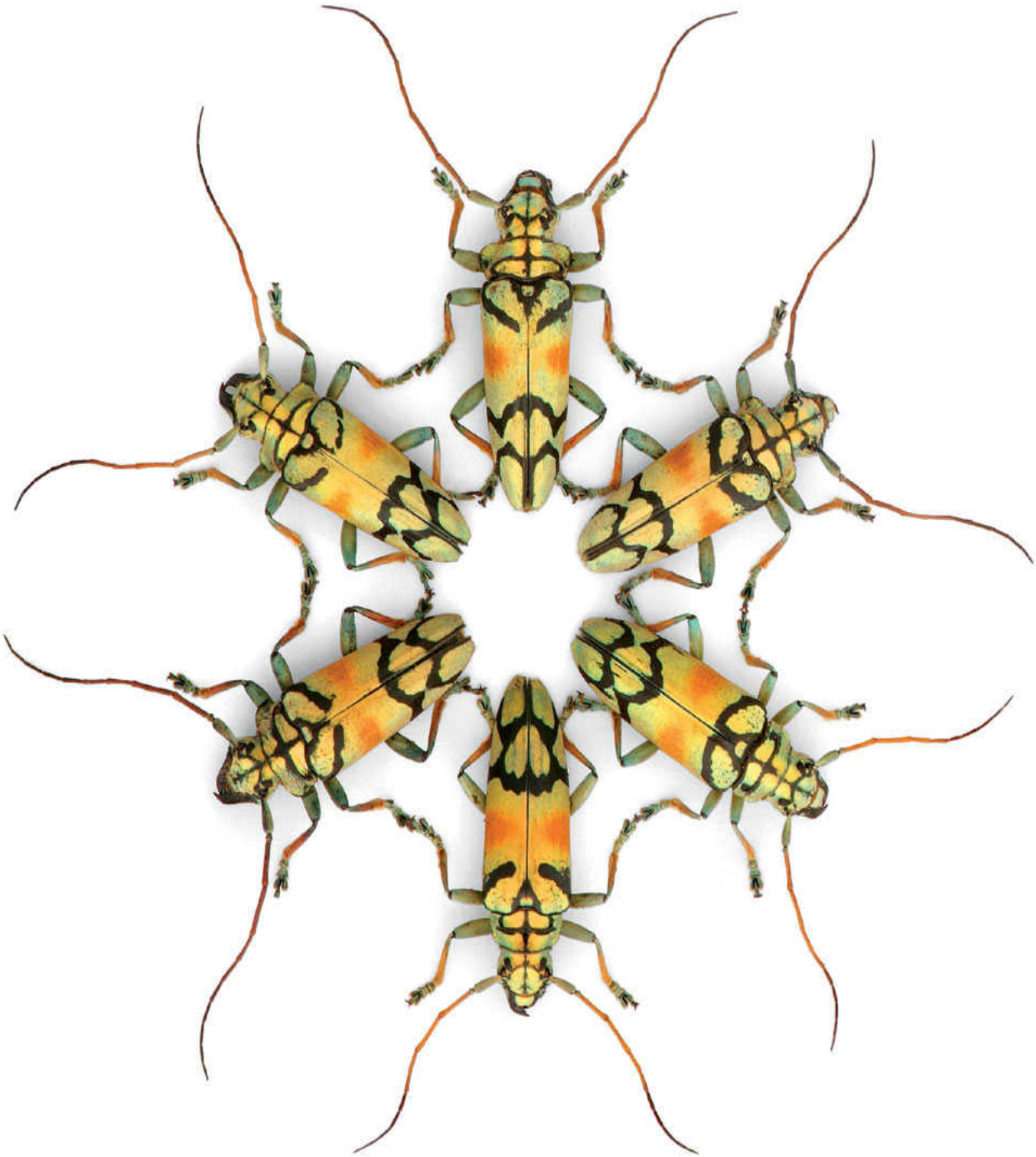

The Analysis of Biological Data

WHITLOCK · SCHLUTER

THIRD EDITION

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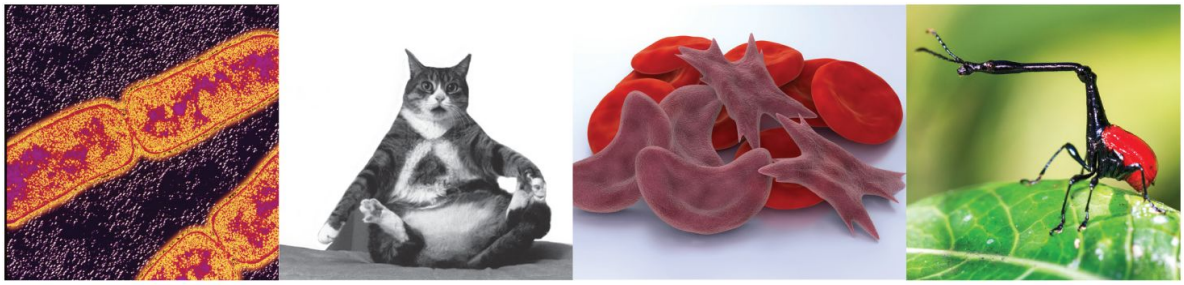

Description

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The Analysis of Biological Data

Third Edition

Michael C. Whitlock and Dolph Schluter

macmillan learning

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Library of Congress Control Number:
2019948174

ISBN-13: 978-1-319-22629-9 (epub)

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In 1946, William Freeman founded W. H. Freeman and Company and published Linus Pauling's General Chemistry, which revolutionized the chemistry curriculum and established the prototype for a Freeman text. W. H. Freeman quickly became a publishing house where leading researchers can make significant contributions to mathematics and science. In 1996, W. H. Freeman joined Macmillan and we have since proudly continued the legacy of providing revolutionary, quality educational tools for teaching and learning in STEM.

To Sally and Wilson, Andrea and Maggie

Contents in brief

Contents

Preface

Modern biologists need the powerful tools of data analysis. As a result, an increasing number of universities offer, or even require, a basic data analysis course for all their biology and premedical students. We have been teaching such a course at the University of British Columbia for the last three decades. Over this period, we have sought a textbook that covered the material we needed in an introductory course at just the right level. We found that most texts were too technical and encyclopedic, or else they didn't go far enough, missing methods that were crucial to the practice of modern biology and medicine. We wanted a book that had a strong emphasis on intuitive understanding to convey meaning, rather than an overreliance on formulas. We wanted to teach by example, and the examples needed to be interesting. Most importantly, we needed a biology book, addressing topics important to biologists and health care providers handling real data.

