

Mathematical Population Biologist

Joel E. Cohen

When asked my profession, I usually respond with a telescoping sequence: scientist – biologist – mathematical biologist – mathematical population biologist. Most people look away with regret after the first word, and I stop there. I proceed, step by step, only on provocation.

What does this mathematical population biologist profess? I try to understand biological populations – humans, bacteria, trees, fish, viruses, trypanosomes that cause Chagas disease, bugs that transmit infection, and food webs, but normally not populations of light bulbs or buildings – by using mathematics in the broadest sense, which includes mathematics, statistics, and computation. As a tool-maker, I try to create new mathematics to understand questions in population biology.

For example? Shrimp are generally more numerous than whales per square kilometer of ocean surface where both occur. In a single species of oak, seedlings are more numerous per square kilometer of land than mature giants. Bigger organisms are rarer than smaller organisms. Almost always, the population density of organisms declines as their average body mass increases. Here's the surprise: the relationship of population density to average body mass can be described well by a simple mathematical formula, a power law.

What is a power law? In elementary geometry, the area of a square increases as the second power (the square) of the length of an edge: $\text{area} = (\text{edge length})^2$. This is a power law with exponent two. The volume of a cube increases as the third power (the cube) of the length of an edge: $\text{volume} = (\text{edge length})^3$. This is a power law with exponent three. Since a cube has six square faces, the surface area of a cube is six times the area of one face of the cube: $\text{surface area of cube} = 6 \times (\text{edge length})^2$; another power law with exponent two. It follows that the surface area per unit volume of a cube is $6 \times (\text{edge length})^2 / (\text{edge length})^3 = 6 / (\text{edge length})$. This power law (with exponent negative one, for those at ease with such details) explains why, when you take a baby out of doors in cold weather, you should wrap the baby more warmly than you wrap yourself. You have a much bigger edge length (height or girth, for example) than the baby does. Therefore, to the extent that you and the baby are more or less the same shape (even if neither of you is a cube), you have a smaller ratio of surface area to volume than the baby, so you lose relatively less heat through your surface, per unit of your volume, than the baby loses through its surface, per unit of his or her volume.

Ecologists have verified so many times that population density is inversely proportional to some (disputed) power of average body

mass that they've given this power law a name: density-mass allometry. Although density-mass allometry has the same power-law formula as the geometric power laws, there is a major conceptual difference. The geometric power laws relate two attributes of individual squares, cubes, or other geometrical objects of different sizes. By contrast, in density-mass allometry, population density (defined as the number of organisms per unit of area or of volume) is not an attribute of any individual, but is an attribute of a population (ensemble of organisms). Average body mass – the other quantity in density-mass allometry – is a hybrid of individual and population attributes: body mass is an attribute of an individual, but the average body mass is a statistical attribute of a population.

Mathematical biology is interested in patterns and mechanisms applicable to individuals and populations. Mathematical population biology focuses on patterns and mechanisms applicable to the attributes of populations that are not attributes of individuals. In that difference lies scientific opportunity. Population thinking in biology is less than two hundred years old. The mathematical tools for population thinking are also young, and in many cases, much younger. Far more mathematical tools for population thinking remain to be invented and discovered than we now possess.

In 2007, I had the good fortune to spend the summer in the laboratory of evolutionary biologist Michael Hochberg at the University of Montpellier. That his laboratory was located in a beautiful old city in southern France near the Mediterranean coast was not irrelevant, but was not my primary motivation for going there. Montpellier has perhaps the world's largest concentration of population biologists in basic and applied fields. I had known and admired Hochberg's work over decades.

He and two graduate students were designing experiments with bacterial populations to test theoretical predictions published in 2003 about Taylor's law. By 2007, Taylor's law had been the subject of an estimated one thousand papers. Hochberg invited me to join the design and analysis of the experiments. For starters, he asked, what did I think about Taylor's law?

Truth be told, I knew nothing about it, but on first exposure, I was fascinated. Initially, Taylor's law seemed magical; simple but widely applicable. Though his examples were not the first, ecologist L. Roy Taylor published in *Nature* in 1961 twenty-four examples of the power law that would later unjustly be named after him. Chester I. Bliss published examples in 1941, S. B. Fracker and H. A.

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Brischle in 1944, B. I. Hayman and A. D. Lowe in 1961. These examples ranged from aphids to zooplankton.

