Newton Rules Biology: A Physical Approach to Biological Problems, C. J. Pennycuick

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How can a book entitled NEWTON RULES BIOLOGY *not* be reviewed in *Biophysical Journal?* If anything speaks more directly to the interface between physics and biology, what can it be? Unfortunately, the book's title is more enticing than accurate, and the amount of physics it contains is rather slim, idiosyncratic and elementary. Nonetheless, this is an interesting book, well written and well worth reading for what it contains, rather than for what its title may seem to promise. It shows in quirky but enjoyable fashion how a few simple physical and mathematical principles can give useful insight into biological behavior, and should provide some good ideas for undergraduate lectures in general biology, physiology and ecology. The aims and flavor of this book are best conveyed by a few quotations from the Preface:

"Among the multitudes of biochemists and molecular biologists, those who study biomechanics are considered to be the lunatic fringe. Very few among this band of eccentrics have commanded universal respect, and foremost of those was the legendary physiologist A. V. Hill. . . . [It] has been one of my objectives in writing this book to show how Hill's way of thinking created a thread which links biological events at the cellular level, through animal locomotion, to the large-scale properties of ecosystems. Hill's scientific style is very unlike that usually associated with the science of physiology. The reader is never in doubt about the exact physical nature of the quantities he measures, or of the meaning of the units with which he measures them. . . . Hill starts from the premise that organisms, and parts of organisms, obey the rules of Newtonian mechanics, which is a difficult point to make to those who have forgotten (or never knew) the difference between weight and mass. . . . It is not my purpose in this book to review Hill's contributions to science, but rather to take a careful look at his Newtonian starting point, and then to see whether his method of reasoning can be extended a little bit, to give a window on the dynamics of ecosystems."

Pennycuick lays the foundation for his program in Chapter 1, which, after a brief reminder of the length scales pertinent for biology, introduces dimensions, systems of units, and the necessity of keeping track of dimensions. Emphasis is placed on SI units, and on the confusion engendered by the engineering metric system, in which the kilogram is a unit of weight rather than mass. Chapter 2 makes these issues more concrete by introducing gravity and frequency as variables, developing a succinct treatment of dimensional analysis, then using it to show that the fundamental frequency of a pendulum does not depend on its mass, but only on $\sqrt{(g/l)}$. Familiar enough, but then we are told that the same argument applies to the stepping frequency of walking mammals. When more than three variables are involved, the Buckingham pi-theorem may be invoked, leading to dimensionless variables such as the Reynolds number. This is not unique, however, and resort must be taken to relations between groups of exponents of variables (that is, to scaling relations). Such relations, coupled with plausible physical arguments, are used to obtain scaling equations for the wing-beat frequencies of birds and the tail-beat frequencies of fish. Lifting body weight against gravity through repetitive motion then leads to considerations of power output.

Chapter 3 applies these general concepts to "muscles as engines." The resolutely mechanical focus is reiterated: "The power output of muscles . . . is often seen as being limited by the rates at which enzyme systems can supply energy. This is putting the cart before the horse, however. The rate at which muscles can do work is limited by three variables and three only, the stress which it can exert, the strain through which it can shorten, and the contraction frequency. These are mechanical variables, and their maximum values are set by mechanical limitations. Adaptations of enzyme systems and so on is a secondary matter." This assertion is qualified a few pages later, however, by the admission that "an aerobic muscle is ultimately limited by the rate at which unit volume of mitochondria can process energy." Most of this chapter deals in lucid, economical and witty fashion with such matters as definitions of stress and strain, the Hill equation relating force and velocity of contraction, maximum strain rate and power, efficiency, maintenance of tension in tonic muscles, and matching "slow" and "fast" muscle to the required contraction frequencies. Applications range from the ability of orangutans to hang by their fingers for long periods, to the explanation why, contrary to popular belief, fleas are such poor jumpers.

Chapter 4 deals with those implications of scaling which follow from the mechanical view of muscular contractions. It begins with the familiar relations between mass, length, and surface area; but quickly gets more interesting by noting that neither the wing spans nor wing areas of Procellariiform birds (albatrosses, petrels,

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etc.) vary quite as predicted with body mass. Scaling arguments are then applied to jumping work (geometrically similar animals all jump the same height), scaling frequency (top speed is independent of body length, but natural or cruising frequency varies as the $-1/2$ power of shoulder height), energy consumption (varies with 0.75 power of mass in steady locomotion), and similar initially puzzling regularities. This last result is extended to all forms of energy usage by animals, and is used as the bridge between the whole animal and ecosystem levels.

Pennycuick takes up fractals in Chapter 5, using the concept of fractal dimension to generalize the scaling arguments of the previous chapter. An ecological example is the relation of the spacing of eagle's nests to the ruggedness of the coastlines of Alaskan islands. Physiological applications are the surfaces of lungs and intestines. If the lung has a fractal dimension of 2.17, then the relation between oxygen consumption and body mass should be $2.17/3 = 0.723$, closer to the 0.75 observed than the $2/3$ expected from simple surface area arguments. Similar considerations, it is suggested, should relate the fractal dimensions of intestines and the grinding surfaces of teeth to the digestion of food.

The book culminates with two chapters applying these concepts to ecosystems. Instead of attempting to model ecosystem dynamics by systems of nonlinear differential equations (whose solution often leads to chaotic behavior), Pennycuick proceeds resolutely with his program of scaling analysis of mass and energy flows (on the way twitting ecologists about whether biomass has units of mass, or mass/length^2, and whether the latter is properly called biomass density). He formulates Darwin's principle of natural selection as a mass accumulation principle: ". . . every organism is adapted to maximize its own power surplus [i.e.] to convert as much material as possible into the biomass of its own offspring. . . ." Some counterintuitive insights arise: e.g., since big animals consume less per unit mass, a habitat where the availability of food is uncertain exerts a selection pressure favoring large body size. In many cases, what appears to be drastic ecosystem disruption is simply a shift of species in a self-regulating system. Matters become dramatically different, however, when the human species, which has "in recent years achieved a world-wide degree of success at biomass accumulation . . . unprecedented in the history of the biosphere," appears on the scene. The human biomass density worldwide is estimated at 1.6 g/m^2, within a factor of three of the density of the herds of wildebeest in the Serengeti. Urban densities are 100 times higher, and the market agriculture needed to sustain them removes nutrients from the food-producing regions. While these losses can be replaced by huge imports from mineral reserves (fertilizer), we face increasing danger of large-scale famine synchronized by long-distance interdependence. This modern version of Malthus looks all too plausible unless humans curb their population growth and instinctive urge to completely dominate nature.