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978-0-521-70271-3 - Introduction to Conservation Genetics: Second Edition

Richard Frankham, Jonathan D. Ballou, David A. Briscoe and Karina H. McInnes

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## Introduction to Conservation Genetics, Second edition

This established author team brings the wealth of advances in conservation genetics into the new edition of this introductory text, including new chapters on Population Genomics and Genetic Issues in Introduced and Invasive Species. They continue the focussed learning features for students – main points in the margin, chapter summaries, strong support with the math, and further reading – and now guide the reader to software and databases. Many new references reflect the expansion of this field. With examples from mammals, birds, reptiles, fish, amphibians, plants and invertebrates, this is an ideal introduction to conservation genetics for a broad audience. The text tackles the quantitative aspects of conservation genetics, and has a host of features to support students learning the numerical side of the subject. Combined with being up to date, its user-friendly writing style and an elegant illustration program make this a robust teaching package.

Emeritus Professor DICK FRANKHAM holds honorary appointments at Macquarie University, James Cook University and The Australian Museum and was Hrdy Visiting Professor at Harvard University in 2004. He began his career in quantitative genetics, achieving international recognition for his work on *Drosophila* before turning to conservation genetics in the early 1990s. He has made many significant contributions to the field via modelling problems in *Drosophila*, meta-analyses and computer simulations. He is a major figure in the discipline and was awarded a D.Sc. by Macquarie University in 2006 for his scientific contributions to conservation and evolutionary genetics.

Dr JON BALLOU is Population Manager and Research Scientist at the Smithsonian Institution's National Zoological Park in Washington, DC, USA and for 2003–2006 was Head of its Department of Conservation Biology. He is also an adjunct member of the Faculty of the University of Maryland. His research has focused on the genetic and demographic problems confronted by small populations, especially of threatened species. He is recognized as a leader in developing the theoretical basis for the genetic management of small populations and in developing population management tools (software, applied theory) that are widely and internationally used by wildlife and zoo managers.

Professor DAVID BRISCOE retired in 2009 after 34 years at the Department of Biological Sciences, Macquarie University, Sydney, Australia where he was Head of Department 2006–2009. He collaborated with Dick Frankham on *Drosophila* research for 34 years, as well as working on the evolutionary genetics of rock wallabies, lizards, velvet worms, social insects and slime moulds. An outstanding communicator, his inspirational teaching enthuses students at all levels and reaches beyond the academic sphere through television appearances and popular books.

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# Introduction to Conservation Genetics

Second Edition

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## Preface to the second edition

Much has changed since we began the first edition of *Introduction to Conservation Genetics* 10 years ago. The human population has exceeded 6.6 billion, with consequent increased pressure on the natural world. The number of threatened species has increased by 55% to 16 306. Over the same time, global climate change has moved from being a somewhat abstract concern to perhaps the pre-eminent global political focus. The impact of climate change is now clearly discernable on the distribution and behaviour of many species. Sea-level increases are impacting on the viability of low-lying nations and the biota they contain. On a smaller scale, three-quarters of species of bears are now considered to be in danger and the Yangtze River dolphin (referred to in the first edition) has become extinct. Further, invasive species are having an ever more important impact on biodiversity, especially with rapidly increasing trade.

While our objectives in preparing this book are fundamentally those that motivated the first edition, accelerating human impacts bring into even sharper focus the need to integrate genetics into the broader conservation effort.

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## Preface

The World Conservation Union (IUCN), the leading international conservation body, recognizes the crucial need to conserve genetic diversity as one of the three fundamental levels of biodiversity. This book provides the conceptual background for understanding the role of genetic factors in extinction and managing to avoid such extinctions.

Conservation genetics encompasses:

- genetic management of small populations to maximize retention of genetic diversity and minimize inbreeding,
- resolution of taxonomic uncertainties and delineation of management units, and
- the use of molecular genetic analyses in forensics and to understand species' biology.

### Purpose of the book

We have endeavoured to make this book appealing to a wide readership. However it is primarily directed towards those encountering the discipline for the first time, either through formal coursework or by self-instruction.

