds for population size, which will facilitate management decisions by the Government of the Bahamas. In Chapter 5, I produce two estimates, eight years apart, of population size for bottlenose dolphins around the coast of NE Scotland. Direct comparison of these two probability distributions for successive population sizes allows a previous prediction of a population decline (Sanders-Reed *et al.*, 1999) to be tested, and provides an updated report on the status of the dolphin population using the Moray Firth SAC.

The analysis and communication of uncertainty that these methods provide is pragmatic when making inference from sparse data. However, this explicit treatment of uncertainty may also constrain the identification of changes in abundance and conservation needs. As a solution to this problem, in Chapter 6 I introduce a method of model-supervised smoothing to borrow strength across a time series of abundance estimates. Specifically, by tying repeated estimates together through an assumed random effects model, I demonstrate how it is possible to obtain more precise estimates of abundance. The method also allows an estimate of the annual rate of population change in the form of a probability distribution that communicates the remaining uncertainty associated with this estimate of abundance trend. This method is applied to a 10-year photo-identification data set to monitor bottlenose dolphin abundance trends within the Moray Firth SAC.

This Bayesian approach of borrowing strength is intuitively attractive. However, pooling over years may introduce some bias through shrinkage towards the assumed random effects model. This focuses attention on the choice of model for the assumed random effect variability between repeated abundance estimates, and necessitates the testing of alternative model forms. Therefore, in Chapter 6, I also present a framework for fitting alternative models to repeated abundance estimates, and I introduce a Bayesian approach for selecting between (and averaging over) candidate models. Specifically, I assess whether the abundance of dolphins within the Moray Firth SAC has changed either at a constant rate, or alternatively through abrupt shifts. I model abrupt non-linearity through the use of step functions in change-point models, to assess both the timing and magnitude of possible shifts.

However, in addition to selecting the most appropriate model for smoothing the abundance estimates, I also show how Bayesian model averaging allows this smoothing to reflect a compromise between the candidate models.

Each of these case studies has been developed to inform current management issues. Individually, the chapters provide opportunities to better incorporate the data from previous and ongoing research to address management issues of importance both in the UK and overseas. Together, they develop generalised approaches for the application of Bayesian methods to marine mammal population data, and the wider field of wildlife population assessment. In the General Discussion (Chapter 7), I highlight some of the fundamental principals that have emerged in these case studies, and I suggest computational advances that may lead to the more widespread application of Bayesian analysis to environmental data. Finally, I describe the potential for extending these approaches to develop more transparent frameworks for integrating varied sources of environmental data to facilitate the management of natural resources.

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CHAPTER 2

AN INTRODUCTION TO BAYESIAN DATA ANALYSIS

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CHAPTER TWO

An introduction to Bayesian data analysis

2.1. BACKGROUND

Effective use of environmental data places great demands on our methods of data analysis and inference (Ludwig *et al.*, 2001). The most commonly used approach is to fit models to the data, and then to make inferences by estimating the parameters of the models (Hilborn and Mangel, 1997). However, model parameters will not be estimated precisely, and two main sources of uncertainty will intervene in the process of model-based data analysis. Firstly, sample data may be sparse and consequently there will be uncertainty associated with estimates of model parameters; and secondly, the specific model structure itself will be uncertain (Buckland *et al.*, 1997). Explicit recognition of this uncertainty is essential, particularly where models are to be used to provide advice for resource management (e.g. Hilborn *et al.*, 1993).

Producing estimates of model parameters and associated statements of uncertainty involves statistical procedures and is known as statistical inference. Statistical inference most commonly takes a parametric form, where probability theory is used to model the data generating mechanism (i.e. relate the data to the parameters) in what is known as the *likelihood function*. However, there are differing views as to how the likelihood function should be interpreted. A major division occurs between the proponents of the conventional or frequentist statistical method (e.g. Dennis, 1996), and those advocating the use of Bayesian statistical approaches for ecological data analysis (e.g. Ellison 1996; Durban *et al.*, 2000). This chapter provides an overview of the practical (rather than philosophical) issues that make the Bayesian statistical paradigm a suitable framework for inference in model-based analysis of ecological data. It begins by briefly contrasting the Bayesian philosophy with the more widely used frequentist approach, proceeds by elaborating on the fundamental advantages offered by Bayesian methods, and finally describes the recent computational advances that have made the these methods more accessible to ecologists.

2.2. STATISTICAL PHILOSOPHIES

Inference about model parameters

Suppose we have data x, and a collection of unknowns θ ($=\theta_1 \ldots \theta_n$), about which we want to make inferences. These unknowns might be model parameters, missing data, or events which we did not observe directly (latent variables). The commonest approach to this inference problem is through parametric statistical inference, where probability models are used for the data-generating mechanism to specify a *likelihood function*, which quantifies the probability of observing the data x given the values of the model parameters θ:

$$p(x \mid \theta)$$

The frequentist philosophy is to treat the parameter values as fixed but unknown and ascribe all of the randomness to the data. Parameters are estimated by maximising the likelihood, with confidence intervals being obtained by a mathematical consideration of what other data could have been drawn and finding functions of these data with the correct coverage probabilities. In complex situations where the