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978-0-521-19028-2 - Parasitism: The Diversity and Ecology of Animal Parasites: Second Edition

Timothy M. Goater, Cameron P. Goater, Gerald W. Esch

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Parasitism

The Diversity and Ecology of Animal Parasites

SECOND EDITION

Reflecting the enormous advances made in the field over the past 10 years, this text synthesizes the latest developments in the ecology and evolution of animal parasites against a backdrop of parallel advances in parasite systematics, biodiversity, and life cycles. It has been thoroughly revised to meet the needs of a new generation of parasitology students, whether their interest is in ecology, conservation biology, evolution, immunology, or health sciences.

Balancing traditional approaches in parasitology with modern studies in parasite ecology and evolution, the authors present basic ecological principles as a unifying framework to help students understand the complex phenomenon of parasitism. Richly illustrated with over 300 figures, the text is accompanied by case study boxes designed to help students appreciate the complexity and diversity of parasites and the scientists who study them. This unique approach, which is presented clearly and with a minimum of jargon and mathematical detail, encourages students to think generally and conceptually about parasites and parasitism.

Timothy M. Goater is Professor and former Chair in the Biology Department at Vancouver Island University, British Columbia, Canada. During the past 20 years he has taught courses in introductory biology, parasitology, ecological parasitology, invertebrate zoology, and entomology. His research interests focus on the population and community ecology of parasites.

Cameron P. Goater is Associate Professor and former Chair in the Department of Biological Sciences at the University of Lethbridge, Alberta, Canada. His parasitological research roots are in the community ecology of helminths of waterfowl on the Canadian prairies, and over the past 15 years he has taught courses in introductory biology, invertebrate biology, field biology, and symbiotic interactions. His current research interests are in the experimental ecology of helminth–host interactions.

Gerald W. Esch is Charles M. Allen Professor of Biology at Wake Forest University, North Carolina, USA, where he has taught for 47 years. He is widely regarded to be one of the world's leading ecological parasitologists, and served as Editor of the *Journal of Parasitology* for 19 years.

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Advance praise for *Parasitism: The Diversity and Ecology of Animal Parasites, Second Edition*

“Their approach is synthetic, refreshingly original and effectively blends coverage of long-standing fundamentals of parasitology with modern advances in the field.”

Janine N. Caira, University of Connecticut, USA

“This is an extremely well written book that does an excellent job of integrating conceptual and organismal aspects of parasitology.”

Dale H. Clayton, University of Utah, USA

“There is a wealth of detail for well-selected examples, building on the rich experience of the authors as top-notch researchers and educators.”

Mark R. Forbes, Carleton University, Canada

“*Parasitism* gives the student both the systematic and zoological background to understand parasitology and the ecological and evolutionary context to understand why it is important. . . As a team, their approach is clear and scholarly, with many important updates since the first edition.”

Kevin D. Lafferty, US Geological Survey, University of California, Santa Barbara, USA

“This new edition will be a wonderful resource for teachers of undergraduate parasitology courses. The well-illustrated and easy-to-read text is unrivalled at the moment and will be a great tool to turn on a new generation of young minds to the wonders of parasitic organisms. A true parasitological tour de force!”

Robert Poulin, University of Otago, New Zealand

“A well-organized integration of the diversity of ideas and methods that characterize this new field of parasite ecology. The style is easily readable, the details extraordinary, and the story is told from the perspective of evolutionary thought. . . even the pros will learn from this book.”

Michael V. K. Sukhdeo, Rutgers University, USA

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TIMOTHY M. GOATER

Vancouver Island University, British Columbia, Canada

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University of Lethbridge, Alberta, Canada

GERALD W. ESCH

Wake Forest University, North Carolina, USA

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*We dedicate this book to our students,
past, present, and future*

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FOREWORD

The ability of parasites to cause disease has always been an important reason to study them, and the teaching of parasitology has almost always been stimulated by conditions conducive to disease, such as war or climate change. Currently, zoonotic diseases emerging from altered ecosystems, or carried by arthropod vectors spreading their ranges due to climate changes, supply that stimulation. However, most of us who teach, or have taught, parasitology have chosen that topic because of the fascinating life cycles of many parasites and their complex interactions with their hosts. Much of that fascination stemmed from learning how parasites can affect the population dynamics of their hosts, or the behavior of the hosts, or even the evolution of their hosts. In addition, that fascination was based on how much parasites could tell us about the life of their hosts, such as their diet, travels, or evolution. Or even of the earth itself – some of the earliest evidence for continental drift was the similarity in parasites of amphibians in Africa and South America. Examples of all of these influences are provided in this book.