Conservation genetics is a relatively young discipline. While it is founded on more than a century of advances in evolutionary genetics, including population and quantitative genetics and plant and animal breeding, it has developed its own unique attributes, specialist journals, etc. In particular, conservation genetics focuses strongly on processes within small and fragmented populations and on practical approaches to minimize deleterious effects within them. It has implications for organizations and individuals with very different immediate concerns. These include zoo staff undertaking captive breeding programs, wildlife and fisheries biologists and ecologists, planners and managers of National Parks, reserves, water catchments and local government natural areas, foresters and farmers. Perhaps of most importance to the future, conservation genetics is of concern to a growing body of undergraduate and postgraduate students, on whom will fall much of the onus of implementing practical measures. Their enthusiasm was a major stimulus to our preparing this volume.

To make *Introduction to Conservation Genetics* accessible to this broad array of readers, we have placed emphasis on general principles, rather than on detailed experimental procedures which can be found in specialist books, journals and conference proceedings. Further, considerable attention has been devoted to clarity of presentation. We have assumed a basic knowledge of Mendelian genetics and basic statistics. Readers requiring a simpler version are referred to our *A Primer of Conservation Genetics*. Conservation genetics is a quantitative discipline as much of its strength lies in its predictions. However, we

Conservation genetics is the use of genetics to aid in the conservation of populations or species

This book is intended to provide an accessible introduction to conservation genetics with an emphasis on general principles

have restricted use of mathematics to simple algebra to make it accessible to a wide audience.

The material is suitable for a full tertiary course on Conservation Genetics. Further, it provides evolutionary geneticists and evolutionary ecologists with conservation examples to enthuse their students. Finally, we have endeavored to create an easily accessible and formalized reference book for both professional conservation geneticists and a wider readership.

### Précis of contents

**Chapter 1** provides an overview of the contemporary conservation context and the reasons why genetic theory and information are crucial in the management of endangered species. **Chapter 2** explores the central issue in the application of genetics to conservation biology, the relation of genetic factors to extinction risk. Inbreeding reduces reproductive capability and survival, and thereby increases extinction risk in the short term, while loss of genetic diversity reduces the long-term capacity of species to evolve in response to environmental changes.

We have divided the book into three subsequent sections: **Section I** describes the evolutionary genetics of natural populations, **Section II** explores the genetic consequences of reduced population size and **Section III** focuses on applications of genetic principles to management of threatened species in wild, semi-wild and captive situations. The relationships of genetics with broader issues in conservation biology conclude this section.

Section I (Chapters 3–10) covers essential background material in evolutionary genetics. **Chapter 3** deals with the extent of genetic diversity and methods for measuring it. Special attention is paid to comparisons of genetic diversity in threatened versus non-threatened species. **Chapters 4** and **5** describe methods and parameters used to characterize genetic diversity. As major genetic concerns in conservation biology are centred on reproduction and survival, we have placed considerable emphasis on quantitative (continuously varying) characters, as reproductive fitness is such a character (**Chapter 5**). Molecular measures of genetic diversity, for which vast data sets have accumulated, have a disturbingly limited ability to predict quantitative genetic variation. The paramount importance placed on the functional significance of genetic diversity distinguishes conservation genetics from the related field of molecular ecology, where selectively neutral variation is frequently favoured. **Chapters 6** and **7** introduce factors affecting the amount and evolution of genetic diversity in large populations. The same processes in small populations are detailed in **Chapter 8**. Chance (stochastic) effects have a much greater impact on the fate of genetic diversity in small, endangered populations than in very large populations, where natural selection has far greater influence. Since conservation genetics focuses on retention of evolutionary potential, **Chapter 9** examines the maintenance of genetic diversity. **Chapter 10** on population genomics (new to the

This book provides a broad coverage of all strands of conservation genetics



second edition) presents important insights into genome evolution that have been revealed by whole genome sequencing and studies of gene expression using RNA expression microarrays, and considers the relevance of these new technologies to conservation management.

