



LIFE ON THE SCALES

Simple mathematical relationships underpin much of biology and ecology

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A mouse lives just a few years, while an elephant can make it to age 70. In a sense, however, both animals fit in the same amount of life experience. In its brief life, a mouse squeezes in, on average, as many heartbeats and breaths as an elephant does. Compared with those of an elephant, many aspects of a mouse's life—such as the rate at which its cells burn energy, the speed at which its muscles twitch, its gestation time, and the age at which it reaches maturity—are sped up by the same factor as its life span is. It's as if in designing a mouse, someone had simply pressed the fast-forward button on an elephant's life. This pattern relating life's speed to its length also holds for a sparrow, a gazelle, and a person—virtually any of the birds and mammals, in fact. Small animals live fast and die young, while big animals plod through much longer lives.

"It appears as if we've been gifted with just so much life," says Brian Enquist, an ecologist at the University of Arizona in Tucson. "You can spend it all at once or slowly dribble it out over a long time."

Scientists have long known that most biological rates appear to bear a simple mathematical relationship to an animal's size: They are proportional to the animal's mass raised to a power that is a multiple of $1/4$. These relationships are known as quarter-power scaling laws. For instance, an animal's metabolic

rate appears to be proportional to mass to the $3/4$ power, and its heart rate is proportional to mass to the $1/4$ power.

The reasons behind these laws were a mystery until 8 years ago, when Enquist, together with ecologist James Brown of the University of New Mexico in Albuquerque and physicist Geoffrey West of Los Alamos (N.M.) National Laboratory proposed a model to explain quarter-power scaling in mammals (SN: 10/16/99, p. 249). They and their collaborators have since extended the model to encompass plants, birds, fish and other creatures. In 2001, Brown, West, and several of their colleagues distilled their model to a single formula, which they call the master equation, that predicts a species' metabolic rate in terms of its body size and temperature.

"They have identified the basic rate at which life proceeds," says Michael Kaspari, an ecologist at the University of Oklahoma in Norman.

In the July 2004 *Ecology*, Brown, West, and their colleagues proposed that their equation can shed light not just on individual animals' life processes but on every biological scale, from subcellular molecules to global ecosystems. In recent months, the investigators have applied their equation to a host of phenomena, from the mutation rate in cellular DNA to Earth's carbon cycle.

Carlos Martinez del Rio, an ecologist at the University of Wyoming in Laramie, hails the team's work as a major step forward. "I think they have provided us with a unified theory for ecology," he says.

The biological clock

In 1883, German physiologist Max Rubner proposed that an animal's metabolic rate is proportional to its mass raised to the $2/3$ power. This idea was rooted in simple geometry. If one animal is, say, twice as big as another animal in each linear dimension, then its total volume, or mass, is 2^3 times as large, but its skin surface is only 2^2 times as large. Since an animal must dissipate metabolic heat through its skin, Rubner reasoned that its metabolic rate should be proportional to its skin surface, which works out to mass to the $2/3$ power.

In 1932, however, animal scientist Max Kleiber of the University of California, Davis looked at a broad range of data and concluded that the correct exponent is $3/4$, not $2/3$. In subsequent decades, biologists have found that the $3/4$ -power law appears to hold sway from microbes to whales, creatures of sizes ranging over a mind-boggling 21 orders of magnitude.

For most of the past 70 years, ecologists had no explanation for the $3/4$ exponent. "One colleague told me in the early '90s that he took $3/4$ -scaling as 'given by God,'" Brown recalls.

The beginnings of an explanation came in 1997, when Brown, West, and Enquist described metabolic scaling in mammals and birds in terms of the geometry of their circulatory systems. It turns out, West says, that Rubner was on the right track in comparing surface area with volume, but that an animal's metabolic rate is determined not by how efficiently it dissipates heat through its skin but by how efficiently it delivers fuel to its cells.

Rubner should have considered an animal's "effective surface area," which consists of all the inner surfaces across which energy and nutrients pass from blood vessels to cells, says West. These surfaces fill the animal's entire body, like linens stuffed into a laundry machine.

