PERSPECTIVES: ECOLOGY

Elephants, Mice, and Red Herrings

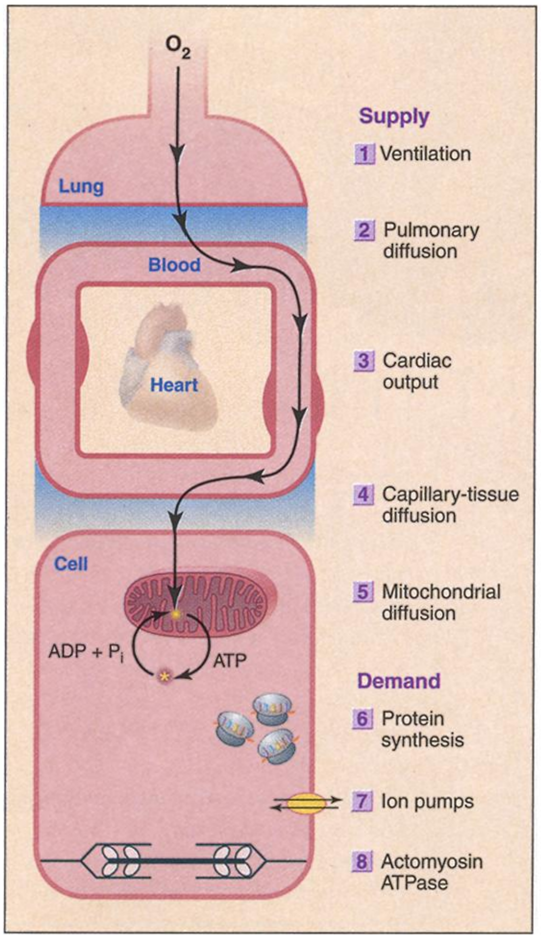
Gary P. Burness

The equation that describes the dependence of basal metabolic rate (BMR) on body mass in mammals is probably the most widely discussed of all scaling relationships (*1*). This relationship is often called the mouse-to-elephant curve to denote the large range in body sizes that it represents. BMR increases with body mass according to the equation BMR = aM^b, where a is the scaling constant (intercept), M is body mass, and b is the scaling exponent. In the 1930s, the exponent b was shown to be closer to 0.75 than to 0.67 (as predicted from surface area–to–volume ratios). Since then, biologists have been fascinated with the $^3/_4$ power law and with understanding the scaling of what Kleiber called "the fire of life" (*2*). Writing in a recent issue of *Nature*, Darveau *et al.* (*3*) may have identified the basis for this most fundamental of scaling relationships.

To date, most studies of metabolic scaling have sought to identify the single factor, or single rate-limiting step, that enforces its own scaling exponent on BMR. Recent examples of this approach include studies claiming that the fractal-like nature of biological distribution systems (such as the mammalian respiratory and circulatory systems) enforces an exponent of 0.75 on BMR (*4*). Darveau *et al.* argue that all such "single-cause" explanations for the scaling of BMR are, in fact, flawed. They reason that metabolic rates in vivo are not controlled by a single rate-limiting step, but rather, control is shared among many steps in metabolic pathways or in physiological systems (*5*). Although the field of metabolic regulation recognized this 40 years ago, with a few exceptions (*6*) it has been largely overlooked in studies of metabolic scaling.

BMR is frequently estimated by measuring whole-body O_2 consumption because rates of O_2 consumption correlate with rates of ATP synthesis and ATP use by cells. Darveau *et al.* recognized that each step in the pathways of ATP synthesis and use has its own scaling behavior with body mass, and its own degree of control over whole-animal metabolic rates. Could it be that many linked steps, rather than a single step, determine Kleiber's 0.75 scaling exponent? Darveau and co-workers think so.

