

PREFACE

One hundred years ago, Sir Ronald Aylmer Fisher (1918), in a paper that was rejected by the Royal Society of London, laid the foundations for the field that has come to be known as quantitative genetics. This paper, and subsequent work by Fisher and others (often in the search of biologically motivated problems), also gave birth to much of modern statistics. The past century has seen quantitative genetics flourish, and indeed, the field has never been stronger or more vibrant as it moves seamlessly into the post-genomics era with an ever-broadening reach. If Fisher were alive today, we believe that he would be fascinated, and somewhat pleased, both at how much the field has grown, and also at how much it remains very familiar to him, even after all these years.

This text is the second part (out of three) of our treatment of the modern field of quantitative genetics from its humble, but path-breaking, beginnings 100 years ago. Some 20 years ago, we remarked in the introduction to the first part of our treatment (Lynch and Walsh 1998) that “today’s quantitative genetics is not the science that it was 25 (or even 10) years ago,” a statement that is even truer today. Our further comment that “the current machinery of quantitative genetics stands waiting (and its practitioners willing) to incorporate the fine genetic details of complex traits being elucidated by molecular and developmental biologists” has certainly been proven true over the past two decades. Modern quantitative genetics is the glue that connects many disciplines, especially given its ability to model uncertainty while fully accounting for known genetic and genomic features.

The first part of our treatment (Volume 1) dealt with genetics, which is the underpinning of complex traits. While we also remark on some recent developments in this area in this volume, our main focus is on the evolution of such traits, with applied evolution (plant and animal breeding) as an important application. To address these concerns, we have attempted to merge modern population-genetics theory with quantitative genetics and genomics. As a result, some of our treatment is more technical than was presented in Volume 1, as it provides a much fuller development of mathematical models of evolution. We have strived to present a holistic treatment, showing the interplay between theory and data, with extensive discussions on statistical issues relating to the estimation of the biologically relevant parameters for these models. We view quantitative genetics as the bridge between complex mathematical models of trait evolution and real-world data, and have tried to frame our treatment as such.

As with our first volume, a key goal in producing this volume is to increase communication among the various disciplines that make up the very diverse field of quantitative genetics. Twenty years ago, this included plant and animal breeders, evolutionary biologists, human geneticists, and statisticians. This list has only grown with the advent of genomics, which attracts an ever-widening array of those who use quantitative genetics (many of whom may not even be aware of it).

Given a project of this size and scope, and despite our own best efforts, excellent copy editors, and wonderful colleagues, it is likely that errors have escaped scrutiny. Hopefully, most will be obvious and trivial, but the posterior for this process often has a long tail, and, therefore, the potential for some interesting outliers. Please report any errors you find to BW (jbwalsh@email.arizona.edu). Likewise, we have a facebook group, **Quantitative Genetics Book**, whose file section will contain updated pdf files for current errata, as well as a forum for discussing issues related to the book. Finally, the final part of our treatment, which deals largely with multivariate issues, will be forthcoming in a more timely manner than this volume!

Acknowledgments

As numerous seasoned readers will know, various components of this book have been in the works for over three decades. For a project of this magnitude, there is a host of people to thank, and we have undoubtedly forgotten to credit individuals who provided us with critical feedback in the earliest years. We profusely apologize for any such slights and blame our slowly fading memories.

As we moved into the field of quantitative genetics in earnest in the 1980s, critical foundational support in the development of our ideas was provided by our colleagues and teachers Stevan Arnold, Reinhard Burger, James Crow, Joe Felsenstein, Wilfried Gabriel, Daniel Gianola, Thomas Hansen, William Hill, Elizabeth Housworth, Alex Kondrashov, Russell Lande, Bill Muir, Tom Nagylaki, Tim Prout, Monty Slaktin, Michael Turelli, and Michael Wade.