We couldn't find the book that we needed, so we decided to write this one to fill the gap. We include several unusual features that we have discovered to be helpful for effectively reaching our audience:

Interesting biology examples and exercise sets.

Our teaching has shown us that biology students learn data analysis best in the context of interesting examples drawn from the medical and biological literature. Statistics is a means to an end, a tool to learn about the human and natural world. By emphasizing what we

can learn about the science, the power and value of statistics becomes plain. Plus, it's just more fun for everyone concerned.

Every chapter has several biological or medical examples of key concepts, and each example is prefaced by a substantial description of the biological setting. The examples are illustrated with photos of the real organisms, so that students can look at what they're learning about. The emphasis on real and interesting examples carries into the problem sets; each chapter has many questions based on real data about biological and medical issues. These include Calculation Practice Problems that take the student step-by-step through the important procedures described in the chapter. Two or three such problems are at the start of most of the chapter problem sets. We include three sections of review problems (after Chapters 9, 13, and 17) to allow cumulative review of the important concepts up to that point in the book. In this third edition, we have added dozens of new problems.

Intuitive explanations of key concepts.

Statistical reasoning requires a lot of new ways of thinking. Students can get lost in the barrage of new jargon and multitudinous tests. We have found that starting from an intuitive foundation, away from all the details, is extremely valuable. We take an intuitive approach to basic questions: What's a good sample? What's a confidence interval? Why do an experiment? The first several chapters establish this basic knowledge, and the rest of the book builds on it.

Practical data analysis.

As its title suggests, this book focuses on data rather than the mathematical foundations of statistics. We teach how to make good graphical displays, and we emphasize that a good graph is the beginning point of any good data analysis. We give equal time to estimation and hypothesis testing, and we avoid treating the P-value P-value as an end in itself. The book does not demand a knowledge of mathematics beyond simple algebra. We focus on practicality over nuance, on biological usefulness over theoretical hand wringing. We not only teach the "right" way of doing something but also highlight some of the pitfalls that might be encountered.

We demonstrate how to carry out the calculations for most methods so that the steps are not mysterious to students. At the same time, we know that a computer will be available for most calculations. Hence, we focus on the concepts of biological data analysis and how statistics can help extract scientific insight from data. With the power of modern computers at hand, the challenge in analyzing data becomes knowing what method to use and why.[1] We imagine and hope that every course using this book will have a component encouraging students to use computer statistical packages. The diversity of such packages is immense, and so we have not tied the book to any particular program. Nevertheless, many biologists and users of this book analyze data with the R statistical computing package. Accordingly, we provide R scripts for all the examples in this book at the book's web site (whitlockschluter3e.zoology.ubc.ca). This site also includes a series of self-guided labs to teach students

the basics of using R at a reasonable pace, and in an order that matches the presentation of the concepts in the book.

Practical experimental design.

A biologist cannot do good statistics—or good science—without a practical understanding of experimental design. Unlike most books, our book covers basic topics in experimental design, such as controls, randomization, pseudoreplication, and blocking, and we do it in a practical, intuitive way.

Coverage of modern topics.

Modern biology uses a larger toolkit than the one available a generation ago. In this book, we go beyond most introductory books by establishing the conceptual principles of important topics such as likelihood, non-linear regression, permutation tests, survival analysis, and the bootstrap.

Useful summaries.

Near the end of each chapter is a short, clear summary of the key concepts, and most chapters end with Quick Formula Summaries that put most equations in one easy-to-find place.

Interleaves.

Between chapters are short essays that we call interleaves. These interleaves cover a variety of conceptual topics in a nontechnical way—ideas that are nevertheless crucial for the interpretation of statistical results in scientific research. Several of them focus on

common mistakes in the analysis and interpretation of biological data and how to avoid them. Although the interleaves are pressed between the chapters, they complement the material in the core chapters in important ways. We believe that the interleaves discuss some of the most important topics of the book, such as the difference between correlation and causation (Interleaf 1), the meaning of statistical significance (Interleaf 3), why control treatments are necessary (Interleaf 6), and the distortions caused by publication bias (Interleaf 10). Interleaf 7 summarizes what statistical test should be used and when, and it is a good place to start when reviewing for exams.

We think *The Analysis of Biological Data* provides a good background in data analysis for biologists and medical practitioners, covering a broad range of topics in a practical and intuitive way. It works for our classes; we hope that it works for yours, too.

Organization of the book

The Analysis of Biological Data is divided into five parts, each with a handful of chapters as indicated in the table of contents. We recommend starting with the first part, because it introduces many basic concepts that are used throughout the book, such as sampling, drawing a good graph, describing data, estimating, hypothesis testing, and concepts in probability. These early chapters are meant to be read in their entirety.

After the first block, most chapters progress from the most general topics at the start to more specialized topics by the end. Each chapter

is structured so that a basic understanding of the topic may be obtained from the earliest sections. For example, in the chapter on analysis of variance (Chapter 15), the basics are taught in the first two sections; reading Sections 15.1 and 15.2 gives roughly the same material that most introductory statistics texts provide about this method. Sections 15.3–15.6 explain additional twists and other interesting applications.

The last block of chapters (Chapters 18–21) is mainly for the adventurous and the curious. These chapters introduce topics, such as likelihood, bootstrapping, and a brand-new chapter on survival analysis (Chapter 21), that are commonly encountered in the biological and medical literature but not often mentioned in an introductory course. These chapters introduce the basic principles of each topic, discuss how the methods work, and point to where you might look to find out more.

A basic course could be taught by using only Chapters 1–17 and, within this subset of chapters, by stopping after Sections 5.8, 7.3, 8.4, 9.4, 12.6, 13.6, 15.2, 16.4, and 17.6 in their respective chapters. We suggest that all courses highlight specific topics covered only in the interleaves.