To test their "multiple-causes model," Darveau *et al.* tackled the scaling of both BMR and maximal metabolic rate (MMR), two metabolic states that differ in their scaling exponents. When an animal is running at its BMR, steps that supply O_2 and fuel to cells have an excess capacity and exhibit little control over BMR (see the figure, steps 1 to 5). An excess capacity is necessary at BMR, because if these steps were rate limiting, an animal would be unable to elevate its metabolic rate above basal levels. Darveau *et al.* argue that this excess capacity is fatal for all models claiming that distribution systems (*4*), or other "energy supply side" processes, determine the scaling of BMR. BMR is determined by "energy demand side" processes, chiefly protein synthesis and the pumping of Na^+ ions, which scale with individual exponents of 0.77 and 0.72, respectively (see the figure, steps 6 and 7). With their model, Darveau *et al.* calculated that BMR should scale with body mass with an exponent b of between 0.76 and 0.79. This is certainly within the range of Kleiber's 0.75 exponent (*2*).



Multiple causes for the scaling of metabolic rate. O_2 enters the lungs and is transported through the circulation into the mitochondria to produce ATP. Key energy-supply processes (contributing directly or indirectly to ATP synthesis) and energy-demand processes (that use ATP) are numbered and listed on the right. Each process scales with body mass, and contributes some control over O_2 flux at BMR and MMR. At BMR, the scaling exponents of energy-demand processes dominate the global scaling exponent b; at MMR, energy-supply processes dominate b. [Modified from (*6*)]

In an exercising animal, MMR is achieved when a continued increase in exercise intensity does not result in a further increase in whole-body O_2 consumption. At MMR, "energy supply side" processes dominate the control of O_2 flux, each scaling with an exponent between ~0.7 and ~1.0 (see the figure, steps 1 to 5). The primary "energy demand side" processes are involved in muscle contraction, but because of an excess capacity in these steps, which allows for high anaerobic power output during sprinting, they offer little control over O_2 flux (see the figure, steps 7 and 8). On the basis of Darveau *et al.*'s model, MMR should scale with body mass with an exponent b in the 0.8 to 0.9 range. This is steeper than the exponent for BMR, in accordance with empirical data, and is astonishingly close to a recent estimate of $b = 0.88$ (*7*).

Currently, this is the only model that can explain the different scaling exponents of BMR and MMR. At BMR, the exponent b is determined largely by "energy demand side" processes, whereas at MMR, most control is on the "energy supply side." The crucial difference between the Darveau *et al.* model and all previous models is that instead of a single physiological system serving as a rate-limiting step, control is shared among many linked steps.

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By applying current concepts in metabolic regulation to the study of scaling, Darveau *et al.* are left to conclude that most previous attempts at understanding the mouse-to-elephant curve were simply red herrings. If their approach holds up to the intense scrutiny that it will no doubt receive, their contribution will fan studies of Kleiber's "fire of life," as would a breath of fresh air.

References

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PERSPECTIVES: GEOCHEMISTRY

Tiny Tracers Tell Tall Tales

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Recent advances in seismic tomography and dynamic modeling of Earth's interior have reopened the question of how Earth's mantle has evolved. Did the mantle evolve as a chemically layered system, or has it always convected as a whole? And what are the consequences for the preservation and location of its geochemical components?

Noble gases trapped in the silicate mantle may hold the key to resolving this question. These volatile, unreactive, and silicate-incompatible elements give us information about the origin of terrestrial volatiles and the processes and conditions in early Earth history that have incorporated these elements into the silicate mantle (rather than partitioning them into the atmosphere). They further constrain how much of the mantle's volatiles have escaped to the atmosphere over Earth's history, and they preserve a record of volatile-rich regions still existing in the mantle today.

