Introduction to Population Biology

How do plant and animal populations change genetically to evolve and adapt to their local environments? How do populations grow and interact with one another through competition and predation? How does behaviour influence ecology and evolution? This second edition of Dick Neal's unique textbook on population biology addresses these questions and offers a comprehensive analysis of evolutionary theory in the areas of ecology, population genetics and behaviour. Taking a quantitative and Darwinian perspective, Neal uses mathematical models to develop the basic theory of population processes.

Key features to this edition include new chapters on inbreeding and species interactions and community structure, a modified structure in Part II, more recent empirical examples to illustrate the application of theoretical models to the world around us and end-of-chapter problems to help students with self-assessment. A series of spreadsheet simulations has also been conveniently located online for students to further improve their understanding of such models.

Dick Neal is Professor Emeritus at the University of Saskatchewan, Canada, having taught undergraduate ecology for almost 40 years. His thesis on Uganda rodents was conducted at the Nuffield Unit of Tropical Ecology in Uganda, and he continued this research on the breeding of African rodents with sabbaticals in National Parks in Kenya (1974–5) and Zimbabwe (1987–8, 1990). Other research areas have included the impacts of uranium mine effluent on aquatic ecosystems, effects on the structure and function of plankton communities, and the bioremediation of contaminated pits.

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PREFACE

WHY I WROTE THIS BOOK

In 1979, I developed an introductory semester course on population biology because I had been inspired by three books: Wilson and Bossert's (1971) *A Primer of Population Biology*, Emlen's (1973) *Ecology: An Evolutionary Approach* and Wilson's (1975) *Sociobiology*. Each of these texts used an evolutionary perspective to synthesize such areas as population ecology, population genetics and behavioural ecology, an approach that my students and I found both intellectually stimulating and exciting.

Over the next two decades, I became increasingly frustrated in my attempts to find an appropriate text for my course. There were excellent texts on evolution, ecology, population genetics and behaviour, and some included two of these areas, but none covered the breadth of material that I taught in my course. Consequently, I wrote a draft copy of a book for my course during a sabbatical in 1998–9, and then tried it out in my class for the following 2 years. The student feedback was both encouraging and enlightening, and was a great help when I revised it and submitted it for publication in 2002. The first edition was published in 2004 by Cambridge University Press.

OBJECTIVES OF THE BOOK

The book was designed for second- or third-year students seeking a broad introduction to population biology. Beginning with a historical account of how Darwin developed his evolutionary theories, particularly natural selection, the book uses this as an underlying theme to introduce some basic principles in three main areas: population ecology (basic population growth models including matrix models, and the evolution of life histories), population genetics and some aspects of behavioural ecology (evolution of altruism, limitation of aggressive behaviour, sexual selection and mating systems). Students require a background in Mendelian genetics, algebra and calculus, although the latter is not essential.

The book provides a brief historical perspective of the various subject areas to show how our understanding has developed, and continues to develop, over time. In addition, most areas are treated quantitatively, developing mathematical models in a step-by-step manner that students can follow and understand. This is augmented by providing spreadsheet instructions in Excel for most of the basic equations, so that students can explore the outcomes or predictions of the various models and see how they may change when the variables are modified. In addition,

there are many worked examples in the text to show how the equations are applied to biological questions, and students can test their understanding by answering the problems at the end of many of the chapters. Their solutions are detailed at the end of the book. Finally, each chapter ends with a series of empirical examples to illustrate how our mathematical models apply to the world around us.

WHAT IS DIFFERENT IN THIS SECOND EDITION

Organization of the Book

The second edition is similar in structure to the first edition, but I have made three significant changes.

New Chapters

There are two new chapters in the second edition: one on inbreeding (Chapter 12) and an entirely new chapter (Chapter 20), which investigates how different interactions between species (competition, predation, herbivory, parasitism and various mutualisms) can influence the structure of communities. The subject of inbreeding was part of the chapter on genetic drift in the first edition, but has now been expanded and includes the consequences of inbreeding in populations.

Unified Coverage for Growth Models of Single Populations

In response to suggestions by some instructors who used the first edition, the exponential and logistic growth models in Part II and the life tables, demographic growth models and review of life histories in Part IV of the first edition have been combined into Part II in the second edition, which now contains five chapters.