Each chapter ends with a series of problems that are designed to test students' understanding of the concepts and the practical application of statistics. The problems are divided into Practice Problems and Assignment Problems. Short answers to all Practice Problems and Review Problems are provided in the back of the book; answers to

the Assignment Problems are available to instructors only from the publisher. For a copy, please send an email to DL-WhitlockSchluter3e@macmillan.com. Other teaching resources for the book are available online at whitlockschluter3e.zoology.ubc.ca.

A word about the data

The data used in this book are real, with a few well-marked exceptions. For the most part, these data were obtained directly from published papers. In some cases, we contacted the authors of articles who generously provided the raw data for our use. Often, when raw data were not provided in the original paper, we resorted to obtaining data points by digitizing graphical depictions, such as scatter plots and histograms. Inevitably, the numbers we extracted differ slightly from the original numbers because of measurement error. In rare cases, we generated data by computer that matched the statistical summaries in the paper. In all cases, the results we present are consistent with the conclusions of the original papers. Most of the data sets are available online at whitlockschluter3e.zoology.ubc.ca.

About the authors

Michael Whitlock is an evolutionary biologist and population geneticist. He is a professor of zoology at the University of British Columbia, where he has taught statistics to biology students since 1995. Whitlock is known for his work on the spatial structure of biological populations, genetic drift, and the genetics of adaptation. He has worked with fungus beetles, rhinos, and fruit flies; mathematical theory; and statistical genetics. He is a member of the American Academy of Arts and Sciences and a Fellow of the Royal Society of Canada. He has been editor-in-chief of *The American Naturalist* and on the editorial boards of nine scientific journals.

Dolph Schluter is a professor and Canada Research Chair in the Zoology Department and Biodiversity Research Center at the University of British Columbia. He is known for his research on the ecology and evolution of Galapagos finches and threespine stickleback, and on the evolution of large-scale biodiversity gradients. He is a Fellow of the Royal Societies of Canada and London and a foreign member of the U.S. National Academy of Sciences.

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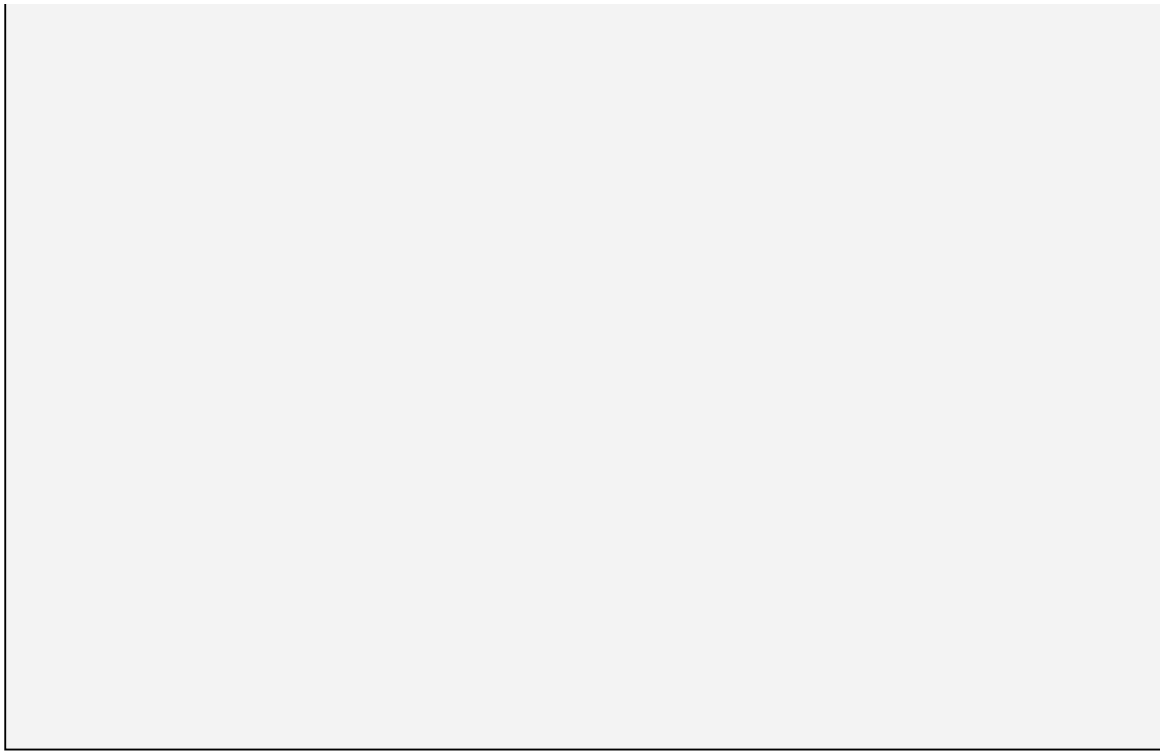


Acknowledgments

This book would not have happened had the two of us had been left to do it by ourselves. Many people contributed in substantial ways, and we are forever grateful. The clarity and accuracy of its contents were improved by the careful attention of a lot of generous readers, including Anwar Ahmad, Arianne Albert, Sulekha Anand, Corey Devin Anderson, Brad Anholt, Cécile Ané, Eric Baack, Mitchell Baker, Brandon Barton, Arthur Berg, Kelly Bodwin, Eline Boghaert, Yaniv Brandvain, Chad Brassil, James Bryant, Martin Buntinas, Mark Butler, Brett C. Byram, Chao Cai, Ashley J.R. Carter, Carrie Case, C. Ray Chandler, Laurel Chiappetta, Mark Clemens, Bradley Cosentino, Erika Crispo, Perry de Valpine, Flo Débarre, Tony Desmond, Eric Dewar, Abby Drake, Christiana Drake, Joseph E. Duchamp, Jonathan Dushoff, K. M. Flanagan, Matthias W. Foellmer, Demba Fofana, Steven George, Aleeza Gerstein, George Gilchrist, Brett Goodwin, Steven Green, B.E. Hagerty, Amanda Hale, Tim Hanson, R.N. Hartnett, Mike Hickerson, Lisa Hines, Eric S. Ho, Heather J. Hoffman, Dominique Ingato, Darren Irwin, Nusrat Jahan, Philip Johns, Roger Johnson, John Kalbfleisch, Istvan Karsai, Karry Kazial, Robert Keen, John Kelly, Rex Kenner, Ben Kerr, Yoon G. Kim, Jamie Kneitel, Laura Kubatko, Joseph G. Kunkel, Terri Lacourse, Robert Laird, Bret Larget, Theo Light, Todd Livdahl, Heather J. Lynch, Rene Malenfant, Mike Marin, Michelle Marvier, Virginia Matzek, Brian C. McCarthy, Kevin Middleton, Eli Minkoff, Robert Montgomerie, Panagis Moschopoulos, Spencer Muse, Courtney Murren, Claudia Neuhauser, Liam O'Brien, Maria Orive, Sally Otto, Iain Pardoe, Elise Pasles, Patrick C. Phillips, Jay

