

Book Reviews

ANIMAL LOCOMOTION. By Andrew Biewener. New York: Oxford University Press. 2003. 296pp. ISBN 0-19-850022-X. \$97.50 (paper).

Animal locomotion has captured human interest and imagination throughout history. Physical anthropologists in particular have been drawn to the study of movement, perhaps as a result of the remarkable diversity of locomotor and postural modes exhibited by the order Primates. Its members display above-, below-, and between-branch behaviors ranging from ponderous knuckle-walking to rapid scurrying, cautious climbing, to ricochetal leaping, bounding quadrupedalism, acrobatic brachiation, and, perhaps most curious of all, bipedalism.

Biewener's richly figured volume provides an excellent broad-based introduction to how different movement patterns are achieved in a vast range of biological organisms. Although the text centers around principles gleaned from hallmark studies on vertebrates and insects, the occasional consideration of ciliated unicellular organisms and such exotic movers as aggregated slime molds stimulates the reader's imagination about the underpinnings of locomotion in other branches of life. Full of real-life examples, the text is ideal for advanced undergraduates and graduate students alike. Yet accessibility does not limit utility; this book serves as an equally excellent reference for professional interests. Most importantly for the physical anthropologist, this volume helps place primate locomotion into a broader context, considering not only how primates are unique, but also how their movement patterns obey physical and physiological laws that govern all manners of animal locomotion.

Supplemented with more detailed articles about particular aspects of primate locomotor behavior, this book constitutes a robust framework for a course in primate biomechanics. Chapter 1 sets the stage with a consideration of common principles associated with movement, mentioning the role of physical properties influencing motion through different environments, outlining biological principles of scaling, loading, and energetics, and introducing basic units and equations employed to describe and study animal locomotion. Chapter 2 provides an essential overview of muscular and skeletal systems, beginning with a description of crossbridge cycling, and proceeding quickly to address relationships between muscle force, length, and contractile velocity. Excitation-contraction coupling, muscle fiber types, and their architecture are discussed prior to an introduction to the skeletal lever systems to which muscles attach. Chapters 3–7 consider different manners of animal locomotion, with an emphasis on the different environmental media across which animals propel themselves. Of these, the treatment of movement on land and the chapter on jumping, climbing, and suspension are of particular interest to students of primate locomotion.

For example, Chapter 3 introduces limb use and posture during terrestrial locomotion, exploring the support and swing phases of the stride cycle and describing how limb postural data may be combined with ground reac-

tion forces in order to better understand joint moments and mechanical advantages of the limbs. Along with increasing velocity, this interaction between a limb's configuration and the strains it experiences is presented as a partial explanation for the selection of different gait patterns, here defined following mechanical and not kinematic standards as the walk, trot, run, and gallop. Mechanisms that influence velocity, including stride length, stride frequency, and body size, are discussed, as are potential tradeoffs between stability and maneuverability in relation to substrate type, body size, and limb design. A number of other concepts significant to the study of primate locomotion are introduced, including limb compliance through the lens of the mass-spring model, and use of the Froude number to compare forward velocity across animals differing in body size. Fluctuations in kinetic and potential energy as a function of the movement of an animal's center of mass are examined, as are mechanisms for reducing the work performed by muscles via the use of energy storage structures such as viscoelastic tendons. Students of paleo-anthropology will enjoy the discussion regarding inferences about velocity and gait, using fossil trackways of animals long extinct. What the book lacks in terms of a detailed treatment of arboreal quadrupedalism, it more than makes up for with its comprehensive overview of the principles of terrestriality, providing a rich backdrop for discussions regarding how and why the locomotor strategies of arboreally adapted animals such as primates depart from patterns observed in terrestrial forms.

Chapters 4 and 5 address movement through fluid environments, namely water and air. A host of locomotor considerations are addressed, including the importance of overcoming inertia, basic elements of thrust, lift, and drag, and the anatomical structures responsible for propelling animals through media of different densities. Along with the cellular crawling mechanisms introduced in Chapter 6, these discussions provide an additional comparative biomechanical context in which to place arboreal and terrestrial locomotion.

Aspects of Chapter 7 may appeal more directly to physical anthropologists, as they address leaping, suspension, and climbing as locomotor strategies. Of these, jumping is most comprehensively considered, beginning with an introduction to ballistic motion and relationships between the distance covered in a given leap and factors such as force magnitude, take-off angle, and limb length. Preparatory countermovements and energy storage in elastic structures such as ligaments, tendons, and muscle aponeuroses are also discussed as potential ways of increasing leap distances. Mechanisms that assist with climbing, and pendular aspects of brachiation, are also briefly mentioned in the chapter, but will require supplementary readings to satisfy the interests of primate specialists.

The remaining chapters consider metabolic pathways and energy costs associated with locomotion, addressing sensorimotor integration and neuromuscular control. These chapters provide students with direct links between the mechanics of locomotion and the mechanisms by which animals power their movements using highly conserved anaerobic and aerobic pathways. Energy cost is

examined in relation to body size, locomotor velocity, and gait pattern, prior to comparisons of the costs of different forms of locomotion. An overview of sensory input from muscle spindles and Golgi tendon organs is followed by a mention of the complex integration of sensory input and motor control using muscle reflex pathways. The book concludes with a consideration of muscle recruitment patterns, and a discussion of how movements can be coordinated by simplified circuitry, resulting in reciprocal inhibition of muscle antagonists, and coordination of muscle timing patterns among limbs, using central pattern generators.

Common threads shaping the fabric of this text include the use of comparative analyses to understand common biomechanical principles, the influence of body size upon animal locomotion, and the use of an integrative evolutionary perspective to examine why convergences or new designs work. At times conversational yet always con-

cise, the author's elegant discourse on each of these themes lends insight into the study of animal locomotion and provides ample opportunities for classroom discussion about promising areas for future research.

Biewener lists three primary goals in constructing this volume: to synthesize general biomechanical, physical, and physiological principles governing animal movement, to provide an accessible discussion of animal locomotion for undergraduates without compromising value for graduate students and professionals, and to create a springboard to address future directions in the study of animal locomotion. These three objectives are accomplished with ease, in a text that is as pleasant to read as it is informative. This volume will no doubt serve as a fine reference for years to come.

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