Simulations Moved Online

In the first edition, eight chapters had appendices with instructions to format spreadsheets to simulate the outcomes of various population models. These are now conveniently gathered on a website that can be accessed at www.cambridge.org/IPB. More simulations have been added, particularly where data from the literature has been analysed. For example, Olaus Murie's (1944) data for the life table of Dall mountain sheep has been completely reanalysed so that the life tables for data collected at two different time periods can be compared for the first time.

The website also includes the figures (some in colour) and tables from the text that can be downloaded for PowerPoint presentations by both students and instructors.

More Empirical Examples Throughout the Text

Much of the text has been rewritten to include more empirical examples, many of them recent, to illustrate the application of theoretical models to the world around us. Two examples illustrate some of this new material. First, the topic of epigenetics, where gene expression is modified in response to the environment, is introduced in Chapter 3 and then expanded in Chapter 8 to show how it may influence the rate of senescence, and finally Chapter 16 demonstrates how it may influence the success rate of small new immigrant populations. Secondly, in Chapter 20 we explore how the ecological niches of populations may evolve over time, and use the magnificent research of Peter and Rosemary Grant (2014) on how the beak size of the medium ground finch (*Geospiza fortis*) has changed over a 40-year period.

Making Space for the New Material

To include all the new examples, I needed to streamline some of the material from the first edition. The transfer of the appendices in eight of the chapters to the new website helped, and I also reduced the amount of biographical information in Part I (Darwin and natural selection) by approximately 25 per cent, as students should already understand what led Darwin to seriously consider the subject of transmutation.

The purpose of the new edition remains unchanged from the first edition: a one-semester course for upper-level students that provides an up-to-date survey of some of the major areas of population biology. It will be difficult to cover all areas of the book in that time, but will allow instructors to pick and choose to some extent, concentrating on various topics and either omitting or briefly reviewing others according to their particular interests and objectives. I sincerely hope that instructors and students alike share my interest and enthusiasm for this area of biology.

ACKNOWLEDGEMENTS

First and foremost, I wish to thank my wife, Jenny, for her help, support, encouragement and endless patience throughout the 8 years it has taken me to develop and write this book. My time of disappearing upstairs to the back bedroom, which has become my office over the past 11 years and where I worked on my book, is drawing to an end.

I am particularly grateful for the constant support and guidance of Cambridge University Press. So many people have helped me over the years, but I will name only six. My Commissioning Editor, Dominic Lewis, was very supportive and understanding during the early years when I was struggling. I went through a series of Content Managers until Jenny van der Meijden took over the task in the seventh year and skillfully guided me through the steps required to transform my numerous files into a form required for submission. Somehow she made it enjoyable. Then I was passed on to the Development Team of Lisa Pinto and Melissa Shivers, who led me through a series of other tasks, including the dreaded Marketing Questionnaire. They had a light touch and a delightful sense of humour as we worked together on the various tasks. I even began to think I could go into marketing. The one task I eventually refused to do personally was the request for permissions; I was appalled by how the process had changed since writing the first edition of this book. Fortunately, Lisa put me in contact with Diane Kraut of DK Research Inc. to complete this task and I hired her immediately. She was superbly organized and efficient, and to my surprise was inexpensive. Finally, it is important to have a fresh pair of eyes to carefully edit the book. Cambridge University Press hired Jane Hoyle to do this task and I am eternally grateful. I soon lost count of the number of errors that she spotted and improvements that she made as we worked on the book. However, I am responsible for any errors that may remain. In conclusion, the thing that impressed me about all of the above is that we worked together and I felt a very real connection to them. They are like old friends and I have confidence in their judgement.

I retired from academic life 4 years before starting to work on this book. Of course, like almost all retired professors, I retained a connection with the Department of Biology and valued the interest of my former colleagues. In particular, I wish to thank Phil McLoughlin for reading the 15th draft of Chapter 8 that I had been working on for over a year. His sage advice helped break the logjam that had bedevilled me for over a year, particularly with the theory of the evolution of senescence. As a result, I was able to complete the final 15 chapters of the book in just over 2 years.

I am indebted to individuals who have given permission to use their figures: Mr D. W. Miller (Figure 1.1) who also provided a digital copy so that it could be modified, Dr Lawrence Cook

(Figure 15.1) and Vanessa Bourhis (Figure 19.12), who was a former student in my population biology class. My son, Tim Neal, developed all of the figures in the first three chapters. Marlynn Mierau, the graphics technician in the Department of Biology, copied figures from various publishers, and improved my hand-drawn line drawings and photographs to make them suitable for my book. Their technical help was invaluable.