Pitocchelli, Danielle Presgraves, Angelica Pytel, Nathan Rank, Bruce Rannala, Diann Reischman, Mark Rizzardi, James Robinson, Simon Robson, Michael Rosenberg, Noah Rosenberg, Anirudh V. S. Ruhil, Colin Rundel, Michael Russell, Ronald W. Russell, Paul Sajda, Johnny Sellers, Andrew Schaffner, Andrea Schluter, Aimee Schwab-McCoy, James Scott, Ye Shen, Joel Shore, Andrew Skelton, John Soghigian, Drew M. Talley, William Thomas, Andrew Tierman, Michael Travisano, Thomas Valone, Christopher Vitek, Bruce Walsh, Claus Wilke, David H. Wise, Melissa Wuellner, Michael Wunder, Grace A. Wyngaard, George Yanev, Sam Yeaman, and Amanda Zellmer. Many of these good people read multiple chapters, and we thank all for their invaluable aid and considerate forebearance. Sally Otto, Allan Stewart-Oaten, and Maria Orive earned our undying gratitude by reading and commenting on the entire book. Of course, any errors that remain are our own fault; we didn't always take everyone's advice, even perhaps when we should have. If we have forgotten anyone, you have our thanks even if our memories are poor.

We owe a debt to the students of BIOL 300 at the University of British Columbia, who class-tested this book over the last several years. The book also benefited by class testing at several colleges and universities. George Gilchrist and his students gave us a very detailed and extremely helpful set of comments at a crucial stage of the book.

Many students and faculty from UBC and other institutions uncovered errors in earlier versions of the book; we thank them by

name at whitlockschluter3e.zoology.ubc.ca/acknowledgments.html. We send special thanks to Nick Cox, who graciously read a previous printing of this book with extraordinary care.

The book has benefited enormously from the efforts of a large team of able people in the first two editions: John Murdzek, Gunder Hefta, Kathi Townes, Tom Webster, Lori Heckelman, Mark Ong, and Kristina Elliott all helped the book look and feel as nice as it does. We are grateful to the team at Lumina for keeping the standards high. Eric Baack, Holly Kindsvater, and Laura Melissa Guzman all carefully checked answers to the Practice and Assignment Problems. Steven Green pointed out several improvements to the answer key and reviewed the answers to the review problem sets. For this third edition, we are very grateful to the team at Macmillan, who made this edition and the online media resources possible; thanks to Jennifer Edwards (Program Manager), Andrew Dunaway (Program Director), Elizabeth Dziubela (Content Project Manager), Natasha Wolfe (Design Services Manager), Daniel Lauve (Director of Content), Doug Newman (Associate Media Editor), and Justin Jones (Assistant Editor). Our special thanks to Ms. Fabulous, Michele Mangelli, who kept us on schedule and on point. Finally, Ben Roberts has our thanks for all of his support and vision for the first editions of this book and especially Clause 24.

The book was started while MCW was supported by the Peter Wall Institute for Advanced Studies at UBC as a Distinguished-Scholar-in-Residence, and the majority of the final stages of the book were written while he was a Sabbatical Scholar at the National

Evolutionary Synthesis Center in North Carolina (NSF #EF-0423641). DS began working on the book while a visiting professor in Developmental Biology at Stanford University. The second edition was aided by a sabbatical leave at the University of Texas (MCW) and a Canada Council Senior Killam Fellowship (DS), which included a wonderful stay at La Selva Biological Station. The University of British Columbia has been a wonderful academic home through all three editions. The scholarly support and environment provided by each of these institutions were exceptional —and greatly appreciated.