The idea, West says, is that a space-filling surface scales as if it were a volume, not an area. If you double each of the dimensions of your laundry machine, he observes, then the amount of linens you can fit into it scales up by 2^3 , not 2^2 . Thus, an animal's effective surface area scales as if it were a three-dimensional, not a two-dimensional, structure.

This creates a challenge for the network of blood vessels that must supply all these surfaces. In general, a network has one more dimension than the surfaces it supplies, since the network's tubes add one linear dimension. But an animal's circulatory system isn't four dimensional, so its supply can't keep up with the effective surfaces' demands. Consequently, the animal has to compensate by scaling back its metabolism according to a $3/4$ exponent.

Though the original 1997 model applied only to mammals and birds, researchers have refined it to encompass plants, crustaceans, fish, and other organisms. The key to analyzing many of these organisms was to add a new parameter: temperature.

Mammals and birds maintain body temperatures between about 36°C and 40°C, regardless of their environment. By contrast, creatures such as fish, which align their body temperatures with those of their environments, are often considerably colder. Temperature has a direct effect on metabolism—the hotter a cell, the faster its chemical reactions run.

In 2001, after James Gillooly, a specialist in body temperature, joined Brown at the University of New Mexico, the researchers and their collaborators presented their master equation, which incorporates the effects of size and temperature. An organism's metabolism, they proposed, is proportional to its mass to the 3/4 power times a function in which body temperature appears in the exponent. The team found that its equation accurately predicted the metabolic rates of more than 250 species of microbes, plants, and animals. These species inhabit many different habitats, including marine, freshwater, temperate, and tropical ecosystems.

The equation gave the researchers a way to compare organisms with different body temperatures—a person and a crab, or a lizard and a sycamore tree—and thereby enabled the team not just to confirm previously known scaling laws but also to discover new ones. For instance, in 2002, Gillooly and his colleagues found that hatching times for eggs in birds, fish, amphibians, and plankton follow a scaling law with a 1/4 exponent.

When the researchers filter out the effects of body temperature, most species adhere closely to quarter-power laws for a wide range of properties, including not only life span but also population growth rates. The team is now applying its master equation to more life processes—such as cancer growth rates and the amount of time animals sleep.

"We've found that despite the incredible diversity of life, from a tomato plant to an amoeba to a salmon, once you correct for size and temperature, many

of these rates and times are remarkably similar," says Gillooly.

A single equation predicts so much, the researchers contend, because metabolism sets the pace for myriad biological processes. An animal with a high metabolic rate processes energy quickly, so it can pump its heart quickly, grow quickly, and reach maturity quickly.

Unfortunately, that animal also ages and dies quickly, since the biochemical reactions involved in metabolism produce harmful by-products called free radicals, which gradually degrade cells.

"Metabolic rate is, in our view, the fundamental biological rate," Gillooly says. There is a universal biological clock, he says, "but it ticks in units of energy, not units of time."

Scaling up

The researchers propose that their framework can illuminate not just properties of individual species, such as hours of sleep and hatching times, but also the structure of entire communities and ecosystems. Enquist, West, and Karl Niklas of Cornell University have been looking for scaling relationships in plant communities, where they have uncovered previously unnoticed patterns.

The researchers have found, for instance, that in a mature forest, the average distance between trees of the same mass follows a quarter-power scaling law, as does trunk diameter. These two scaling laws are proportional to each other, so that on average, the distance between trees of the same mass is simply proportional to the diameter of their trunks.

"When you walk in a forest, it looks random, but it's actually quite regular on average," West says. "People have been measuring size and density of trees for 100 years, but no one had noticed these simple relationships."

The researchers have also discovered that the number of trees of a given mass in a forest follows the same scaling law governing the number of branches of a given size on an individual tree. "The forest as a whole behaves as if it is a



Newly discovered scaling laws have revealed an unexpected relationship between the spacing of trees and their trunk diameters in a mature forest.

very large tree," West says.

Gillooly, Brown, and their New Mexico colleague Andrew Allen have now used these scaling laws to estimate the amount of carbon that is stored and released by different plant ecosystems.

