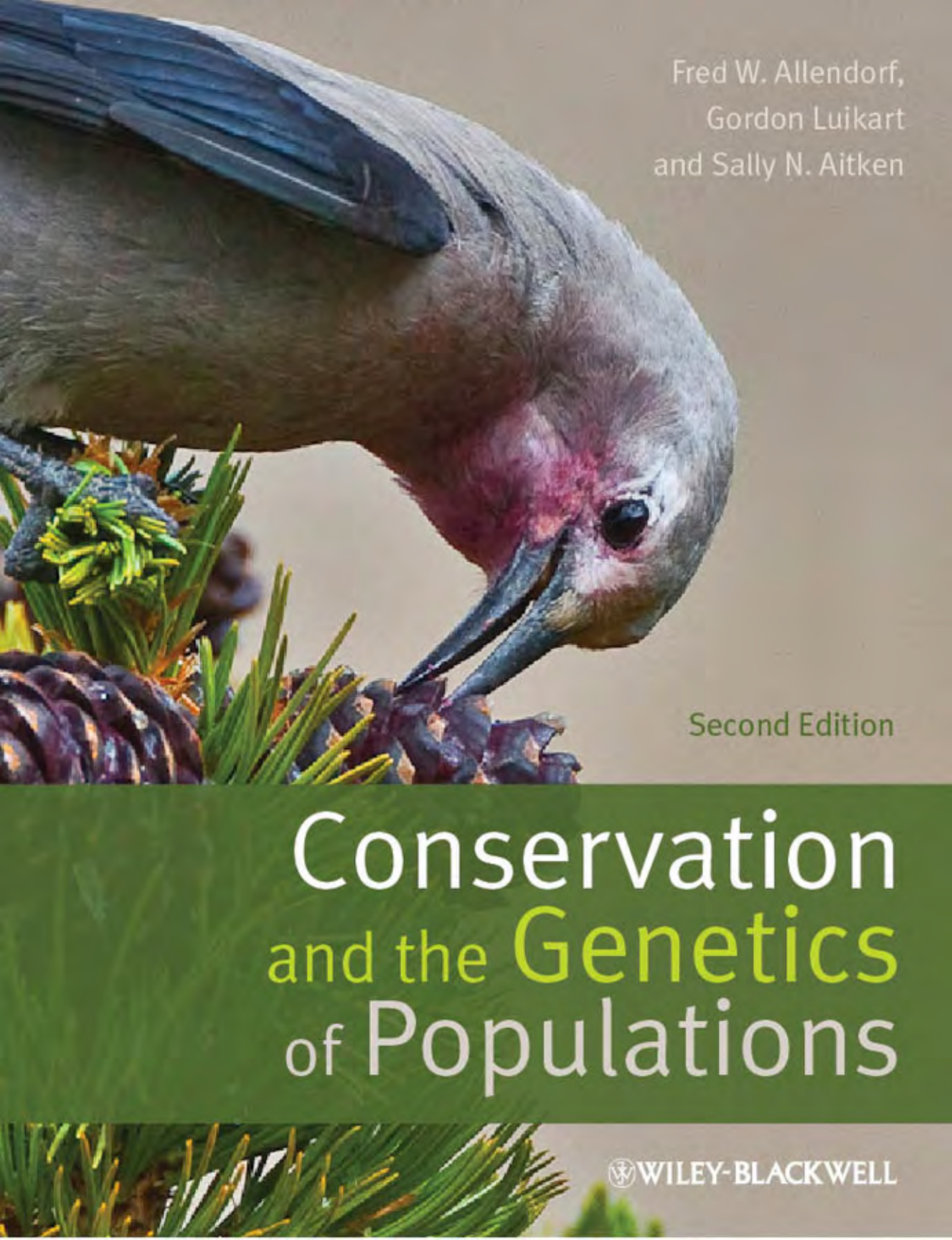

Fred W. Allendorf,
Gordon Luikart
and Sally N. Aitken

Second Edition

Conservation and the Genetics of Populations

WILEY-BLACKWELL

CONSERVATION AND THE GENETICS OF POPULATIONS

Companion website

This book has a companion website at:

www.wiley.com/go/allendorf/populations

with additional resources

CONSERVATION AND THE GENETICS OF POPULATIONS

Second Edition

Fred W. Allendorf
Division of Biological Sciences, University of Montana, Missoula, MT 59812, USA