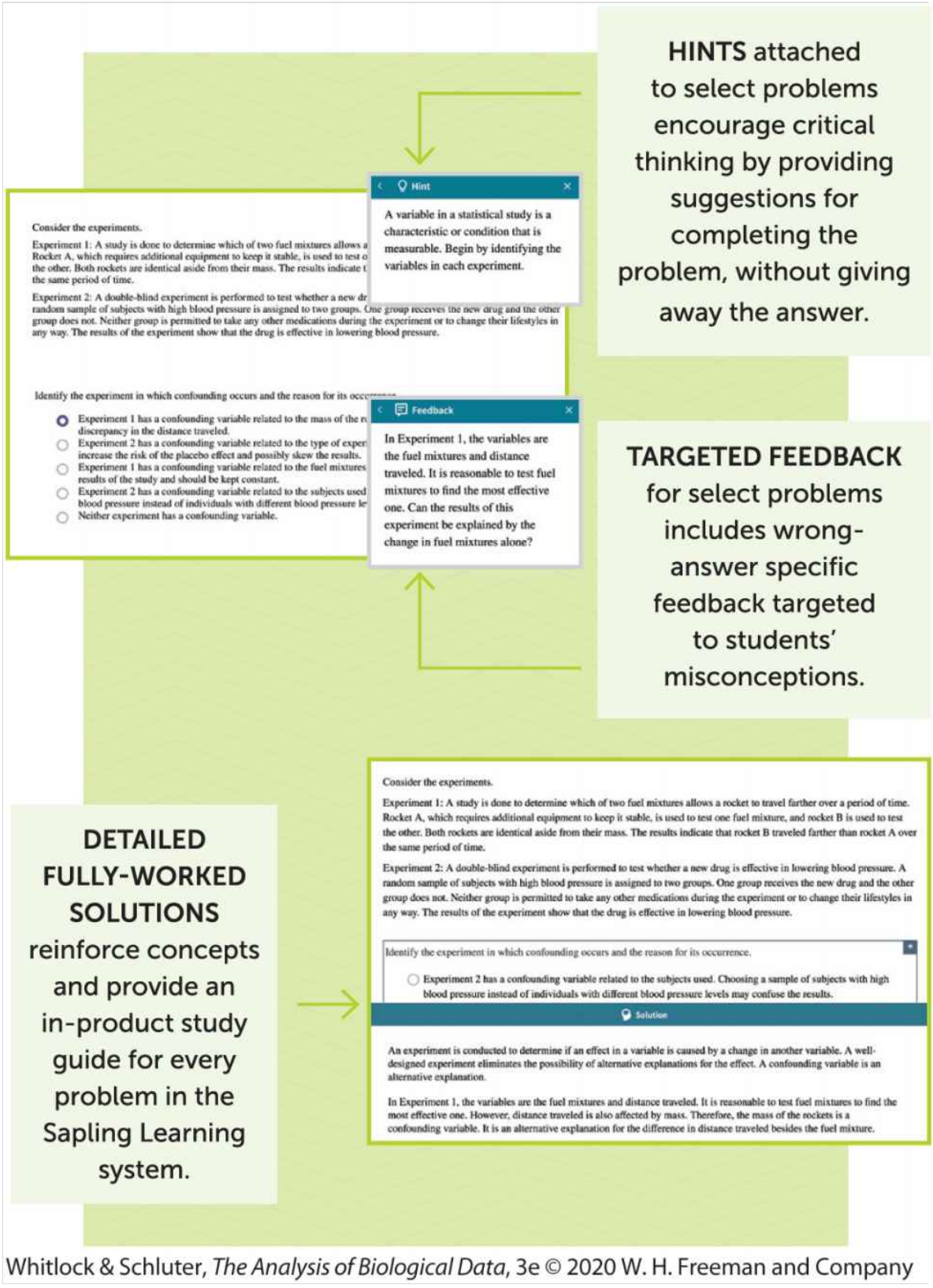
Finally, we would like to give great thanks to all of the people that have taught us the most over the years. MCW would like to thank Dave McCauley, Mike Wade, Nick Barton, Ben Pierce, Kevin Fowler, Patrick Phillips, Sally Otto, and Betty Whitlock. Nancy Heckman and Don Ludwig enlightened DS on many things about data and the theory and practice of statistics.

Statistics: Course Resources

The Analysis of Biological Data, Third Edition, is accompanied by a media and supplements package that facilitates student learning and enhances the teaching experience. Fully loaded with our interactive e-book and all student and instructor resources, **SaplingPlus** is organized around a set of pre-built units available for each chapter.

Formative Assessment

SaplingPlus provides online questions, including select assignment problems, for every chapter and on every important learning objective in the book. For select questions, students' incorrect answers receive error-specific feedback based on common misconceptions about the topics.



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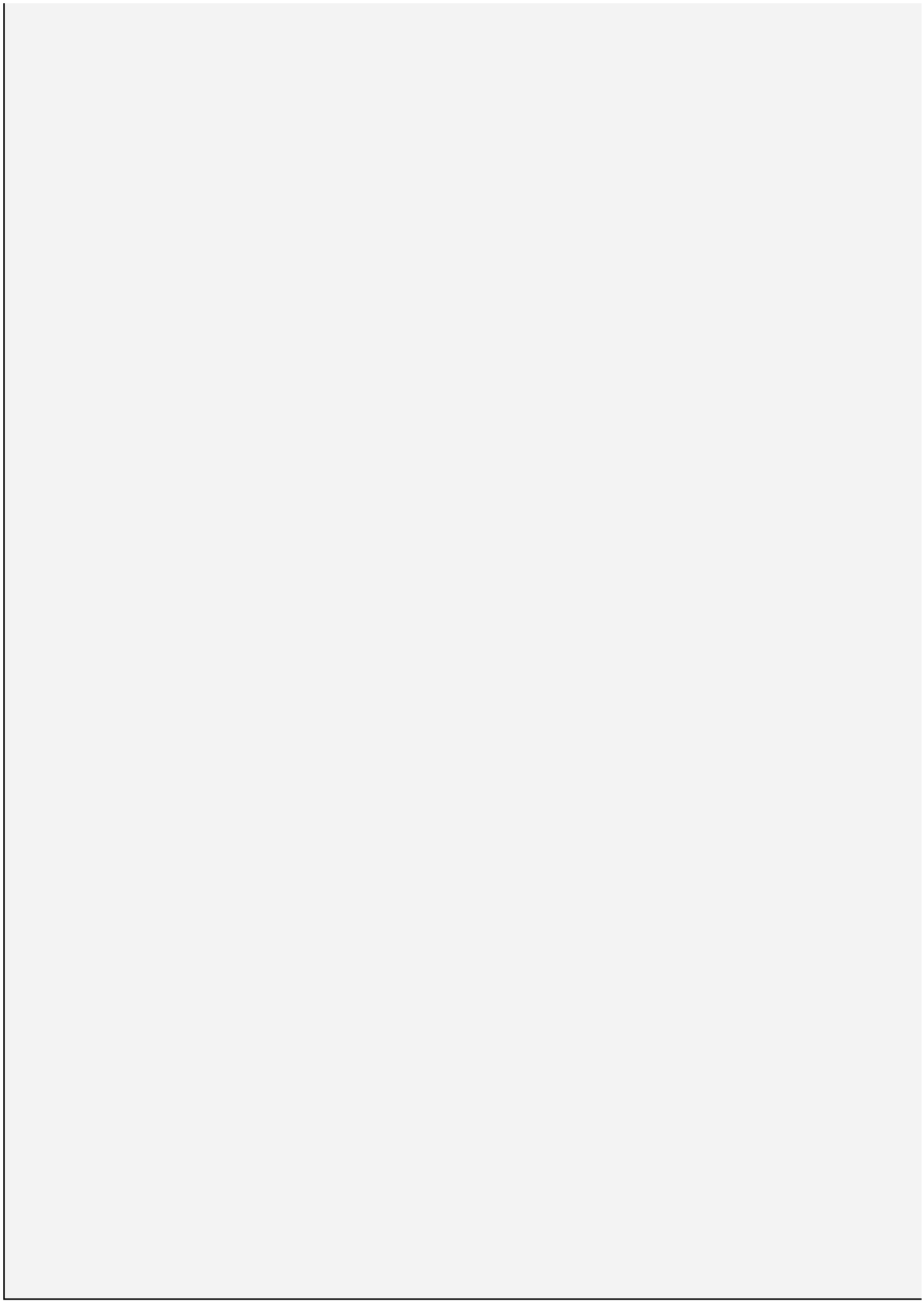
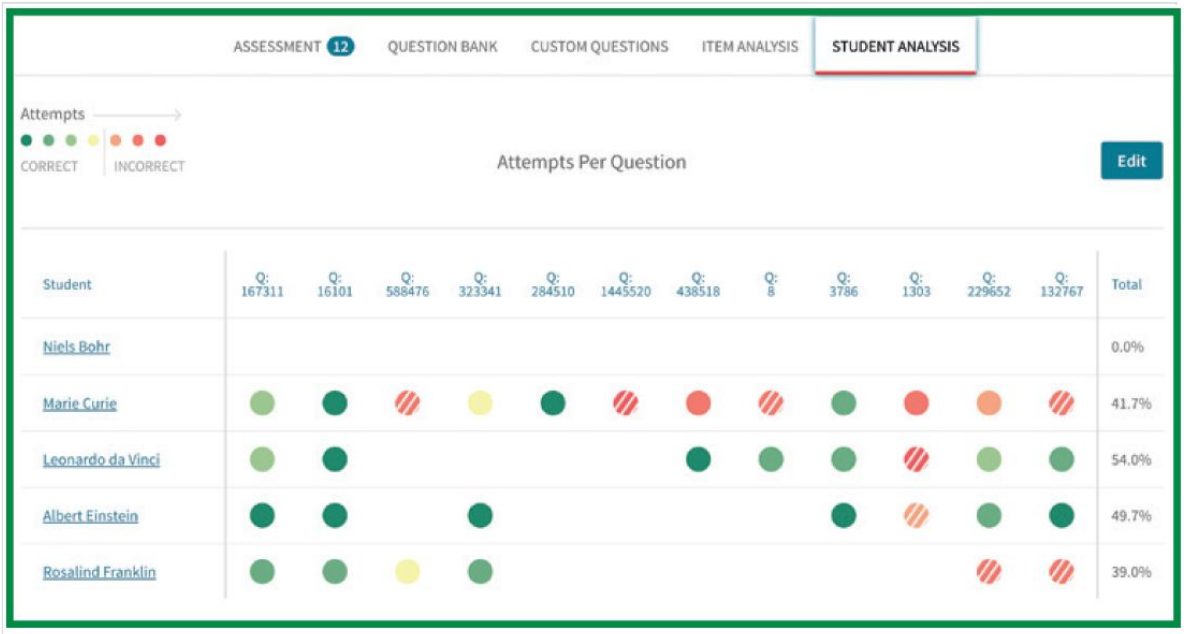


