



BIOLOGIST JAMIE GILLOOLY THINKS
METABOLISM OFFERS NEW INSIGHTS INTO
THE RELATIONSHIPS BETWEEN ORGANISMS

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'Master' Equation

BY JOHN PASTOR

"I went to the woods because I wished to live deliberately, to front only the essential facts of life, and see if I could not learn what it had to teach, and not, when I came to die, discover that I had not lived."

—Henry David Thoreau

When Jamie Gillooly received his bachelor's degree in English Literature from the University of Michigan in 1988, he had no intention of becoming a biologist, and not the remotest idea that he would one day help construct a mathematical model that reduces all forms of life, from weeds to whales, to a few essentials.

Literature and poetry were Gillooly's passions. His one undergraduate science course — Introduction to Biology — didn't inspire him.

"Science was dry to me, so boring compared with a great novel. I didn't appreciate science until I realized it is a process of discovery, not just a bunch of stuff people figured out a long time ago," he says. That realization didn't begin to dawn on Gillooly until his final semester as an undergraduate, when he was reading Thoreau, Ralph Waldo Emerson and other transcendentalist writers.

Like Thoreau, whose path to becoming nature's poet laureate began with a canoe trip along the Concord and Merrimack rivers, Gillooly took paddle in hand and retraced that journey of discovery as part of UM's New England Literature Program.

"We would canoe down the river, actually follow Thoreau's path, and read his writings," Gillooly says. "We lived in the woods for eight weeks — and I felt I was totally in my element. When you read those things and you are in those places, it's so powerful."

But Gillooly's new-found appreciation for the natural world did not lead immediately to the service of science. He worked as a middle school teacher for a few years first. Eventually, however, the pull was too great. He earned a doctorate in zoology from the University of Wisconsin-Madison and in 2000 took a position as a post-doctoral associate in biologist James H. Brown's lab at the University of New Mexico.

Brown, a member of the National Academy of Sciences, had gathered scientists from fields as diverse as physics, ecology and mathematics to try to understand relationships between individual organisms and ecosystems.

Gillooly says the team "would literally lock ourselves in a room for eight-hour shifts. We'd just write notes on the board, write equations and look at data. It was pretty intense."

Another member of the team, Van Savage, says Gillooly's background in literature brought a unique perspective to the discussions.

"Jamie is a very open communicator, and that's important because people from different fields speak different languages," says Savage, now an assistant professor of biomathematics at UCLA Medical Center. "Scientifically, he is always finding a new aspect of biology to ask questions about."

Out of those cram sessions came a realization that nature was acting in a more predictable — albeit unexpected — way across species than many scientists had thought.

"I was focused on temperature, and Jim was focused on body size," Gillooly says. "My first six months there, we realized body size and temperature come together to explain tremendous variation in all kinds of biological rates and times, from cell lifespan in individuals to rates of nutrient cycling in whole ecosystems. It just worked."

Between 2001 and 2004, the group published numerous papers in prestigious journals like *Science* and *Nature*, including "Toward a Metabolic Theory of Ecology" in *Ecology* in 2004. That paper's abstract summed up their thinking: "Metabolism provides a basis for using principles of physics, chemistry and biology to link the biology of individual organisms to the ecology of populations, communities and ecosystems."

As for the mathematical model discussed in the research, supporters refer to it as the "master equation," but Gillooly shrugs at both the tone and implications.

However, it does provide a baseline for scientists to compare creatures as far-flung as elephants and fruit flies. What's more, the model apparently applies to societies as well as individual organisms.

"What's nice about the model is it's really simple, even though it may not look like it," Gillooly says of the equation $B = b_0 M^{3/4} e^{-E/kT}$, which predicts the size and temperature dependence of metabolic rate. "If you give me an organism's body size and temperature — two things that are very easily measured — I can tell you about processes like growth rate, lifespan and rates of molecular evolution. The reason is size and temperature control metabolic rate and, in turn, metabolic rate governs these other processes."

"Once you start viewing biological questions through this window, you have a perspective that is different from most other scientists, and that's an advantage," Gillooly says. "It provides a lot of novel insights. It's funny, every time we think we have

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covered the big ideas and applications of this theory, new things emerge. I would have never guessed two years ago that I would have gotten into broad-scale comparisons of acoustic communication.”

Gillooly has worked with other researchers to look at a variety of subjects through this lens of metabolic scaling — which basically says an organism’s lifespan, growth rate and rate of reproduction are largely determined by its size, temperature and the amount of energy it consumes.

What they found is that the same rules apply whether an organism is a plant, a fruit fly or an elephant. Life’s immense diversity, which has always made it difficult to compare drastically different organisms, may have a few common denominators after all.

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Photo Illustration: K. Kinsley-Momberger

Even the sounds animals make seem to be scalable.

