Fred W. Allendorf, Gordon Luikart and Sally N. Aitken

### Second Edition

# Conservation and the Genetics of Populations

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CONSERVATION AND The genetics of Populations

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## CONSERVATION AND The genetics of Populations

### Second Edition

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#### **R.H. Blyth**

This second edition is an updated and expanded version of our book published in 2007. The need for applying genetics to problems in conservation has continued to increase. In addition, many important technological and conceptual developments have changed the field of conservation genetics over the least five years. We have added new chapters on climate change and on genetic effects of harvest (e.g., hunting and fishing), and have extensively revised all other chapters. In an effect to restrict the size of this new edition, we have moved the end of the chapter questions to the book's website. A new edition is needed to keep pace with the changes, to remain a useful overview and synthesis, and to help advance the field. Nearly one-third of the over 1800 references in this book were published after the first edition.

We are excited to have added Sally Aitken as a coauthor. Sally was a reviewer of our first edition for Wiley-Blackwell. Sally's review and suggested changes were so helpful that she should have been an author of that edition!

As we said in the Preface of the first edition, this book is not an argument for the importance of genetics in conservation. Rather, it is designed to provide the reader with the appropriate background and conceptual understanding to apply genetics to problems in conservation. The primary current causes of extinction are anthropogenic changes that affect ecological characteristics of populations (habitat loss, fragmentation, introduced species, etc.). However, genetic information and principles can be invaluable in developing conservation plans for species threatened with such effects. Phil Hedrick (2007) suggested in his review of the first edition that we should have made more of a sales pitch for the successes of conservation genetics, rather than our very even-handed approach. We do not agree. We are advocates for conservation, not genetics.

We have strived for a balance between theory, empirical data, and statistical analysis in this text. Empirical population genetics depends upon this balance (see Figure i.1). The effort to measure and understand the evolutionary significance of genetic variation in natural populations began with the rediscovery of Mendel's principles in the early 1900s. For many years, empirical observation of genetic variation lagged far behind the development of sophisticated theory by some of the greatest minds of the twentieth century (e.g., J.B.S. Haldane, R.A. Fisher, and Sewall Wright). Today it is relatively easy to obtain and analyze enormous amounts of information on genetic variation (e.g., markers or genome sequences) in any species.

There are a wide variety of computer programs available to analyze data and estimate parameters of interest. However, the ease of collecting and analyzing data has led to an unfortunate and potentially dangerous reduction in the emphasis on understanding theory in the training of population and conservation geneticists. Understanding theory remains crucial for correctly interpreting outputs from computer programs and statistical analyses. For example, the most powerful software programs that estimate important parameters, such as effective population size (Chapter 7) and gametic disequilibrium (Chapter 10), are not useful if their assumptions and limitations are not understood. We are still disturbed when we read statements in the literature that the loci studied are not linked because they are not in linkage (gametic) disequilibrium.

The tools being used by molecular population geneticists are changing rapidly. Deciding which techniques



**Figure i.1** The application of population genetics to understand genetic variation in natural populations relies upon a balance of understanding the appropriate theory, collecting appropriate data, and understanding its analysis.

to include in Chapter 4 was difficult. We have added new genomics (and other 'omics') information and still include some techniques that are no longer in use (e.g., minisatellites) because they are crucial for understanding previous literature. On the other hand, we have not included older techniques that are now known to provide data that are not reliable (e.g., RAPDs).

#### ACKNOWLEDGMENTS

We would like to thank again everyone acknowledged in the Preface to the previous edition of this book. FWA thanks the Hatfield Marine Science Center and the Hawai'i Institute of Marine Biology for hosting his extended visits to work on this edition. Chapter 18 is based partially on work supported by the US National

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#### DEDICATION

We dedicate this book to James F. Crow, who died just before his 96<sup>th</sup> birthday as we were putting the finishing touches on this book. Jim was a great scientist and wonderful human being whose contributions were enormous. We were honored that he agreed to write a Guest Box for the Statistical Appendix. Over the years, we always appreciated Jim's clear and useful reviews of our papers when they were sent to him. FWA got to know Jim in the last few years while his daughter was attending graduate school in Madison. My most vivid memory of talking with Jim in his tiny office was finding Sewall Wright's National Medal of Science haphazardly placed on a filing cabinet behind the office door.

12 February 2012

Fred W. Allendorf Gordon Luikart Sally N. Aitken The many beings are numberless; I vow to save them all.

#### **Traditional Zen vow**

The one process now going on that will take millions of years to correct is the loss of genetic and species diversity by the destruction of natural habitats. This is the folly our descendants are least likely to forgive us.

#### Edward O. Wilson, 1984

This book is about applying the concepts and tools of genetics to problems in conservation. Our guiding principle in writing has been to provide the conceptual basis for understanding the genetics of biological problems in conservation. We have not attempted to review the extensive and ever growing literature in this area. Rather we have tried to explain the underlying concepts and to provide enough clear examples and key citations for further consideration. We also have strived to provide enough background so that students can read and understand the primary literature.

Our primary intended audience is broadly trained biologists who are interested in understanding the principles of conservation genetics and applying them to a wide range of particular issues in conservation. This includes advanced undergraduate and graduate students in biological sciences or resource management, as well as biologists working in conservation biology for management agencies. The treatment is intermediate and requires a basic understanding of ecology and genetics.

This book is not an argument for the importance of genetics in conservation. Rather, it is designed to provide the reader with the appropriate background to determine how genetic information may be useful in any specific case. The primary current causes of extinction are anthropogenic changes that affect ecological characteristics of populations (habitat loss, fragmentation, introduced species, etc.). However, genetic information and principles can be invaluable in developing conservation plans for species threatened with such effects.

The usefulness of genetic tools and concepts in conservation of biological diversity is continually expanding as new molecular technologies, statistical methods, and computer programs are being developed at an increasing rate. Conservation genetics and molecular ecology are under explosive growth, and this growth is likely to continue for the foreseeable future. Indeed we have recently entered the age of genomics. New laboratory and computational technologies for generating and analyzing molecular genetic data are emerging at a rapid pace.

There are several excellent texts in population genetics available (e.g., Hedrick 2005, Hartl and Clark 1997, Halliburton 2004). Those texts concentrate on questions related to the central focus of population and evolutionary genetics, which is to understand the processes and mechanisms by which evolutionary changes occur. There is substantial overlap between those texts and this book. However, the theme underlying this book is the application of an understanding of the genetics of natural populations to conservation.

We have endeavored to present a balanced view of theory and data. The first four chapters (Part I) provide an overview of the study of genetic variation in natural populations of plants and animals. The middle eight chapters (Part II) provide the basic principles of population genetics theory with an emphasis on concepts especially relevant for problems in conservation. The final eight chapters (Part III) synthesize these principles and apply them to a variety of topics in conservation.

We emphasize the interpretation and understanding of genetic data to answer biological questions in