BIOPHYSICS

New Clues to Why Size Equals Destiny

Dueling theories aim to explain why larger organisms tend to live longer; both conclude that the physics of nutrient distribution is key

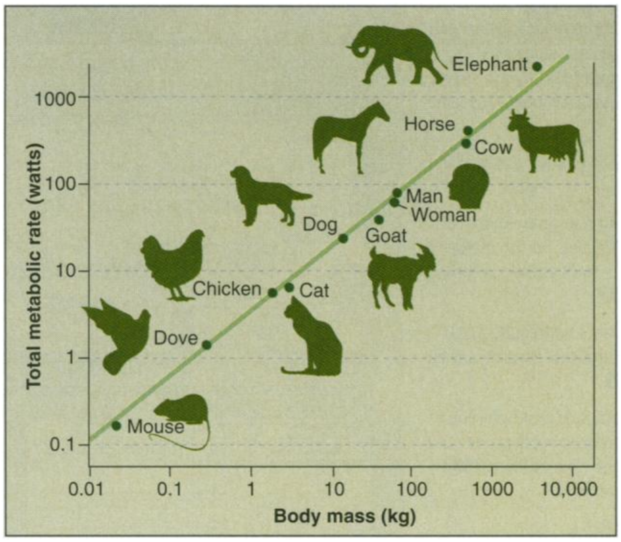
Turning 50 inevitably gets you thinking about how much time you have left in the world. For Geoffrey West, reaching the half-century mark in 1990 set him grappling with an extraordinary equation that predicts how long an organism might live: the quarter-power scaling law. In general, the larger the species, the longer the life. This relationship holds true with remarkable precision: Life-span tends to lengthen—and metabolism slows down—in proportion to the quarter power of an animal's body weight. "If you could understand the origin of these scaling laws," says West, a high-energy physicist at Los Alamos National Laboratory in New Mexico, "you'd understand something about aging and death."

One of the few all-encompassing principles in biology, the quarter-power law helps scientists work out, for example, how to adjust drug doses in rats for use in humans. But the law's universality is baffling: Why should so many species, with their variety of body plans, follow the same rules on longevity? "Either there is some fundamental physical reason for it," says Peter Dodds, a geophysicist at the Massachusetts Institute of Technology, "or evolution has found only one of many mechanisms that could work, and this has pervaded all of biology."

Physicists, of course, would prefer a physical explanation, and there are signs that they could be homing in on one. On page 1677, West and his colleagues propose that the quarter-power law derives from the physical constraints of an ideal system for distributing nutrients, whether it's the blood conduits running through our body or the vascular network nourishing a plant. An alternative theory from a second group (*Nature*, 13 May, p. 130) differs in details but comes to the same conclusion: The constraints on life-span and metabolism lie within an organism and have nothing to do with outward size and shape.

Late last century, biologists sought to explain why smaller animals spend life in the fast lane and die young, while larger ones burn energy more slowly and live longer. Grab a chicken, and you will feel its pulse racing at about 300 beats a minute. Sidle up to an elephant about 10,000 times as massive as a chicken, and the thumping clocks in at 30 beats per minute. Because nearly all mammals expire after anywhere from 1 billion to 2 billion heartbeats, an elephant, naturally, should outlive a chicken.

In 1883, biologist Max Rubner proposed an explanation. If an animal is N times as big (in height or length) as another, then its skin surface should be N^2 times as big, he argued, and its mass (M) N^3 times as big. Because the heat an animal can shed is proportional to skin surface, its *total* metabolic rate—the energy an animal burns in an hour—is proportional to N^2, which is itself proportional to $M^{2/3}$. Finally, the *specific* metabolic rate—the energy burned per unit mass, which controls pulse rate—is obtained by dividing by M, giving $M^{-1/3}$. Thus, Rubner concluded, specific metabolic rate should decrease with size as the cube root of mass.



Slow pulse, long life. The baffling correlation between body size and total metabolic rate may stem from nutrient distribution.

This argument would work if chickens and elephants were spheres. Alas, they are not. Although the cube-root law does sometimes hold when comparing metabolisms of individuals in a species or among closely related species, it fails when extended to a divergent set of species. In 1932, Max Kleiber, a Swiss-American animal scientist, plotted the first accurate measurements of size versus metabolic rate, discovering that the correct scaling law was nearer to the fourth root. (The exponents he measured were 0.74 for total metabolic rate, and –0.26 for specific rate.) Thus it is no accident that an elephant, with 10^4 times the mass of a chicken, has a pulse rate about 1/10 as fast. Kleiber's law has been confirmed in a broad spectrum of animals (see chart).