LearningCurve

Put “testing to learn” into action. Based on educational research, **LearningCurve** really works: Game-like quizzing motivates students and adapts to their needs based on their performance. It is the perfect tool to get students to engage before class and review after class. Additional reporting tools and metrics help instructors get a handle on what their class knows and doesn’t know. Available in **SaplingPlus.**

Analytics

Through our heatmap dashboard, instructors can get a quick visual representation of student performance on a given question. Instructors can also evaluate an aggregate view of their class’s performance on a problem.



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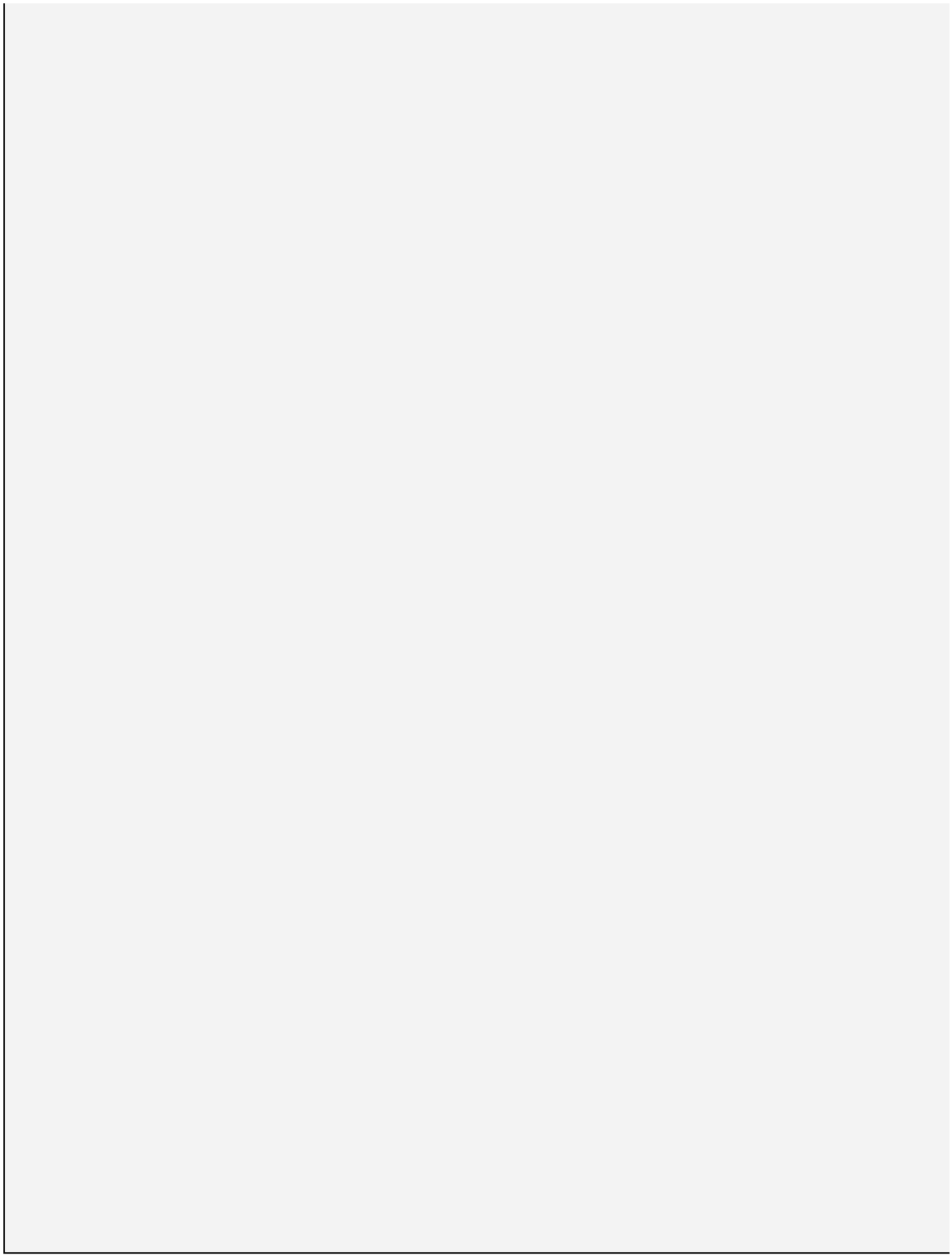