Many of the systems that parasitologists have used to show these fascinating features have become relatively easy to study due to new techniques, such as those in genomics and proteomics, which have provided new and more powerful ways to study systematics, evolution, and host–parasite relationships. This has attracted the attention of biologists with a wide variety of backgrounds, so that much of the very interesting work done on host–parasite systems recently has been done by those trained in other specialties, such as ecology, behavior, neurophysiology, and evolutionary biology. Very few of the students in senior-level parasitology courses will go on for further study in parasitology, but many more will go on for

further study in other biological specialties. Our courses, books, readings, and other materials used in our classes should be chosen to expose those students to the usefulness of parasites in investigations in their chosen fields.

This book is the best I have seen for that purpose. The authors have provided a wide-ranging review of the diversity of parasites, emphasizing those which provide examples of the insights provided by the use of the new techniques or examples of how parasites can provide new and exciting insights into other aspects of biology. One of the best features of this book is that it emphasizes the complexity of host–parasite systems, with full recognition that most of the outcomes are markedly dependent on the conditions in which that system is embedded. This emphasis on complexity starts with a chapter on immunity, which is the best and most succinct coverage I have ever seen of those aspects of immunity that are important in host–parasite interactions. This emphasis is most apparent in the most integrative chapters – those on the influence of parasites on their hosts, and parasite evolutionary ecology.

This is the book I would have loved to have been available when I was teaching. But, of course, it could not have been written then. Most of the more provocative insights, and especially the evidence for complexity and conditional outcomes of host–parasite encounters, have come in the past two decades since I retired. The field of parasitology has become increasingly fascinating, and its implications for other fields of biology more significant, in those two decades. Enjoy this book, as I have, and see where it leads you.

John C. Holmes

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PREFACE AND ACKNOWLEDGMENTS

In this second edition, we stay true to the philosophical approach that was adopted in the first. Thus, we continue to see a need for a single text with dual focus on the diversity *and* ecology/evolution of parasites. At the core, we feel that an ideal strategy for senior undergraduate and beginning graduate students to understand and appreciate breakthroughs in parasite ecology is through a solid understanding of parallel advances in parasite diversity, life-cycle variation, systematics, and functional morphology. By way of example, we suggest that an understanding of the role of falciparum malaria in determining the worldwide distribution of the human sickle-cell gene, and thus the role of parasites in mediating natural selection (Chapter 16), comes from an understanding of life-cycle variation, functional morphology, and biodiversity of the apicomplexans (Chapter 3). Likewise, real understanding of the evidence in support of the parasite hypothesis for the evolution and maintenance of sexual reproduction in molluscs (Chapter 16) comes from a detailed understanding of variation in life cycles and life histories of the platyhelminths (Chapter 6). This dual focus, under one cover, is the hallmark of this text.

Our aim is to provide students with a synthetic understanding of the biodiversity, ecology, and evolution of animal parasites. Thus, throughout most of the text, we unabashedly take a parasite-centered view of the phenomenon of parasitism. Yet, we also aim to provide insights on the nature of the host–parasite interaction itself. It is for this reason that following a brief introductory chapter, we provide an overview of vertebrate and invertebrate immunity, and the new discipline of ecological immunology. We turn again and again to the importance of fundamental immunological principles throughout the text.

There are now nine biodiversity chapters (Chapters 3–11). We have added chapters on the Myxozoa, Microsporida, and Nematomorpha,

reflecting developments in their systematics, and their value as models in parasite ecology and evolution. By necessity, the ‘phylogenetic relationships and classification’ sections for all of the diversity chapters have been updated, adopting the most current molecular-based taxonomic schemes. The protist chapter in particular has been completely revised from the first edition, reflecting the monumental changes in protist systematics. New text boxes that highlight key areas of development, and the scientists behind them, are integrated into each of these chapters. New life cycle diagrams and dozens of new photographs and micrographs have also been incorporated. A color plate section has been added, showcasing dramatic photographs of parasites in or on their hosts.

Armed with a solid background in parasite biodiversity, systematics, and functional biology, Chapters 12–17 cover advances in the ecology and evolution of parasites. The titles and content of these chapters have been completely revised from the first edition, reflecting in part, the interests and backgrounds of the new authors. Yet the substantial revisions also reflect the pace of development in methodologies and in overall approaches that have matured the field over the past decade. While some of these developments have confirmed earlier ideas, others have revolutionized our understanding of even the most fundamental aspects of the parasitic way of life. Thus, the incorporation of new model host–parasite interactions that are amenable to manipulation in the laboratory and field have provided key insights into how parasite populations are regulated and how they are distributed among hosts in space and time (Chapter 12). Studies at the community level (Chapter 13) have also benefited from rigorous empirical approaches involving key model systems where the composition of component species can be manipulated. In Chapter 14, we see how advances in molecular biology, genomics, and remote sensing have

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transformed our understanding of parasite biogeography and phylogeography. Coverage in Chapter 15 is focused on the diverse manner in which parasites can affect the biology of their hosts, whether it is at the level of the host individual, or on the structure of entire host ecosystems. Again, key advances stemming from empirical, hypothesis-testing approaches involving selected model systems have markedly advanced our understanding of the magnitude of these effects, and their underlying mechanisms. The focus in Chapter 16 takes the next logical step, covering the manner in which parasites affect the evolutionary and coevolutionary trajectory of their hosts. We conclude the text by summarizing the nature of the parasite/human/habitat interface, and how the multidisciplinary field of environmental parasitology (Chapter 17) can assist in interpreting the nature of host–parasite interactions in the face of anthropogenic change.