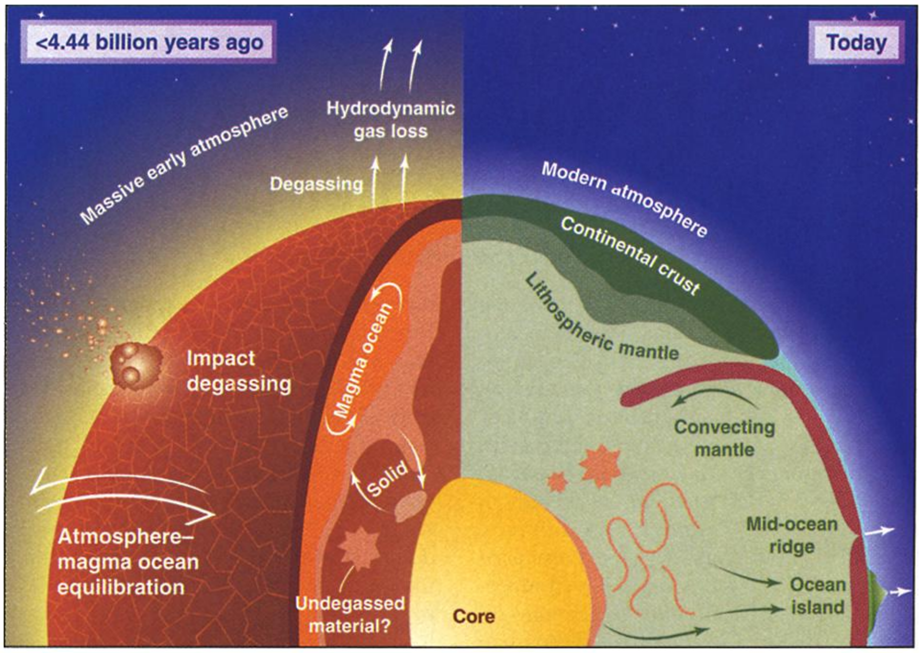
The noble gases He, Ne, Ar, Kr, and Xe produced by radioactive decay (mostly from U, Th, and K) differ in their isotopic composition from the original or "primordial" noble gases. Primordial noble gases in today's Earth originate either directly from the solar nebula or from volatiles trapped in accreting material (such as meteorites hitting the early Earth). Compared with these sources, the primordial noble gases in today's terrestrial atmosphere are enriched in their heavy isotopes.

The enrichment may be a result of the loss of an early, dense atmosphere in the first 100 million years of Earth's history (*1*). During a high-energy phase of the early Sun, hydrogen streamed from this atmosphere into space, carrying with it lighter volatile elements and isotopes (*2*). However, different noble gases have varying degrees of enrichment that cannot be caused by a single event. Differential release of noble gases from the mantle into the atmosphere because of their different solubilities in magma, combined with various stages of atmosphere loss, may provide the answer (*3*).

Noble gases trapped since accretion are still degassing from the mantle into the atmosphere today. The ratio of primordial to radiogenic noble gas isotopes in mantle material, for example, $^3He/^4He$, reflects the ratio of noble gas to U and Th. Basalts from mid-ocean ridges, which sample the upper mantle, have a remarkably uniform $^3He/^4He$ ratio. In contrast, $^3He/^4He$ ratios of ocean island basalts may be lower or higher than at the ridges. Major ocean island "hot spots," such as Hawaii and Iceland, have a higher $^3He/^4He$ ratio than mid-ocean ridges, an observation that has been a cornerstone of the "layered mantle" model that has dominated mantle geochemistry for the last 20 years. In this model, ocean island volcanoes sample a lower, more volatile-rich layer that has been preserved over Earth's lifetime below the seismic discontinuity at 670 km depth.

This model has recently come under scrutiny. Tomographic images have provided evidence for subducted material passing through the 670-km discontinuity (*4*). And numerical models of mantle convection show that neither the high viscosity of the lower mantle nor the phase change at 670 km can preserve layering or large-scale geochemical heterogeneity in the deep mantle (*5*). The models also show that the observed mass balance of radiogenic noble gas between atmosphere and mantle is not unique to a layered mantle (*5*). This presents us with a fundamental problem: How and where are primordial noble gases preserved in the mantle?

The problem is compounded by the fact that a large portion of ocean island basalt stems from material that has been subducted and recycled into the mantle (*6*). Recy-



Then and now. During accretion, large bodies are efficiently degassed on impact (**left**), yet noble gas measurements suggest that reservoirs within Earth's mantle remain volatile-rich today (**right**). Possible causes include equilibration between a magma ocean and an early massive atmosphere, or incorporation of undegassed material into the mantle, perhaps from an early stage of accretion. Any model describing the evolution of the mantle must account for why different regions in the mantle preserve distinct geochemical signatures in a dynamic convecting regime.

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