Quantifying the role of plants in the carbon cycle is critical to understanding global warming, which is caused in large part by carbon dioxide released to the atmosphere when animals metabolize food or machines burn fossil fuels.

Plants, by contrast, pull carbon dioxide out of the air for use in photosynthesis. Because of this trait, some ecologists have proposed planting more forests as one strategy for counteracting global warming.

In a paper in an upcoming *Functional Ecology*, the researchers estimate carbon turnover and storage in ecosystems such as oceanic phytoplankton, grasslands, and old-growth forests. To do this, they apply their scaling laws to the mass distribution of plants and the metabolic rate of individual plants. The model predicts, for example, how much stored carbon is lost when a forest is cut down to make way for farmlands or development.

Martinez del Rio cautions that ecologists making practical conservation decisions need more-detailed information than the scaling laws generally give. "The scaling laws are useful, but they're a blunt tool, not a scalpel," he says.

Scaling down

The team's master equation may resolve a longstanding controversy in evolutionary biology: Why do the fossil record and genetic data often give different estimates of when certain species diverged?

Geneticists calculate when two species branched apart in the phylogenetic tree by looking at how much their DNA differs and then estimating how long it would have taken for that many mutations to occur. For instance, genetic data put the divergence of rats and mice at 41 million years ago. Fossils, however, put it at just 12.5 million years ago.

The problem is that there is no universal clock that determines the rate of genetic mutations in all organisms, Gillooly and his colleagues say. They propose in the Jan. 4 Proceedings of the National Academy of Sciences that, instead, the mutation clock—like so many other life processes—ticks in proportion to metabolic rate rather than to time.

The DNA of small, hot organisms should mutate faster than that of large, cold organisms, the researchers argue. An organism with a revved-up metabolism generates more mutation-causing free radicals, they observe, and it also produces offspring faster, so a mutation becomes lodged in the population more quickly.

When the researchers use their master equation to correct for the effects of size and temperature, the genetic estimates of divergence times—including those of rats and mice—line up well with the fossil record, says Allen, one of the paper's coauthors.

The team plans to use its metabolic framework to investigate why the tropics are so much more diverse than temperate zones are and why there are so many more small species than large ones.

Most evolutionary biologists have tended to approach biodiversity questions in terms of historical events, such as landmasses separating, Kaspari says. The idea that size and temperature are the driving forces behind biodiversity is radical, he says.

"I think if it holds up, it's going to rewrite our evolutionary-biology books," he says.

Enthusiasm and skepticism

While the metabolic-scaling theory has roused much enthusiasm, it has its limitations. Researchers agree, for instance, that while the theory produces good predictions when viewed on a scale from microbes to whales, the theory is rife with exceptions when it's applied to animals that are relatively close in temperature and size. For example, large animals generally have longer life spans than small animals, but small dogs live longer than large ones.

Brown points out that the metabolic-scaling law may be useful by calling attention to such exceptions. "If you didn't have a general theory, you wouldn't know that big dogs are something interesting to look at," he observes.

Many questions of particular interest to ecologists concern organisms that are close in size. Metabolic theory may not explain, for example, why certain species coexist or why particular species invade a given ecosystem, says John Harte, an ecologist at the University of California, Berkeley.

Some scientists question the very underpinnings of the team's model. Raul Suarez, a comparative physiologist at the University of California, Santa Barbara disputes the model's starting assumption that an animal's metabolic rate is determined by how efficiently it can transport resources from blood vessels to cells. Suarez argues that other factors are equally important, or even more so. For instance, whether the animal is resting or active determines which organs are using the most energy at a given time.

"Metabolic scaling is a many-splendored thing," he says.

Suarez' concern is valid, agrees Kaspari. However, he says, the master equation's accurate predictions about a huge range of phenomena are strong evidence in its favor.

Ecologists, physiologists, and other biologists appear to be unanimous on one

point: The team's model has sparked a renaissance for biological-scaling theory.

"West and Brown deserve a great deal of credit for rekindling the interest of the scientific community in this phenomenon of metabolic scaling," Suarez says. "Their ideas have stimulated a great deal of discussion and debate, and that's a good thing."

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