As with all projects of this scope, this book is a collaborative effort. We extend sincere thanks to the authors of the first edition, Al Bush, Jackie Fernández, and Dick Seed for their initial vision and dedication. Several of their line drawings and photographs, incorporating the image-editing skills of Maggie Bush, have been retained here. Numerous colleagues offered valuable suggestions on specific sections/chapters, especially Carter Atkinson, Mark Blaxter, Katharina Dittmar, Eric Hoberg, Jens Høeg, Kayla King, David Marcogliese, Jim Mertins, Beth Okamura, George Poinar, John Webster, Chris Whipps, and Stephen Yanoviak. We also appreciate the insightful comments John Holmes provided for several chapters. Several of our former students, especially Martin Anglestad, Melissa Beck, Aaron Jex, Chelsea Matisz, Phillip Morrison, Vanessa Phillips, Brad van Paridon, and Chris Whipps helped to review and edit chapters. Their perspectives helped clarify and focus our efforts.

This revision contains many new drawings, as well as new photographs and micrographs. Bill Pennell spent many hours of his retirement taking several new photographs, as well as editing countless others. Doug

Bray and Brad van Paridon took several of the new scanning electron micrographs. We thank our colleagues for contributing extensive new data figures, photographs, and micrographs for the new edition. Their generous contributions are acknowledged in the figure captions. John Sullivan is especially thanked for sharing several of his photographs from his excellent parasitological resource, *A Color Atlas of Parasitology*. Several new life-cycle diagrams and line drawings are incorporated into this edition, thanks to Chelsea Matisz, Lisa Esch McCall, and Danielle Morrison. Danielle, in particular, is thanked for her patience and dedication in preparing, labeling, and editing many of the new figures and photographs.

Vancouver Island University is thanked for providing Tim Goater the sabbatical and professional development funds that enabled this revision to take shape. Special thanks also to Mike Steele, David Marcogliese, and Herman Eure for providing office space during his sabbatical, as well as Eric Demers, Larissa Nelson, Wendy Simms, and Jane Watson for their enthusiastic encouragement throughout the project. Likewise, Cam thanks Dean Chris Nicol and Chair Brent Selinger for moral support and teaching relief during the peak phases of this revision, and colleagues Doug Bray, Doug Colwell, Andy Hurly, Joe Rasmussen, and Brian Wisenden for their constant support. Cam also extends thanks to Barb Johnson and staff at Waterton Lakes National Park for access to their cabin during key writing phases. Most sincere thanks also to Lori Goater for her monumental patience and support and to Ben and Ali for frequently reminding their dad, and their uncle, that parasite ecologists come in all ages.

Our primary editor, Katrina Halliday and her assistant, Megan Waddington at Cambridge University Press are thanked for all of their help addressing our many queries and, especially, for their patience and devotion to seeing this project to its completion.

Timothy M. Goater
Cameron P. Goater

About this edition

The first edition of our book was published in 2001. Al Bush, Jackie Fernández, and Dick Seed were co-authors, along with myself. Sadly, Al died in 2010. Further, Jackie stepped aside to raise two sons and Dick retired from his faculty position at the University of North Carolina-Chapel Hill. As the only original author that was still active professionally, it became my responsibility to recruit new co-authors. Given the overall theme and target audience of the text, my choice fell upon brothers, Tim and Cam Goater. Tim was a former Ph.D. student of mine at Wake Forest University, and Cam was a former Ph.D. student with Clive Kennedy at the University of Exeter. Both brothers were mentored by Al Bush at Brandon University in Manitoba, Canada. Tim and Cam have extensive experience teaching senior undergraduate

courses in parasitology and ecology, and Cam extends his teaching perspectives to the mentoring of graduate students. Both have diverse and complementary research backgrounds that, together, span most areas of modern parasitology.

Throughout the writing of both editions, I maintained my duties as Editor of the *Journal of Parasitology*, as well as my teaching. Mrs. Vickie Hennings, my Editorial Assistant for the Journal, continued her responsibilities while I was occasionally subsumed by the book. Cindy Davis and Zella Johnson, both long-term secretaries for the Department of Biology at Wake Forest University, are thanked for their help as well. I especially express my appreciation to Ann for being such a marvelous 'listener' and for her constant support from the book's inception.

Gerald W. Esch