Having established the basic principles, Section II concentrates on the genetic implications of population size reduction, loss of genetic diversity (**Chapter 11**), the deleterious consequences of inbreeding on reproduction and survival (inbreeding depression) (**Chapters 12 and 13**) and the genetic effects of population fragmentation (**Chapter 14**). The section concludes with consideration of the population size required to maintain genetically viable populations (**Chapter 15**).

Section III explores practical issues, genetic resolution of taxonomic uncertainties and delineation of management units (**Chapter 16**), the genetic management of wild populations (**Chapter 17**), genetic issues relating to invasive species and their control (**Chapter 18**, new to the second edition), genetic management of captive populations (**Chapter 19**) and reintroduction (**Chapter 20**). **Chapter 21** addresses the use of molecular genetic analyses in forensics and resolution of cryptic aspects of species biology. **Chapter 22** expands to a broader picture, the integration of demographic, ecological and genetic factors in conservation biology. In particular, we explore the concepts of population viability analysis (PVA) using computer simulations. The final component, **Take home messages** presents a brief summary of the contents of the book, followed by a **Glossary**.

*Introduction to Conservation Genetics* concentrates on naturally outbreeding species of plants and animals, with lesser attention to self-fertilizing plants. Microbes receive limited coverage, as little conservation effort has been directed towards them.

We have used examples from threatened species wherever possible. However, most conceptual issues in conservation genetics have been resolved using laboratory and domesticated animals, non-threatened but related species, or by combined analyses of data sets (typically small) from many species (meta-analyses). Endangered species typically have low numbers and are often slow breeders, and it is imprudent to risk losing them through experimentation.

### Changes in the second edition

Since we began the first edition 10 years ago, there have been major changes to the discipline, both to threat status and to the underlying science. The number of threatened species has increased overall, the most spectacular increase being the 15-fold increase in threatened amphibians, due primarily to a fungal disease and global warming. As a consequence of global climate change, many species will need to move to remain in their favoured climatic envelope and may need to be translocated for this to happen. There has been steady progress in most areas of conservation genetics, but population genomics has arisen since the first edition. Further, invasive species have an

The second edition has been extensively updated and revised to encompass the major advances in conservation genetics since we wrote the first edition, but the general format has been retained

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increasing role as threatening agents and research on them has expanded dramatically. Overall, the field of conservation genetics has developed rapidly, as judged by number of journal papers, number of courses and new methodologies. Further, the sources of information have diversified with the rapid rise of databases and websites. Software tools for statistical analyses and computer simulations have also proliferated.

We have been heartened by the favourable reception to the first edition both as a textbook and as a professional reference book. We have preserved the main organization in this second edition, but updated the content and references throughout and added two new chapters. New topics include material on population genomics, the implications of genomics to conservation genetics, a box on meta-analysis, landscape genetics, proposals for DNA-based taxonomy, DNA barcoding, decline in haplo-diploids due to loss of genetic diversity at the sex locus, the Jurassic Park scenario, the impact of transgenics and genetic issues in invasive species. We have also expanded the coverage of adaptive changes in response to global climate change. The number of references has expanded by 48% in line with the expansion of the field and over half of the references are new to this edition. We have added references to software packages, important websites and databases, as they are now widely available and extensively used. The index has been improved by doubling the number of entries and by using italic numbers for tables and bold ones for figures and illustrations. In spite of the new material, the overall length is similar to that of the first edition. This has been achieved by streamlining the presentation and by omitting a few topics of lesser importance.

### Format

Extensive effort has been made to motivate readers by making the book attractive, interesting, informative and easy to follow

The book is profusely illustrated to make it visually attractive and to tap the emotional commitment that many feel to conservation. To highlight significant points and make it easy to review, the **main points** of each chapter are given in a box at the start of the chapter along with **Terms** used in the chapter. A **Summary** is given at the end of each chapter. Within chapters, the **main points** of each section are highlighted in small boxes. Much of the information is presented in figures (~220), as we find that biology students respond better to those than to information in text or tables. For some figures, the message is highlighted in italics in the caption. Numerous examples and case studies have been used to illustrate the application of theory to real-world conservation applications. These have been chosen to be motivating and informative to our audience. Case studies are given in **boxes** throughout the book. Boxes are also used to provide additional information in a way that does not impede the flow of information for those who wish to skip such detail.

