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BOOK REVIEW

Animals in Motion

Animal Locomotion
By Andrew A. Biewener (2003) New York: Oxford University Press. 296 p. $97.50 (cloth). ISBN 0-198-50023-8. $45.00 (paper). ISBN 0-198-50022-X

Principles of Animal Locomotion
By Richard M. Alexander (2003) Princeton: Princeton University Press. 376 p. $49.50 (cloth). ISBN 0-691-08678-8

Comparative Biomechanics: Life's Physical World
By Steven Vogel (2003) Princeton: Princeton University Press. 582 p. $60.00 (cloth). ISBN 0-691-11297-5

With the exception of the television addict and folivores fortunate enough to forage in repose, primates are constantly on the move, foraging for food, sex, or a safe place to sleep. Because locomotion is energetically costly, any improvements in locomotor design free energy for more productive pursuits, such as sex and child rearing. So it is reasonable to suppose that the principles governing the evolution of locomotor design have been important forces in primate evolution. Certainly, biomechanical principles are central to explanations of the origins of arboreal locomotion in stem primates, vertical clinging and leaping in tarsiers, convergent adaptations to suspensory locomotion in atelines and hominoids, prehensile tails in platyrrhines, ricochetal brachiation in lesser apes, knuckle-walking in the great apes, bipedality in humans, or any of a host of other primate locomotor adaptations. Consequently, any primate-focused biomechanical or functional morphologist will want to have Andy Biewener's *Animal Locomotion* and R. MacNeill Alexander's *Principles of Animal Locomotion* on their shelves. And if you teach biomechanics to graduate students or undergraduates, a copy of Steve Vogel's *Comparative Biomechanics: Life's Physical World* will be invaluable.

Embracing a wide range of writing styles, taxonomic diversity, and technical detail, this triptych of books constitutes a nice cross-section of biomechanics textbooks. Vogel's scope is all of life, swimming, flying, moving, feeding, diffusing, pulsating, circulating, convecting, and more. Comprehensive it is, from the strain of snail slime to swimming down Von Karman Street. Vogel's book is as erudite, charming, and witty as one would expect from having read his previous books. The charm and wit will sometimes perplex you, but they do soften the impact of biomechanics on your undergraduates and the algebraically challenged. One added advantage of Vogel's book is that if you e-mail him, he'll send you an extensive list of problem sets that you can use freely in your own class.

Alexander's and Biewener's volumes are equally erudite, but charm, wit, and snail slime are not in their bailiwick. Alexander aims at advanced undergraduates, graduate students, researchers, and university teachers, so the text is thicker with details, formulae, and references to the literature. He seeks to define the principles governing different modes of animal locomotion and their relative energetic costs, and thereby reveal the logic underlying their recruitment in different lineages by natural selection. Biewener's shares with Alexander's the aim of presenting the principles underlying animal locomotion, but his target audience is principally undergraduates. Hence, brevity is more pertinent; the logic behind the principles is stripped down and asserted rather than developed and expanded.

Consider their contrasting treatments of the Froude number, Fr = $(v/gl)^{0.5}$, a fundamental concept for comparing, for example, the speed at which animals switch from walking to running gaits. Vogel gives two routes to the Froude number.

> Consider, for one, the forces on an appendage swinging back and forth as a pendulum or an alternately rising and falling body, again acting as a pendulum. What keeps it going is what's often called its inertial force—given as mass times acceleration. What makes it stop as it swings upward is gravitational force—mass times the earth's gravitational acceleration. We can write the two as a ratio, cancel masses, and reduce acceleration to speed and length (tacitly assuming steady motion). Sticking to loose dimensional terms $ma/mg = v^2/gl =$ Fr (p. 479).

Alexander presents the Froude number as a tool enabling identification of dynamic similarity in animals of different body sizes. After making an analog between dynamic and geometric similarity, he lays out the conditions for two motions to be dynamically similar.

> Let m_1, m_2 be corresponding masses in the two motions (for example, the masses of corresponding parts of two animals' bodies); let v_1, v_2 be corresponding velocities (for example, the velocities of corresponding body parts at corresponding stages of the motion); let F_1, F_2 be corresponding forces (for example, peak forces on the feet) and let $L1$, $L2$ be corresponding lengths (for example, stride lengths). If the motions are dynamically similar,
>
> $$m_1v_1^2/F_1L_1 = m_2v_2^2/F_2L_2$$
>
> Both motions must have the same value of mv^2/FL.
>
> This must be true for all the kinds of forces that are important for the motion. Suppose, for example, that gravitational forces are important, as they are for running mammals. The force F exerted by gravity on a mass m is mg, where g is the gravitational acceleration. Thus, $mv^2/FL = v^2/gl$. When gravity is important, motions can be dynamically similar only if they have equal values of v^2/gl, a quantity that is called a Froude number (p. 58–59).

