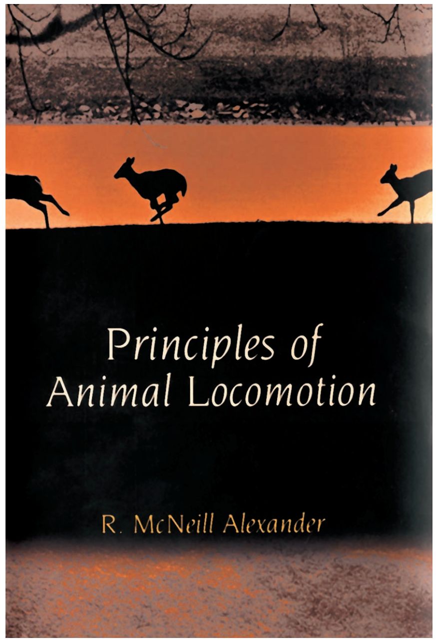
Book Review

SEE HOW THEY RUN, CRAWL, HOP, HOVER, FLY, SWIM…



Principles of Animal Locomotion

By R. McNeill Alexander

Princeton University Press (2003)
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Our efforts to match the extraordinary performance of nature's materials, organ systems, networks and behaviors have revealed the daunting complexity of biological systems. Rather than blindly copying nature, it is clear we must be inspired by general principles that emerge from an integration of disciplines. Fortunately, we are in the midst of a revolution that is removing the barriers between disciplines at a breath-taking pace. The field of animal locomotion, in particular, stands as an exemplar to the power of interdisciplinary integration. R. McNeill Alexander, one of the great zoologists of our time, has written a principle-based synthesis of muscle-powered movement that will engage engineers and physicists, intrigue mathematicians, broaden the perspective of biologists and inspire graduate and undergraduate students.

Principles of Animal Locomotion demonstrates once again that comparing a diversity of animals allows discovery of general principles. Using an array of taxa challenging the breadth of any zoologist, Alexander reveals the secrets of crawling, burrowing, walking, running, hopping, climbing, jumping, gliding, hovering, flying by flapping, and swimming by oars, hydrofoils, jet propulsion and undulation. A comparison with Sir James Gray's still insightful book *Animal Locomotion* (1968; published by Weidenfeld & Nicolson) shows the field's progression from biological descriptions to a synthesis offering quantitative principles. The author presents the principles using simple mathematical models derived from deep quantitative reasoning and with a remarkable ability to collapse dimensions effectively. Alexander's exemplary approach to biological discovery pervades the book. Simply put, he asserts that, "*We cannot expect…these models to be accurate for real animals. The value of the calculations is that they reveal general principles that might be obscured by the complexity of more realistic models.*"

Locomotion by animals is accomplished through a staggering assortment of complex morphologies operating in equally complex environments. Fortunately, common denominators exist. Alexander delineates performance metrics in the first chapter that include speed, acceleration, stability, maneuverability, endurance and economy. Muscles with strikingly similar properties that actuate animal movement are outlined in the second chapter. Regardless of whether feet, fins or feathers are used, animals generate kinetic or gravitational potential energy and often store and return elastic strain energy. Chapter 3 details the muscle energetics required to produce the force, work and power necessary for oscillatory movements. Powerful analytical tools used to reveal principles are presented in Chapter 4. Allometry, the scaling of animals that differ in size, has been remarkably successful in showing trends that cut across diverse taxa. Dynamic, elastic and stress similarity theory provide testable hypotheses of locomotor performance. Optimality, allometry, similarity theory and energy minimization remain dominant themes throughout the rest of the chapters that march through the modes of locomotion.

For those familiar with Alexander's prolific past efforts, *Principles of Animal Locomotion* is an updated and greatly expanded version of *Locomotion of Animals* (1982; published by Blackie), with the clarity of the popular *Exploring Biomechanics: Animals in Motion* (1992;

published by Freeman) and the depth of *Animal Mechanics* (1983; published by Blackwell Scientific), *Mechanics of Animal Locomotion* (1992; published by Springer-Verlag) and the classic compilation *Mechanics and Energetics of Animal Locomotion* (1977; published by Chapman and Hall). Classic examples from these previous publications used to illustrate fundamental principles, such as the Froude number characterization of quadrupedal gaits, stability in turtles and energy minima in running and flying, are not discarded in this new book but instead evaluated, integrated and extended with recent discoveries. To be specific, a few of the many updates and additions include a calculation of muscle stress based on optical tweezer experiments for a single molecule, a novel cost comparison of 10 models of terrestrial locomotion from crawling to wheels to spring-mass running, and an analysis by the author of walking on hills and soft ground. Explanations of extraordinary performance by jumping bushbabies and frogs, brachiating gibbons, climbing geckos and insects, and flying fruit flies and moths using unsteady flow effects are important additions. A new chapter highlights locomotion on water by spiders and basilisk lizards, as well as surface swimming. Recent visualization efforts and simulation of fish fins are included along with new discoveries about tuna tendons and a review and synthesis of the complex subject of fish muscle function. Finally, a unique chapter on human-powered boats, aircraft, bikes and running shoes provides the direct connection needed to our own experiences and capabilities.

Although this comprehensive volume comes surprisingly close, no book can include all areas and approaches. The lack of phylogenetic analyses was defended by Alexander (2001; *Nature* **412**, 591) in a pre-emptive strike arguing the utility of local optimality approaches that provide testable hypotheses. The locomotion of cells and microorganisms by cilia, flagella or amoeboid movements along with their internal motors is absent. Despite the effective additions on stability, the book does not go beyond McMahon's *Muscles, Reflexes and Locomotion* (1984; published by Princeton University Press) with respect to neuromechanical integration. *Principles of Animal Locomotion* is thought provoking for experts in the field. This synthesis will serve as a gateway into a growing body of literature for integrative biomechanists, physiologists and functional morphologists newer to the area. It should be digested by engineers who hope to gain inspiration from biology for the design of novel devices. Perhaps, most importantly, Alexander's *Principles of Animal Locomotion* will serve as a text for graduate and upper level undergraduate courses worldwide, thereby positioning the next generation to lead the unprecedented integration of physics, mathematics and biology.

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