We are deeply indebted to Karina McInnes, whose elegant drawings add immeasurably to our words. She has drawn 20 new illustrations for the second edition and new illustrations drawn for the *Primer* are also used.

The revision of the textbook has been aided by comments from several cohorts of students at Macquarie University and from many colleagues and students throughout the world. We thank these people for their contributions.

The order of topics throughout the book, and within chapters, is based on our teaching experience. We have chosen to introduce practical conservation issues as early as possible, with the details of parameter estimation etc. provided later. We hope that readers will find it more stimulating to appreciate *why* a parameter is important, before understanding *how* it is derived. As an example, Chapter 2 directly addresses the relationship between genetics and extinction, and provides an overview of much of the later material, prior to a detailed treatment of inbreeding in Chapters 12 and 13.

In presenting material, we have aimed for a balance between that necessary for student lectures, and a comprehensive coverage for advanced students and conservation professionals. The material in each chapter is more than adequate for a single lecture, allowing instructors to choose what they wish to emphasize in their course, but the material in each chapter should not prove overwhelming to students. Some topics are too extensive for a single lecture. We have therefore divided evolution in large populations into two chapters. Chapters are designed to be comprehensible on a 'stand-alone' basis, so there is some repetition of material, but this is reduced compared to the first edition.

Everyone who has taught genetics recognizes that mastery of the discipline comes through active participation in problem-solving, rather than passive absorption of 'facts'. Consequently, worked **Examples** are given within the text for most equations presented. **Problem** questions are posed at the end of each chapter, together with **Revision problems** at the end of the book. Problem answers are given on the Cambridge University Press website [www.cambridge.org/9780521702713](http://www.cambridge.org/9780521702713).

Named species are used in many problem questions, to make them more realistic. These are usually fictitious problems, but reflect situations similar to those that have, or reasonably might have, occurred in the named species. Real data are referenced where used.

**Practical exercises** are suggested at the end of chapters covering topics where laboratory exercises are relevant. Most of these have been trialled in our own teaching and are frequently computer exercises, using readily available software.

References are given to reviews and recent papers, these being sufficient to gain access to the most significant literature. Space does not permit direct reference to many other excellent studies by our colleagues. An annotated **General bibliography**, relevant to many chapters, is given at the end of Chapter 1. Readers seeking further detail on specific topics will find an annotated list of suggested **Further reading** at the end of each chapter. We have also included a sprinkling of books written for popular audiences to provide an introduction to some of the, often controversial, characters involved in conservation biology, and the passions that motivate their work.

The order of topics both within and across chapters has been designed to motivate students

Each chapter has been designed to provide instructors with material suitable for one lecture, along with additional information for independent study

Worked examples and problems with solutions are provided

Practical exercises are suggested for several chapters

For clarity and brevity, referencing is mainly restricted to reviews and recent papers

Referencing and data presentation are more extensive for contentious topics.

As most of the principles of conservation genetics apply equally to different eukaryotic species, we primarily use common names in the text. Genus and species names in the **index** are cross-referenced to common names.

### Controversies

The development of conservation genetics has been driven by what many consider to be a global environmental crisis – ‘the sixth extinction’. As a consequence, many other dimensions, economic, political, social, ethical and emotional, impact upon the field. The fate of species, populations and habitats are in the balance. We have flagged these controversies and attempted to provide a balanced, up-to-date view, based upon information available in late 2007. Where feasible, we have consulted experts to corroborate facts and interpretations. Inevitably, some readers will disagree with some of our views, but we trust that they will accept that alternative interpretations are honestly given. New data may alter perspectives and some such changes have occurred since the first edition.

We hope that readers find the book as stimulating to read as we found it to write, but not as tiring! Feedback, constructive criticism and suggestions will be appreciated (email: [dick.frankham@mq.edu.au](mailto:dick.frankham@mq.edu.au)).

We maintain a website with updated information, corrections, etc. at <http://www.cambridge.org/9780521702713>.

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