We have also greatly benefited from all past and current members of our labs for their comments over the years. These especially include Ph.D. students: Matthew Ackerman, Desiree Allen, Stephan Baehr, David Butcher, Chi Chun Chen, Hong-Wen Deng, Suzanne Estes, Allan Force, Jean-François Pierre Gout, Kyle Hagner, Parul Johri, Vaishali Katju, Weiyi Li, Timothy Licknack, Hongan Long, Samuel Miller, Kendall Morgan, Angela Omilian, Michael Pfrender, Taylor Raborn, Sarah Schaack, Ryan Stikeleather, and Ken Spitze; and post-doctoral associates: Charles Baer, Melania Cristescu, Dee Denver, Thomas Doak, Jeffrey Dudycha, Suzanne Edmands, Jean Francois Gout, Kevin Higgins, David Houle, Sibel Kucukyildirim, Niles Lehman, Hong-An Long, Takahiro Maruki, Martin O'Hely, Susan Ratner, Barrie Robison, Stewart Schultz, Douglas Scofield, and John Willis.

BW also wishes to thank the thousands of students who have attended his short courses on various aspects of quantitative genetics over the past two decades, during which he has taught over 5000 students from roughly 60 countries at various locations around the world (25 countries at last count). This international interaction and feedback have greatly sharpened our ability to present the material in this book to a truly universal audience.

We have been exceptionally blessed with outstanding feedback throughout this project from a long list of colleagues, who directly engaged with the manuscript. Sally Otto and Michael Morrissey read whole parts of the manuscript, while critical comments on specific chapters were provided by Steve Arnold, Nick Barton, Piter Bijma, Mark Kirkpatrick, Bill Muir, Shinichi Nakagawa, Guilherme Rosa, Ruth Shaw, John Storey, and Michael Turelli.

We especially want to acknowledge Bill Hill, who has been a major force throughout this project, and in many ways could be considered its third author. Bill read all of both Volume 1 (Lynch and Walsh) and the current volume, offering very detailed and critical comments, and saving us from much embarrassment. Our goal throughout the project was to present the field with the breadth and depth that Bill carries around in his head. He also kept us going by constantly ending his emails with the reminder to "keep writing!" Hence, we are very pleased to codedicate this volume to Bill.

With respect to the production end, we have greatly enjoyed working with the highly professional staff at Sinauer Associates through the bulk of the editing process, and then with their new colleagues at Oxford during the final phase. Copy editor Nicole Balant and production editor Martha Lorantos faced the thankless task of trying to catch typos in a 1400-page technical manuscript where the lead author is rather dyslexic.

Elizabeth Morales and Ann Chiara did a wonderful job with the illustrations and patiently dealt with us, as we frequently changed our minds on how to best illustrate various concepts, while Michele Beckta dealt with copyright issues regarding the figures. Last, but certainly not least, production manager Chris Small thoughtfully guided us through the typesetting of both this and the previous volume (both of which were typeset by BW using Textures). Any less-than-professional appearance of aspects of this volume are there despite the best efforts of Chris!

We save very special thanks for our publisher and friend, Andy Sinauer. Andy initially started this project in the mid-1980s when we (BW and ML) discovered (via Andy) that

we were both working on separate books on the same subject and he logically queried whether it might be better if we worked together. Indeed it was! Andy has shown incredible patience over the past three decades on the pace of this project, and we hope that he will be pleased with the final outcome, despite its long gestation. We are thus extremely pleased to codedicate this volume to Andy for his long and outstanding service as one of the preeminent publishers of biological science textbooks. Upon his retirement, he has left a gap that will be hard to fill, and his impact on a number of fields, particularly evolutionary biology, is hard to overstate.

In closing, ML is especially grateful to the administration and colleagues at the University of Illinois, his place of first employment, for providing him with a safe environment for making an early (and risky) career transition from limnology to evolutionary genetics. And we both thank NSF and NIH for continuing support for research related to the subject matter of the book.

Finally, and especially, we wish to thank our incredible wives, Emília Martins (ML) and Lee Fulmer (BW), for their enduring patience during this long project.

Bruce Walsh, Tucson

Michael Lynch, Tempe

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