

Spherical cows help to dump metabolism law: 3/4-power law is actually 2/3

February 3 2010, by Joshua E. Brown

(PhysOrg.com) -- Apparently, the mysterious "3/4 law of metabolism" -proposed by Max Kleiber in 1932, printed in biology textbooks for decades, explained theoretically in *Science* in 1997 and described in a 2000 essay in *Nature* as "extended to all life forms" from bacteria to whales -- is just plain wrong.

"Actually, it's two-thirds," says University of Vermont <u>mathematician</u> Peter Dodds. His paper in the January 29 edition of <u>Physical Review</u> <u>Letters</u> helps overturn almost eighty years of near-mystical belief in a 3/4 exponent used to describe the relationship between the size of animals and their resting metabolism.

Two-thirds or three-quarters?

To understand the debate between 2/3 and 3/4, assume a spherical cow. "That's what a physicist would do," Dodds says, laughing. Basic geometry shows that the surface area of this difficult-to-milk creature would increase as the square of its radius while the volume would increase as the cube of the radius. In other words, the exponent that describes the ratio of surface area to volume is 2/3.

Next, assume a spherical mouse. OK, now compare the resting metabolic rates of these sorry animals. Since the point of resting metabolism is to keep a warm-blooded animal warm (and alive!) with the lowest necessary <u>energy use</u>, both geometry and common sense suggest that the



cow would have a lower rate of metabolism per cell than the mouse: the mouse, with more surface area relative to its volume, would lose heat faster than our cartoon cow.

And what about in real animals? In 1883, a German physiologist named Max Rubner measured the heat output of some dogs ranging from a few pounds to nearly seventy. He plotted these numbers to show that the dog's metabolic rates were proportional to their mass with an exponent of 2/3 -- just like the geometry of an imaginary spherical beast would suggest.

But, in 1932, Swiss agricultural chemist Max Kleiber presented a paper with a now-famous graph. It plotted, on a <u>logarithmic scale</u>, the body weight of 13 mammals, ranging from rats to cows, against their resting metabolism. Strangely, the line traced through the data points did not conform to Rubner's observation nor common sense. Instead, it hewed to a line with a somewhat steeper slope of about .73. To make it easier for slide rule use, he rounded the exponent to a neat .75. Kleiber's 3/4-power law was born.

"Kleiber's original data is a mess, a complete mess," says Dodds, "but it became something everyone believed in. The idea of quarter-powers begins to take on this spooky, magical quality. Nobody can explain it, but it's a secret law of the universe. It's quarterology!"

Over the next decades, hundreds of animals' resting metabolisms were measured or estimated, from microbes to whales. The results in various groups of animals ranged from slopes of less than 2/3 to greater than 1. But as Vaclav Smil wrote in a sweeping "millennium essay" for Nature they were "close enough to the 0.75 line," and concluded that "the 3/4 slope is representative for all" animals.

"Some data seems to fit this 3/4 line -- if you're looking for it!" says



Dodds. "It was pre-supposed to be true -- and became a universal overarching law that somebody needs to explain."

Instead of explaining it, in the 1960s a Scottish conference on energy metabolism simply voted, 29-0, to enshrine 3/4 as the official exponent. Then, in 1997, an elegant, though controversial, paper by Geoffrey West and colleagues was published in Science that claimed to derive 3/4 from first principles, drawing on ideas about fractals in networks and the growing length of tubes.

"The problem is their paper fell to pieces mathematically. It just didn't work. Unfortunately, I showed that and published a paper with my advisor and a fellow student in 2001," Dodds says. They also reanalyzed data from Kleiber and six other scientists and concluded that there is little empirical evidence for rejecting 2/3 in favor of 3/4. "But we didn't have a better theory," Dodds says, "or some way to clean it all up."

Network matters

Until now. Dodds's new paper explores the geometry of branching networks -- like blood supply -- to show how a material, like blood, can be most efficiently delivered. "If you're going to build organisms with a central source, like a heart, that places physical constraints that evolution has to run up against," he says. "These constraints won't let the ratio be too far away from 2/3."

"My new paper follows the argument that was put forth in 1997 -- that, somehow, networks give rise to the 3/4 law. They were right that supply networks are key to understanding the metabolic limitations of animals. Except my paper shows that networks give rise to the 2/3 law, actually," Dodds says, "If you do the math properly."

"What's good here is that the network supplying to the inside of this



system matches with the 2/3 exponent you'd expect from surface area," he says. And recent statistical analyses continue to show that the 2/3 exponent fits well empirically with large data sets for both mammals and birds. It seems that Rubner got it right in the 1880's after all.

Of course, it may be that biologists -- who delight in detail, local mechanisms and exceptions -- will win out over statistical physicists -- who look for evidence of universal patterns in nature: there may be no single exponent to describe the scaling of metabolism. A line drawn through a confounding scatter of data about specific animals across orders of magnitude may be just a line, not a law. But a confluence of facts -- greater understanding about how a network best minimizes volume, as evolution would favor in the costly production of blood supply; surface area geometry; and re-analysis of Kleiber's and other data -- seem to be pummeling the once-beguiling 3/4 law into dust.

"Especially for smaller guys," Dodds says, "like birds, it's just absolutely, stone-cold 2/3."

More information: Optimal Form of Branching Supply and Collection Networks, <u>DOI:10.1103/PhysRevLett.104.048702</u>

Provided by University of Vermont

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