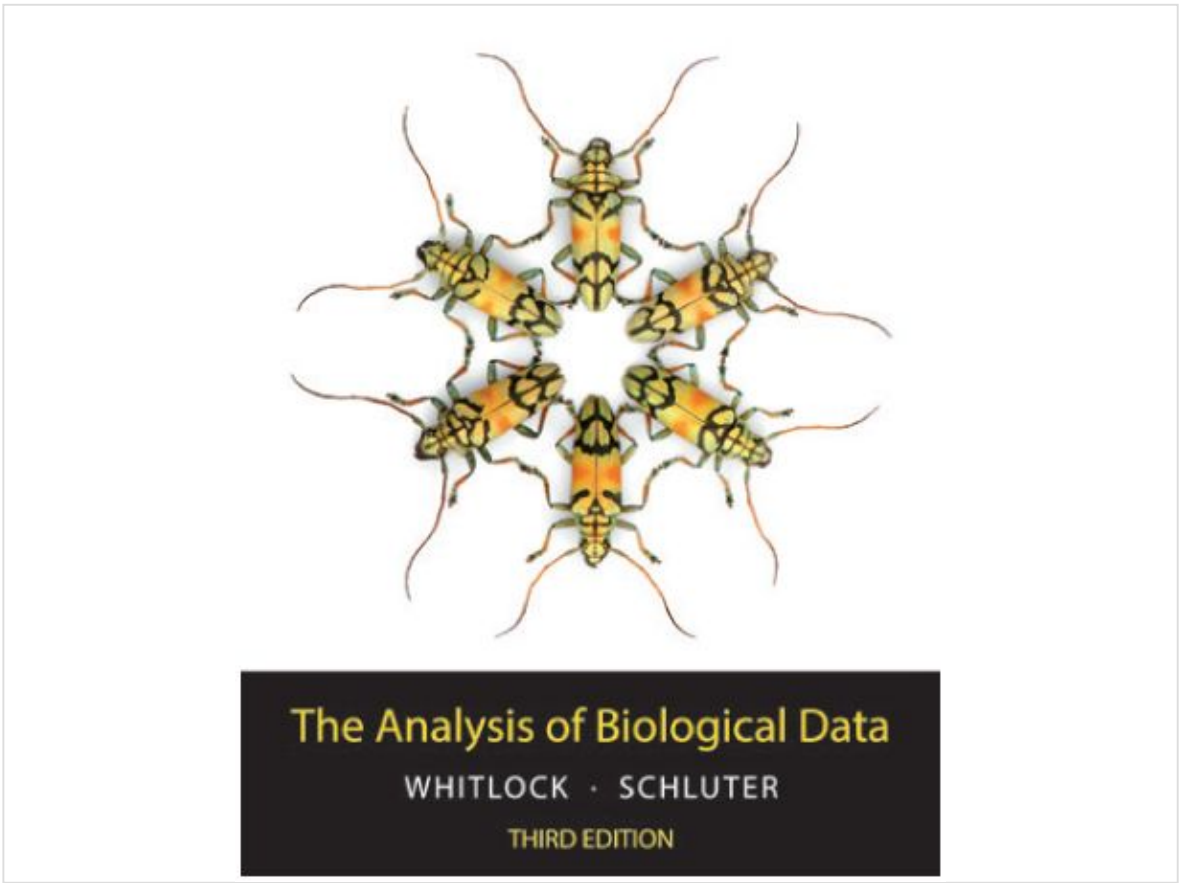
Test Bank, Clicker Questions, and Lecture Slides

For every chapter in the book, instructors are provided with a test bank of relevant questions, clicker questions that address all key concepts, and lecture PowerPoint presentations. All of these materials have been prepared by a team of statistical education specialists.

Online Resources for Students

Many online resources are available to help students learn each of the key concepts and skills in the book. These are located on the authors' website at **whitlockschluter3e.zoology.ubc.ca** and **via www.saplinglearning.com.**

A link to a web page listing all resources available for each chapter is provided near the summary section of each chapter in the book.