Gordon Luikart
Flathead Lake Biological Station, University of Montana, Polson, MT 59860, USA

Sally N. Aitken
Department of Forest Sciences, University of British Columbia, Vancouver, British Columbia, Canada V6T 1Z4

With illustrations by Agostinho Antunes

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111 River Street, Hoboken, NJ 07030-5774, USA

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Cover image: © Lee Rentz Photography. Clark's nutcracker feeding on whitebark pine. Whitebark pine seeds are a crucial food resource for many animal species (e.g., Clark's nutcracker and grizzly bears). Whitebark pine currently are threatened by an introduced pathogen (Chapter 20 Invasive Species) and by climate change (Chapter 21 Climate Change).

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Guest Box authors

C. Scott Baker, Marine Mammal Institute and Department of Fisheries and Wildlife, Oregon State University, Newport, Oregon, USA (scott.baker@oregonstate.edu). Chapter 22.

Louis Bernatchez, Département de biologie, Université Laval, Quebec, Canada (Louis.Bernatchez@bio.ulaval.ca). Chapter 4.

David Coates, Department of Environment and Conservation, Western Australia, Australia (Dave.Coates@dec.wa.gov.au). Chapter 16.

David W. Coltman, Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada (dcoltman@ualberta.ca). Chapter 11.

William A. Cresko, Institute of Ecology and Evolution, Department of Biology, University of Oregon, Eugene, Oregon, USA (wcresko@uoregon.edu). Chapter 8.

James F. Crow, Laboratory of Genetics, University of Wisconsin, Madison, Wisconsin, USA. Appendix (1916–2012).

Chris J. Foote, Fisheries and Aquaculture Department, Malaspina University College, Nainamo, British Columbia, Canada (Chris.Foote@viu.ca). Chapter 2.

Steven J. Franks, Department of Biology, Fordham University, Bronx, New York, USA (franks@fordham.edu). Chapter 21.

Birgita D. Hansen, Arthur Rylah Institute for Environmental Research, Department of Sustainability and Environment, Victoria, Australia (birgita.hansen@dse.vic.gov.au). Chapter 5.

Paul A. Hohenlohe, Institute for Bioinformatics and Evolutionary Studies, University of Idaho, Moscow, Idaho, USA (hohenlohe@uidaho.edu). Chapter 8.

Menna E. Jones, School of Zoology, University of Tasmania, Hobart, Tasmania, Australia (Menna.Jones@utas.edu.au). Chapter 6.

Lukas F. Keller, Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Switzerland (lukas.keller@ieu.uzh.ch). Chapter 13.

Robert C. Lacy, Department of Conservation Science, Chicago Zoological Society, Brookfield, Illinois, USA (rlacy@ix.netcom.com). Chapter 19.

Guðrún Marteinsdóttir, Institute of Biology, University of Iceland, Sturlugata, Iceland (runam@hi.is). Chapter 18.

Craig R. Miller, Departments of Mathematics and Biological Sciences, University of Idaho, Moscow, Idaho, USA (crmiller@uidaho.edu). Chapter 7.

L. Scott Mills, Wildlife Biology Program, University of Montana, Missoula, Montana, USA (lscott.mills@umontana.edu). Chapter 1.

B.G. Murray, School of Biological Sciences, University of Auckland, Auckland, New Zealand (b.murray@auckland.ac.nz). Chapter 14.

Michael W. Nachman, Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona, USA (nachman@u.arizona.edu). Chapter 12.

M. Pickup, Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, Ontario, Canada (melinda.pickup@utoronto.ca). Chapter 14.