In the experiments of Hochberg and his students, clones of a bacterial species were grown in laboratory dishes that had eight different amounts of bacterial food (nutrient concentrations), with eight replicate dishes for each level of nutrient concentration. All dishes started with the same number of bacteria. After twenty-four to thirty-six hours, the students estimated the number of bacteria in each dish. For each level of nutrients, they estimated the mean and the variance of the population density of bacteria in the eight replicates. The mean is simply the average of the bacterial counts (the sum of the counts in all eight dishes, divided by eight). The variance is a standard statistical measure of scatter, that is, of how much the counts varied around the mean: it is the average of the squared difference of each count from the mean count. The bigger the variance, the greater the scatter. Taylor's law connects the mean and the variance: it asserts that the variance of the counts should be a power of the mean of the counts, with an exponent near two. Both variables in Taylor's law – the variance and the mean of counts – are intrinsically population attributes, not attributes of individuals. Sure enough, when the experimental dust settled, the eight points (one for each nutrient concentration) lined up as predicted by Taylor's law with an exponent not statistically distinguishable from two. How did the bacteria know?

My own work, some of it not yet published, with collaborators in many countries, has confirmed Taylor's law in oak forests in New York; mountain beech forests in New Zealand; parasites and hosts in New Zealand lakes; gray-sided voles in Hokkaido, Japan; and humans in Norway and the United States.

Beyond the empirical testing of Taylor's law, theoretical questions beckon. Why is Taylor's law so successful with so many diverse populations, and far beyond population biology? To explain why a simple formula describes so well such a widespread empirical pattern, I have shown mathematically that several well-known models of population dynamics lead to Taylor's law. One of these models was published prominently (by others) in 1969. But it was not until 2013 that my coauthors and I established a connection between that 1969 model and Taylor's law. We showed that the mechanisms assumed in the model described the details of observed tree counts over seventy-five years of censuses from Black Rock Forest, New York, and correctly predicted the form and parameters of Taylor's law for the trees.

In addition to trying to explain Taylor's law, I have been exploring its consequences. Independently, the Chilean ecologist Pablo Marquet and his colleagues and my colleagues and I realized that a combination of Taylor's law and density-mass allometry predicted a new power law, which I called variance-mass allometry: the vari-

ance of population density should be a power of average body mass. My colleagues and I confirmed variance-mass allometry empirically for plants and animals.

Completely unexpectedly, in purely theoretical work, I discovered that the exponent of Taylor's law could pass through a singularity: as one parameter in a highly simplified climate model changed smoothly, the exponent of Taylor's law started at two, grew faster and faster, exploded to positive infinity, jumped to negative infinity, and returned to two. Subsequently, I showed that classical population models like branching processes and linear birth-and-death processes also led to Taylor's law and displayed abrupt changes of the exponent of Taylor's law in response to smooth changes in their parameters. In these examples, abrupt biotic change crawled unbidden out of the theoretical woodwork of smooth environmental change, hissing with teeth bared. A greater investment in understanding the conditions, warning signals, and consequences of abrupt biotic change seems in order.

Many questions remain unanswered. For example, how much of the widespread empirical success of Taylor's law reflects the biology of populations, and how much reflects statistical processes independent of biology? Taylor's law is used in controlling insect pests of economically important crops like cotton and soybeans and in assessing extinction risks in conservation. What are other practical or scientific applications, in mathematical population biology and beyond?

When I was fourteen, living in Battle Creek, Michigan, I knew I wanted to become a composer of music, or a writer of journalism or poetry, or a mathematical biologist. I knew then that biology had irresistible problems and that new mathematics would be required to make sense of them. I've been lucky. Nearly six decades later, I am still in love with music, poetry and prose, and the adventure of mathematical population biology. ■

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Most of Joel E. Cohen's academic publications are freely available for download at <http://lab.rockefeller.edu/cohenje/cohenall>. For more background reading on these topics, see Nicolas Bacaër, *A Short History of Mathematical Population Dynamics* (London; Dordrecht, The Netherlands; Heidelberg, Germany; New York: Springer-Verlag, 2011); Joel E. Cohen, "Mathematics is Biology's Next Microscope, Only Better; Biology is Mathematics' Next Physics, Only Better," *Public Library of Science Biology* 12 (12) (2004): 2017–2023; and Zoltán Eisler, Imre Bartos, and János Kertész, "Fluctuation Scaling in Complex Systems: Taylor's Law and Beyond," *Advances in Physics* 57 (1) (2008): 89–142.



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