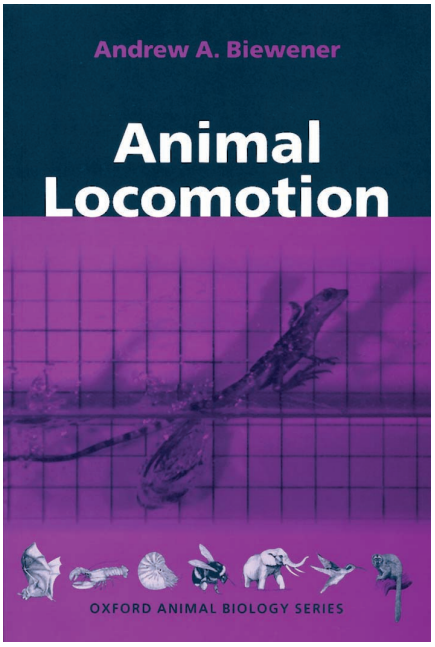
Book Review

ACTIVELY ANIMATED ANIMALS



Animal Locomotion

By Andrew A. Biewener

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'Bright-flaming, heat-full fire,
The source of motion.'
Gullaume de Salluste du Bartas

Locomotion is one of the true hallmarks of animal biology. The ability to self-propel the body and move it large distances without reliance on external forces from wind, waves, or currents is an attribute of animals not possessed by other life forms. Animal locomotion is a complex coordinated activity. It is powered by molecular engines manifest as muscular tissue. Motion is effected through the action of sinuous tendons and rigid, levered skeletons that transmit and magnify the muscular force, and the whole system is controlled with precision by complex neural networks.

Locomotion, however, involves more than the physical constructs of the body working against the environment. Locomotion requires the transformations of energy, from chemical to mechanical at the molecular level, with alternations of internal and external kinetic and potential energies. Speed, strength, acceleration, efficiency, stability, and maneuverability are attributes that determine survival. Therefore, the relationships among the components of musculoskeletal structure, neural coordination, and energy transformation are integrated by evolution to determine the physical performance of animals. Analysis of locomotion, through a synthetic examination of all of these components, is what distinguishes the book *Animal Locomotion* by Andrew Biewener.

Biewener has crafted a text that deals with both sides of the energy equation. The relationship is considered between both metabolically derived energy input and mechanically generated energy output. There is an interplay between the different forms of energy and their rates of usage that strongly influences the evolution of animals. Charles Darwin, in *Origin of the Species*, considered that animals could exist in intermediate forms leading to greater specialization, so long as adequate energy reserves were available. The use and transformation of energy involved in locomotion is paramount to understanding how animals function.

Animal Locomotion is a book on the biomechanics of movement in its broadest sense. Biomechanics has emerged as a synthetic field as barriers have fallen between what were the sacred territories of physiologists and anatomists; even the areas of functional morphology and ecological physiology are still too limited to express the interdisciplinary nature of the field. Perhaps more than any other book on the subject, *Animal Locomotion* highlights the interdependency of the biological systems associated with movement.

The book is basically divided into three parts. The first two chapters highlight the essentials of biomechanics. Topics include the physics of force and work, structural mechanics, scaling, and the physiology of muscles. These chapters lay the foundation on which the structural and functional complexities seen in the diversity of animals and their modes of locomotion can be built. Details of muscle function include the mechanics and control of contraction rate, as well as a lucid discussion of the counter-intuitive concept of negative work.

The bulk of the book contains chapters on movement on land, in water, and in air. Throughout these chapters, common concepts are considered including scaling, elastic energy storage, gait, and stability and maneuverability. Additional chapters

concentrate on the locomotion of animals by hopping, jumping and swinging, and cellular movements using pseudopods, cilia and flagella. For purists noting that the cellular mechanisms are limited for animal locomotion, these mechanisms are still important for internal transport even in the most complex of animals.

The final three chapters shift from a more mechanical approach to a focus on the energetics and control of locomotion. The chapters on energetics examine the various metabolic pathways fueling locomotion and the energetic costs associated with running, flying, and swimming. Biewener notes that these costs are substantial, but behavioral adjustments can increase energy economy.

The chapter on neuromuscular control of movement (chapter 10) was a true surprise that sets *Animal Locomotion* apart from other books on the subject. Other texts have always acknowledged motor units and neural activation of muscles, but Biewener addresses the neural control of locomotion. Much of this control is performed reflexively without input from higher processing centers such as the brain. Many of the intricacies of the controlling neural circuitry are still hypothetical, as is the case with vertebrate central pattern generators. Invertebrate systems provide splendid examples of the direct association between the pattern of neural connections and the coordinated action of the appendages. Despite what are still major gaps in our knowledge in detailing the exact neural networks for control of movement, a compelling case is made that an understanding of locomotion is incomplete without an appreciation of neuromuscular control systems.

The writing of *Animal Locomotion* is lucid and elegant. It is appropriate for biology students at the upper-level undergraduate and graduate levels. Despite the dependency of the subject material on concepts applied from physics and engineering, the book can be appreciated even by the most physics-phobic of readers. There is an economy of mathematics throughout the text, which may be a deficiency. As an introductory text, however, Biewener emphasizes the concepts leaving more equation-based books for future reading. All concepts are clearly illustrated with biological examples. These examples demonstrate how the concept is important ecologically as well as mechanistically. A summary is provided at the end of each chapter, which concisely details the major focus of the chapter while pointing to future directions of research. Although the list of references is not exhaustive, the papers cited throughout the manuscript are many of the most important contributions to the field. For professionals already in the field, Biewener's descriptions of biomechanical concepts are succinct and presented with superb clarity, providing a framework for instruction. The book will also appeal to engineers, who may need an introduction to the biology of locomotion for biomimetic and biorobotic applications.

In the preface of *Animal Locomotion*, Biewener writes that his goal '*was to provide a synthesis of general physical, physiological, and biomechanical principles that underlie the many ways in which animals move*'. By interweaving this suite of principles, Biewener has succeeded in realizing his goal. *Animal Locomotion* is a truly moving book.

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