Why it's a quarter power and not the cube root is the mystery of life that West was pondering when he met biologists Jim Brown and Brian Enquist of the University of New Mexico, Albuquerque, who were turning the same question over in their minds. Enquist had found that the quarter-power scaling law holds for metabolism in plants, which deepened the intrigue. If there were a single explanation, they reasoned, it had to involve a feature shared by species in both kingdoms.

Their suspicions centered on the circulatory system. In animals and plants, circulatory systems resemble branching fractal networks, and capillary size does not depend on organism size: An elephant's capillaries are the same size as a chicken's, and a pine tree's vascular capillaries are the same size as a daisy's. In 1997, the New Mexico trio published a report in *Science* (4 April 1997, p. 122) deriving the quarter-power scaling law from the physics of capillaries and the hydrodynamics in tubes. The model predicts accurately other scaling in mammals: aorta size, capillary density, and heart size, to name a few. "It's phenomenal how well it works," West says.

The revival of the dormant debate over Kleiber's law fascinated physicists. "It really was a paper with a brilliant idea," says Dodds. One enthusiast was Jayanth Banavar, a physicist at Pennsylvania State University in University Park. He heeded Occam's razor and looked for a less complex rationale for Kleiber's law. "When you see something so pervasive, the explanation had better be really, really simple," he says.

Banavar found a way to take fractals, which he saw as an unnecessary complication, out of the picture. In last month's *Nature* paper, he and two Italian physicists—Amos Maritan and Andrea Rinaldo—present the case that the quarter-power law is a feature of any optimally efficient network. They assumed that a network for distributing nutrients has circulation length L, which in three dimensions serves roughly L^3 sites where nutrients leave the system. Any nutrient would, on average, pass L sites on the way to its destination, they figured. Therefore, the total nutrients in the network at any

CREDIT: K. SCHMIDT-NIELSEN, *SCALING: WHY IS ANIMAL SIZE SO IMPORTANT?*

given time must be roughly L^4 (destinations times stops en route). This represents blood volume, which based on empirical observations should be proportional to an organism's mass. The rest of the argument is reminiscent of Rubner's. The total metabolic rate is proportional to sites served (L^3, or $M^{3/4}$), which makes the specific metabolic rate proportional to $M^{-1/4}$, in agreement with Kleiber's law. The argument can also be adjusted to two-dimensional river networks, where it predicts cube-root scaling, in agreement with experimental observations.

Some experts say the simplicity of Banavar's model is a big plus. "I'd be happier if it were this way than the fractal model," says William Calder, a biologist at the University of Arizona, Tucson. But it must be interpreted with care, adds West: For example, a "site" cannot be an individual cell, because this would imply that the proliferation of cells could not keep pace with increasing organism size.

Banavar was not the only researcher trying to simplify the New Mexico team's model. West and his colleagues also felt that there had to be a broader argument that could apply to plants, animals, and even one-celled organisms lacking a vascular system. With that in mind, they scrapped the physics of fluid flow. In their latest *Science* paper, the team makes a case for a quarter-power law based mostly on geometry, particularly the hierarchical nature of circulatory networks. "We traded in the dynamics for the statement that hierarchy gives rise to a power law," West says. They argue that an organism's "internal area"—the total area of its capillary walls—fills up space so efficiently that it, in effect, adds a third dimension. The "internal volume" of all the vessels feeding the capillaries adds an extra dimension as well, scaling as the fourth power of internal length. The distinction between internal and external lengths, areas, and volumes is crucial, West says. "You really have to think in terms of two separate scales—the length of the superficial you and the real you, which is made up of networks."

The new argument by West's team poses its share of head-scratchers: If the internal length of an animal's circulatory system increases less rapidly ($M^{1/4}$) than the external length ($M^{1/3}$), what happens when it becomes too short to reach the skin? The answer, Dodds believes, may be a delicate balancing act: "I would argue that there are different scales in different parts of the animal"—that is, not one internal length scale but several. In the end, simplicity may have its limits. "The final theory will not be as simple as Banavar's but may be around the level of what West has done," Dodds says. "What I am sure of is that they will both be very controversial." **—DANA MACKENZIE**

Dana Mackenzie is a science writer based in Santa Cruz, California.