Looking at data from nearly 500 species, Gillooly and Alexander G. Ophir of Oklahoma State University found the calls of crickets, whales and a host of other creatures are ultimately controlled by their metabolic rates — in other words, their uptake and use of energy.

“Very few people have compared cricket chirps to codfish sounds to the sounds made by whales and monkeys to see if there were commonalities in the key features of acoustic signals, including the frequency, power and duration of signals,” Gillooly says.

They learned that for all species, sounds are primarily controlled by individual metabolism, which in turn varies predictably with body size and temperature. The proof is in an audio file Gillooly plays during scientific presentations, and it is always a crowd-pleaser. When adjusted for metabolism, size and temperature, the chirp from a cricket rubbing its wings and the song emanating from a whale’s larynx sound the same.

Using the same principles to understand more about prehistoric animals, Gillooly says that the size of the largest dinosaurs ultimately may have been limited by their body temperatures. One of the larger animals, a behemoth called *Sauroposeidon proteles*, weighed close to 120,000 pounds and had a body temperature of nearly 118 degrees Fahrenheit — about as hot as most living creatures can get before the proteins in their bodies actually begin to break down.

“The theory is very young. Since the metabolic theory paper came out in 2004, it’s really kind of exploded,” Gillooly says. “It can help to better manage fisheries and oceans and to

understand forests and global warming. Even in the medical sciences, tumors and tumor growth follow these same models, so the possible applications are tremendous.”

What’s more, the theory apparently applies to societies as well as individual organisms.

Take ants, for example. When Gillooly applied the theory to insect colonies, he found that they follow the same biological rules that govern individual organisms.

For more than a century, biologists have marveled at how ants, bees and other social insects work together to determine the survival and growth of a colony.

But taken as a whole, these colonies are nearly indistinguishable from single organisms. Analyzing data from 168 different social insect species including ants, termites, bees and wasps, Gillooly and colleagues found that the lifespan, growth rates and rates of reproduction of whole colonies — when considered as a single, living being — were about the same in terms of their physiology and life cycle as individual organisms that proportionally weigh about the same and use about the same amount of energy — a cat, for example.

The discovery attracted the attention of famed Harvard biologist Edward O. Wilson, co-author of the book “The Super-Organism,” who said the findings were notable in originality and importance, adding new perspective to how insect societies are organized.

For Gillooly, it was another step toward linking different levels of biological organization, from cells to individuals to populations to communities to ecosystems.



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“In life, two of the major evolutionary innovations have been how cells came together to function as a single organism, and how individuals joined together to function as a society,” Gillooly says. “Relatively speaking, we understand a considerable amount about how the size of multicellular organisms affects the life cycle of individuals based on metabolic theory, but now we are showing this same theoretical framework helps predict the life cycle of whole societies of organisms.”

In another example of the power of the theory, Gillooly and colleague Andrew P. Allen, then at the University of California-Santa Barbara, demonstrated that higher temperatures near the equator speed up the metabolic rates of the inhabitants, which in turn influences the rate of DNA evolution, and eventually the actual creation of a new species.

It takes about 10 to the 23rd power — that’s 1 followed by 23 zeros — of energy units called joules to generate a new species of plankton. That’s equivalent to about all the fossil fuel burned on the planet in a year — quite a high cost for the evolution of tiny organisms that drift in the sea. But for the first time, the process of speciation could be quantified in terms of energy.

In time, Gillooly hopes these efforts will lead to a general mathematical theory of ecology; one that will provide a baseline for understanding different ecosystems and help shape sound environmental policy.

John Whitfield, who began covering metabolic theory as a writer for *Nature* and has since written a book on the subject, says the idea that nature can be explained in such broad strokes is foreign to biologists.

“In biology, there is not such a market for grand, ambitious theories as there is in physics,” says Whitfield, author of

In the Beat of a Heart: Life, Energy, and the Unity of Nature.

“Biologists generally are more exploratory; they tend to think there are plenty of things for them to solve before working on some grand, overarching theory. It has kind of meant that metabolic theory has not swept as quickly through all the areas to which it might be applied.”

While proponents of the theory are using it to link the different organizational levels of life — cells, organisms and societies, Gillooly would like to see it used to connect different disciplines.

“I think it will help us address a number of important questions in different branches of biology, everything from longstanding questions of the origin and maintenance of biodiversity — which has always been the Holy Grail of ecology — to better understanding of global change and environmental issues,” he says.

That may seem a lofty ambition for a humble mathematical model and a literature aficionado turned scientist. But Gillooly will not shirk from the woods to front the essential facts of life.

As Thoreau said, “Do not worry if you have built your castles in the air. They are where they should be. Now put the foundations under them.” ☒

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