Preface

The goal of this book is to provide a synthesis of the physical, physiological, evolutionary, and biomechanical principles that underlie animal locomotion. An understanding and full appreciation of animal locomotion requires the integration of these principles. Throughout this book, we present, as broadly as possible and within a reasonable amount of space, a discussion of animal locomotion that is accessible to undergraduates, yet also of value to more advanced graduate students and professionals. Toward this end, we provide the necessary introductory foundation that will allow a more in-depth understanding of the physical biology and physiology of animal movement. In so doing, we hope that this book will illuminate the fundamentals and breadth of these systems, while inspiring our readers to look more deeply into the scientific literature and investigate new features of animal movement.

Animal locomotion is so rich and diverse that it is daunting to try to write an introductory book, even at an upper-level undergraduate or graduate level. The scales of locomoting animals range from microscopic to house-sized and the habitats extend from the moist surface of delicate leaves to the depths of the open ocean. The study of animal locomotion itself extends back thousands of years as humans have performed observational and experimental studies of animal capabilities, whether due to simple fascination or with the desire to emulate nature's capabilities. This is a big, historic field offering a wealth of inspiration, yet the field is grounded in a set of physical rules that unites much of the diversity and allows us to write a concise book about the core principles of animal locomotion.

Several themes run through this book. The first is that by comparing the modes and mechanisms by which animals have evolved the capacity for movement, we can understand the common principles that underlie each mode of locomotion. A second is that size matters. One of the most amazing aspects of biology is the enormous spatial and temporal scale over which organisms and biological processes operate. Within each mode of locomotion, animals have evolved designs and mechanisms that effectively contend with the physical properties and forces imposed on them by their environment. Understanding the constraints of scale that underlie locomotor mechanisms is essential to appreciating how these mechanisms have evolved and how they operate. A third theme is the importance of taking an integrative and comparative evolutionary approach in the study of biology. Organisms share much in common. Much of their molecular and cellular machinery is the same. They also must navigate similar physical properties of their environment. Consequently, an integrative approach to organismal function that spans multiple levels of biological organization provides a strong understanding of animal locomotion. By comparing across species, common principles of design emerge. Such comparisons also highlight how certain organisms may differ and point to strategies that have evolved for movement in diverse environments. Finally, because convergence upon common designs and the generation of new designs result from historical processes governed by natural selection, it is also important that we ask how and why these systems have evolved.

When we decided to write the second edition of this book, which was first published more than a decade ago, our goal was to bring the first edition up to date, increase the diversity of animals covered in the book, and to address the burgeoning fields of evolutionary analysis of locomotion and the application of animal locomotor mechanisms to the development

of novel engineering devices. Naturally, the fundamental rules of physics have not changed, yet the depth of knowledge and development of impressive technical approaches to the study of these systems have moved quickly in particular areas. Some areas covered in the first edition could be written in the span of a few paragraphs, and now an entire chapter of new discoveries could be devoted to the topic. Without a doubt, the biggest challenge of writing and synthesizing this new edition was keeping the book straightforward and focused on guiding, fundamental principles, while trying to figure out how to navigate all of the fabulous discoveries that we simply could not fit in this short volume. As in the first edition, our foremost goal was to capture the fundamentals underling the study of animal locomotion, even if it meant leaving out much of the research and history of this vibrant field.

We have re-organized the book in multiple ways, both in terms of the coverage of the chapters and the topics of the chapters. The book begins with a chapter on the fundamentals of motion, and quickly moves to a chapter focused on muscles, a source of motion unique to animals, and how muscles interact with animal skeletons to transmit force for movement and support. We next consider the energetics of locomotion, focusing on how the metabolic cost of terrestrial movement varies with animal size and speed, and compares with the cost of flying and swimming. We then examine the principles of locomotion through a series of chapters that explore three major habitats - land, water, and air. The seventh chapter probes a suite of locomotor modes that transcend particular habitats and these modes include jumping, suspensory locomotion and adhesion. The eighth chapter examines the neuromuscular control of movement, providing an overview of sensory-motor pathways and motor recruitment that are central to the dynamic nature of complex locomotor systems. We wrap up the book with a chapter on the evolution of locomotion that examines the broad trends in the evolution of locomotion, as well as the methods and levels of analysis for examining locomotor diversity. It is clear that between the first and second edition of this book, there has been exceptional growth in the comparative biomechanics and physiology of animal locomotion.

We have many people to thank for helping with both the first and second editions of this book. We are grateful to our students and colleagues with whom we have shared the fascination and love of animal movement, physiology and biomechanics. These interactions that have come from our work and discussions are the best part of science. For their insights on the first edition of the book, we thank George Lauder, Bob Shadwick, Gary Gillis, Ty Hedrick, Jim Usherwood, Bob Full, Tom Roberts, and Peter Weyand. Michael Dickinson and Bret Tobalske provided feedback on both editions. We thank Walter Federle for his assistance with synthesizing the field of adhesion in this second edition. We thank the students of Duke University's "How Organisms Move" course and Brown University's "Animal Locomotion" course taught by Sharon Swartz for their feedback on the second edition, especially Sarah Beaverson, Aakash Jain and Suzanne Ou. We are grateful to Rachel Crane and Grace Farley for their editorial assistance. We thank our editors for their assistance with the process of writing the first and second editions. Most of all, we are grateful to our families for their support and patience. This book is dedicated to Dick Taylor, Beth Brainerd, Farish Jenkins, Jr. and Karel Liem, whose unbounded enthusiasm for comparative physiology and love of animal locomotion are an inspiration to so many students and scientists.