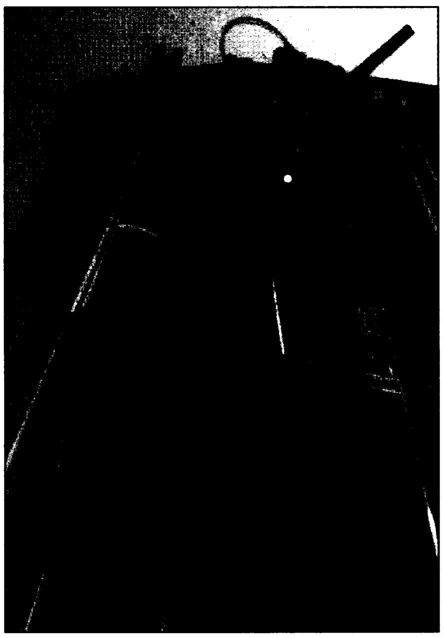
FLUID DYNAMICS

Soap Films Reveal Whirling Worlds of Turbulence

New techniques for studying "soap film tunnels" are giving researchers a glimpse into the surprising world of two-dimensional turbulence

Blowing a killer soap bubble takes a steady hand and a still day, as any child knows. But creating the kinds of soap films that thrill physicists goes far beyond child's play. Their high-tech films, clinging to a pair of wires hung a few centimeters apart, flow toward the floor and stream past strategically placed obstacles that stir roiling patterns in their wakes. The patterns, resembling swirls of smoke, are shedding new light on the intricate physics of turbulence in two dimensions (2D). "Soap films are a brilliant way to produce 2D turbulence," says fluid dynamicist Patrick Tabeling of the Ecole Normale Superieure in Paris. "They are a major contribution."

Two-dimensional dances with whorls, scientists believe, arise in nature when moving liquids or gases are confined to flat or curved surfaces. Cyclones and other large-scale wind flows in the atmospheres of planets fit this bill, says physicist Walter Goldburg of the University of Pittsburgh. These vortices are hundreds of kilometers across but just a few kilometers thick, so their motions are essentially 2D, Goldburg says. Plasmas corralled by magnetic fields in space or in fusion reactors, and ocean currents pinned in a narrow horizontal layer by sharp changes in temperature or salinity, may also be examples of 2D turbulence.



Physics in 2D. A 2-meter-long soap film streams downward between two wires in this apparatus designed by Maarten Rutgers.

CREDIT: BRENT DANIEL AND MAARTEN RUTGERS, THE OHIO STATE UNIVERSITY

At first glance, some of the swirling 2D patterns in these systems look like cross sections of 3D vortices, the more familiar brand of turbulence generated, for example, behind a jet's wings. However, radically different principles of physics govern the two types of turbulence, says physicist Robert Ecke of Los Alamos National Laboratory in New Mexico. And although physicists have plenty of theoretical models and computer simulations of 2D turbulence, testing these models and theories in the lab has proven difficult. A turbulent flow initially confined to a 2D sheet likes nothing better than to unfold into three dimensions, as researchers trying to study 2D phenomena in wind and water tunnels discovered early on. But now, 2D turbulence is beginning to reveal its secrets, such as how its vortices evolve and suddenly swap energy, thanks largely to new techniques for studying "soap film tunnels."

The soap films build upon work in 1986 by French physicist Yves Couder, who dragged objects through stationary films to watch how turbulent patterns decayed to stillness. A few years later, a team led by fluid dynamicist Mory Gharib, then at the University of California, San Diego, pioneered a moving film that could be replenished continuously—a key advance that mimics flows in nature.

Today, in a system devised by Goldburg and Xiao-lun Wu at Pittsburgh and refined by physicist Maarten Rutgers of The Ohio State University in Columbus, nozzles spray dilute dish soap continuously onto a pair of vertical wires. Cords draw the wires apart, stretching the soap into a rectangular patch of film that flows at speeds of a few meters per second. In the middle of the patch, the forces of gravity and air drag balance out so that the film reaches a steady "terminal velocity," like a skydiver with outstretched limbs. The film, a sandwich of soap molecules and water, is sev-