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Biewener's treatment in contrast, is more utilitarian. Under what circumstances is the Froude number important?

> The Froude number normalizes the forward velocity of a moving animal to its limb length and gravitational acceleration. These parameters represent fundamental force interactions of stepping locomotion, in which the centrifugal force ($F = mv^2/r$) acting on the body's mass, as it rotates over a supporting limb, balances the ground reaction force acting on the limb from below . . . . At the same Froude number, geometrically similar animals move in a dynamically similar fashion . . . . The Froude number also represents the ratio of a moving body's kinetic energy ($mv^2/2$) relative to its potential energy (mgl). Therefore, equal Froude numbers imply equal ratios of kinetic to potential energy when an animal moves (p. 65–67).

All three books cover basic concepts such as questions of scale, definitions of work and power, muscle mechanics, gaits and their advantages, and when animals shift from one to another. They also all include detailed treatments of the mechanics of flight and swimming, which although not of direct relevance to most primatologists, are the means of locomotion for the majority of vertebrate species. Being of broader scope, Vogel's book includes a very accessible section on the material properties of solids and the mechanics of solid structures. The basics are all here. Biewener's treatment of muscle physiology is more extensive than that provided by the others, and he includes a nice chapter on neuromuscular control of movement, a topic not addressed by Alexander and Vogel. Alexander includes a brief chapter on methods, including strain-gauge analysis, electromyography, and procedures for measuring pressure, flow, oxygen consumption, and kinematics, and includes a few references to basic literature. Alexander's volume includes an interesting chapter on aids to human locomotion, including shoes, bicycles, and scuba-gear.

I was surprised at the paucity of references to the primate literature. Human walking makes inroads in various places in all three books; gibbon brachiation and spider-monkey suspensory locomotion are also reviewed.[1–4] There are brief treatments of climbing and leaping by both Biewener and Alexander, with Biewener's being the most primate-friendly. He cites Emerson's[5] discovery of common hindlimb scaling trends in frogs and leaping mammals, including primates, and uses Cartmill's[6] treatment of the biomechanical principles underlying climbing as the basis for his treatment of the topic. Biewener[7–9] reviews power amplification via elastic storage in galagos, but Alexander mentions this subject only in passing. This is doubtless a common mechanism for power amplification among primates, although the precise location of the energy storage elements remains to be identified. Alexander notes the need for more data on "the mechanics and energetic of locomotion through trees." This is not a trivial question: Large leapers lose substantial energy to vibrating tree branches because the branches do not recoil before the animal has leaped.[3] However, it is not a trivial exercise to collect these data. Ongoing research by Demes at the Duke University Primate Center is addressing this issue.

Why do nonhuman primates appear so little in these volumes? One reason is that primatologists mostly publish in their own journals, which are seldom read by biomechanists working on other groups. There are, for example, few citations in these volumes to papers in AJPA and JHE. Another reason is that the focus of attention in primatological biomechanics is different from that in other disciplines. In primatology much of the focus is on clade- and adaptation-specific hypotheses; that is, hypotheses regarding the origins of major primate groups and their defining features. Much of this literature is concerned with reconstructing behavior (including locomotion) and ecology in fossils, and such issues are not always of obvious interest outside of primatology. Ideas on the origin and functional significance of bipedalism and brachiation, for example, interest nonprimatologists because these modes of locomotion are so bizarre and of only limited relevance to the general principles of locomotion obtaining in other mammals.

But the flip side of this is why these three books are so valuable to me. They provide detailed and broad-brush reviews of fields that I cannot keep up with in detail. For example, I visited them for entrées to the literature on kinetics and kinematics of gait biomechanics so that I could compare these aspects of locomotion and mastication in my research; I boned up on the material properties of various connective tissues to deepen my understanding of recent work on sutural development; and I used their accounts of fluid mechanics to explain various aspects of fish swimming biomechanics to graduate students. All three books helped in different ways, their differing levels of expertise matching my varying degrees of ignorance in these fields. I am glad to have all three.

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