Loren H. Rieseberg, University of British Columbia, Department of Botany, Vancouver, British Columbia, Canada, and Indiana University, Department of Biology, Bloomington, Indiana, USA (lriesebe@mail.ubc.ca). Chapter 17.

Michael K. Schwartz, Rocky Mountain Research Station, US Forest Service, Missoula, Montana, USA (mkschwartz@fs.fed.us). Chapter 9.

Richard Shine, School of Biological Sciences, University of Sydney, New South Wales, Australia (rick.shine@sydney.edu.au). Chapter 20.

Michael E. Soulé, 212 Colorado Ave, Paonia, Colorado, USA (msoule36@gmail.com). Chapter 1.

Paul Sunnucks, School of Biological Sciences and Australian Centre for Biodiversity, Monash University, Victoria, Australia (Paul.Sunnucks@monash.edu). Chapter 5.

Jody M. Tucker, Sequoia National Forest, US Forest Service, Porterville, California, USA, and Wildlife Biology Program, University of Montana, Missoula, Montana, USA (jtucker@fs.fed.us). Chapter 9.

Elaina M. Tuttle, Department of Biology, Indiana State University, Terre Haute, Indiana, USA (elaina.tuttle@indstate.edu). Chapter 3.

Robert C. Vrijenhoek, Monterey Bay Aquarium Research Institute, Moss Landing, California, USA (vrijen@mbari.org). Chapter 15.

Lisette P. Waits, Fish and Wildlife Sciences, University of Idaho, Moscow, Idaho, USA (lwaits@uidaho.edu). Chapter 7.

Robin S. Waples, Northwest Fisheries Science Center, Seattle, Washington, USA (Robin.Waples@noaa.gov). Chapter 10.

Andrew Young, Centre for Plant Biodiversity Research, CSIRO Plant Industry, Canberra, Australian Capital Territory, Australia (andrew.young@csiro.au). Chapter 14.

Preface to the second edition

Truth is a creation, not a discovery.

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

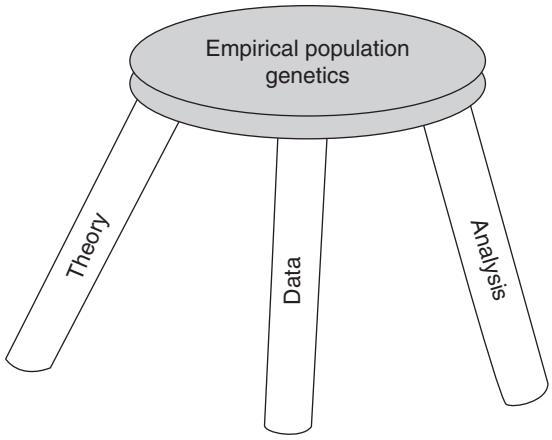

Figure i.1 The application of population genetics to understand genetic variation in natural populations relies upon a balance of understanding the appropriate theory, collecting appropriate data, and understanding its analysis.

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 Science Foundation, Grant DEB 074218 to FWA and GL. In addition, we give special thanks to the Minitab Corporation for providing software through their Author Assistance Program, Paul Sunnucks for his many helpful comments on the previous edition, Nils Ryman for help with the Appendix, and Ian Jamieson for help with Table 13.1. In addition, we thank the many colleagues who have helped us by providing comments, information, unpublished data, and answers to questions associated with this edition: Steve Amish, Peter Beerli, Kurt Benirschke, Des Cooper, Rob Cowie, Kirsten Dale, Pam Diggle, Suzanne Edmands, Zac Forsman, Ned Friedman, Oscar Gaggiotti Roxanne Haverkort, Paul Hohenlohe, Marty Kardos, Meng-Hua Li, Ian MacLachlan, Sierra McLane, Juha Merilä, Gordon Orians, Barb Taylor, Mark Tanaka, Dave Towns, C. Susannah Tysor, and Sam Yeaman.

DEDICATION

We dedicate this book to James F. Crow, who died just before his 96th 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

Preface to the first edition

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