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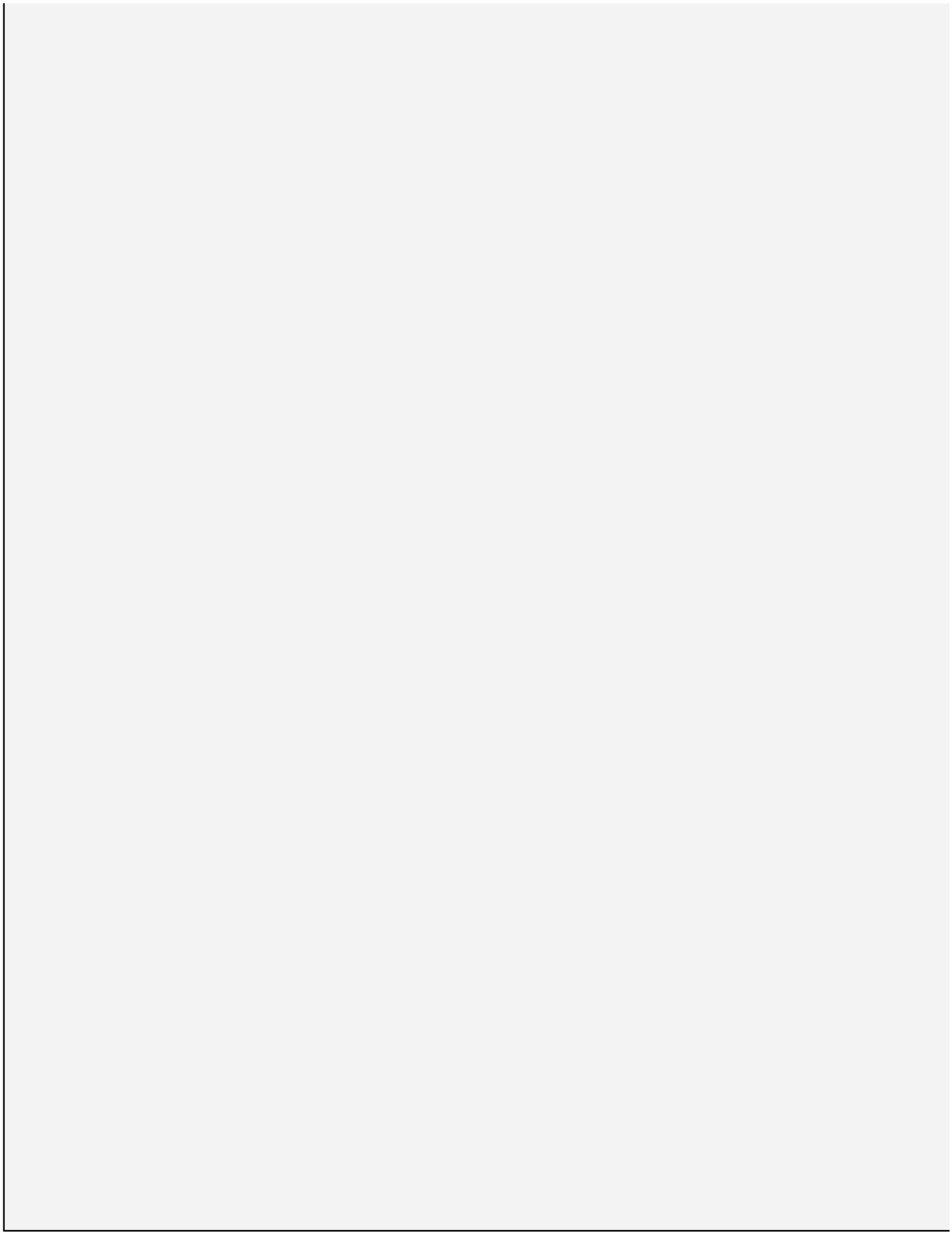


Interactive e-book

With the e-book, students can search, highlight, and bookmark specific information, making it easier to study and access key content. Media assets

such as data sets and glossary terms are linked within the e-book in **SaplingPlus.**

R Code for all Examples in the Book

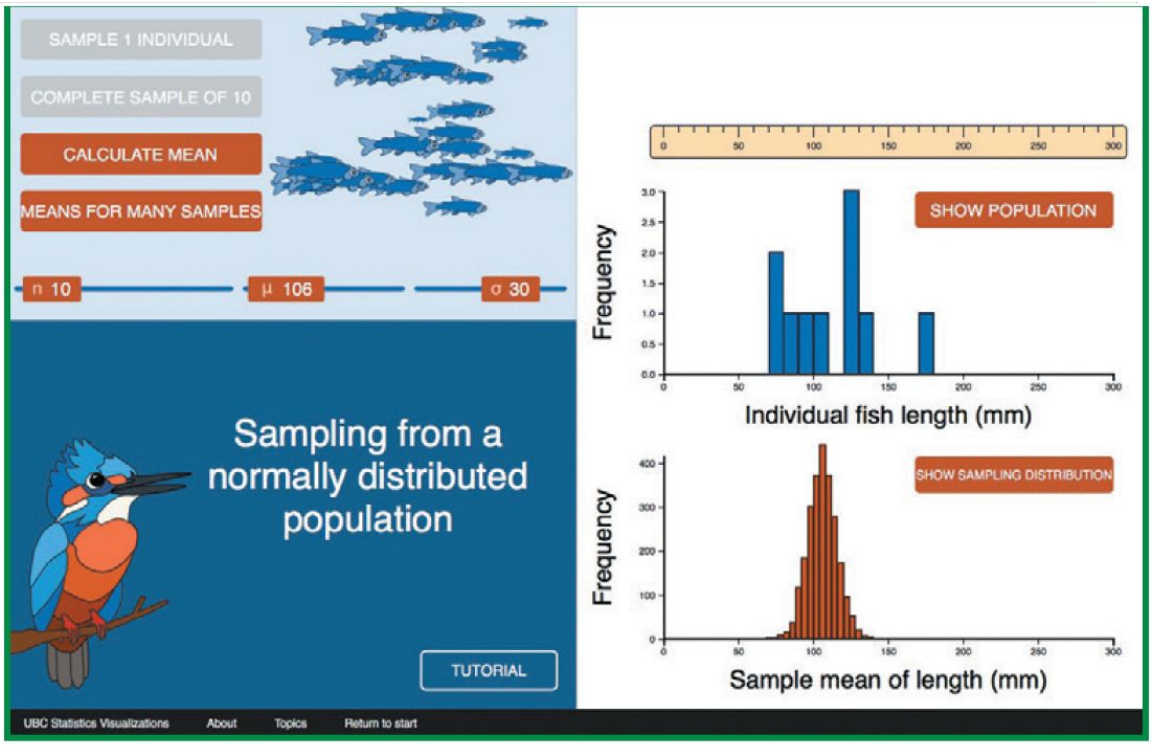
R code is provided to reproduce the complete analysis of all examples presented in the main text of the book. This resource enables students to learn R further by example. The code is available online at **whitlockschluter3e.zoology.ubc.ca.**

Labs Using R

A series of self-guided labs directs students through a week-by-week set of activities to reinforce key concepts and introduce the powerful free statistics package **R**. These labs are available online at **whitlockschluter3e.zoology.ubc.ca.**

Visualizations

A series of interactive web visualizations allow active learning of many of the key difficult concepts in introductory statistics. These resources are available online at **whitlockschluter3e.zoology.ubc.ca.**



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