The Space-Lifetime Hypothesis: viewing organisms in four dimensions, literally

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Abstract

Much of the debate about alternative scaling exponents may result from unawareness of the dimensionality appropriate for different data and questions: in some cases analysis has to include a fourth temporal dimension and in others it does not. Proportional scaling simultaneously applied to an organism and its generation time, treating the latter as a natural fourth dimension, produces a simple explanation for the $3/4$ power in large-scale interspecies comparisons. Analysis of datasets of reduced dimensionality (e.g., ones constructed such that one or more of the four dimensions are fixed), results in predictably lower metabolic exponents of $2/3$ and $1/2$, under one and two constraints, respectively. Our space-lifetime view offers a predictive framework mutually consistent with much of the content of existing "3-dimensional" theories, but does not currently offer an alternate mechanism. Our view is useful as a step in developing a more complete mechanistic theory of metabolic scaling.

Introduction

The ¾ power scaling of metabolism with animal body mass (Kleiber's Law;Kleiber 1932) generalized to all forms of life (Brown et al. 2004; Hemmingsen 1960; Savage et al. 2004), has been not unlike Fermat's Theorem in the theory of integers: it is an observation that has been relatively easy to see but hard to explain.

From the beginning, dimensional arguments have played an important role in attempts to account for metabolic scaling. Before Kleiber, metabolism was thought to scale as the ⅔ power of mass, since organisms metabolize through two-dimensional surfaces but supply a three-dimensional body (Rubner 1883). Recent work has produced a largely satisfactory general explanation of the observed tendency for metabolic rates to scale interspecifically according to Kleiber's law (instead of ⅔) by focusing on the geometry of organisms' internal distribution networks for metabolites or nutrients (Banavar et al. 2002; Banavar et al. 1999; West et al. 1997; West et al. 1999). In this theoretical approach the ¾ exponent results because the network scales as if it has a metaphorical "extra" spatial dimension, related to the extra distances that a functional network requires as it increases in size (but for different reasons, depending on the models of different research groups). This characteristic of networks has been dubbed the "fourth dimension of life" (West et al. 1999). However, here we discuss something different: we argue that there is a distinct and literal sense in which the conventional fourth dimension — time — may be profitably incorporated into biological scaling theory. Our goal here is to adopt this literal (rather than metaphorical) four-dimensional view of organismic scaling and explore novel predictions arising from it.

45 Part of our motivation is that even if network geometry explains the prevalence of
46 Kleiber's law, there is considerable variation in the degree to which different subsets of
47 organisms and taxa conform to it (Glazier 2005; White et al. 2007). The field of
48 Metabolic Ecology, recently "baptized" by Brown and colleagues (Brown et al. 2004),
49 has developed quickly over the last decade and incorporates many previously discovered
50 $\pm 1/4$ power allometries, including those for generation time (Bonner 1965), rate of
51 population increase (Fenchel 1974), population density (Damuth 1987; Damuth 2007)
52 and many others discovered and summarized by earlier workers (Calder 1984; Peters
53 1983; Savage et al. 2004). All exhibit variation and most are interrelated, such that
54 articulating an adequate theoretical account of the empirical complexity of metabolic
55 ecology appears to be a daunting task (Glazier 2005). A four-dimensional approach
56 reveals order and simplicity not readily apparent in the traditional three-dimensional
57 view.
58 Our point of departure is a well-known observation: With respect to body mass
59 (M) in a wide range of taxa, most life history traits scale either as approximately $M^{-1/4}$
60 (rates of physiological processes, and reproduction) or as $M^{1/4}$ (various times, including
61 generation time and lifespan, (Brown et al. 2004; Calder 1984)). It is striking that when
62 combined with the $3/4$ interspecific scaling of metabolism, such life history scaling gives
63 rise to a host of invariants or isometries with respect to body mass (Calder 1984; Charnov
64 1993). For example, lifetime metabolism scales as $M^{3/4} \times M^{1/4} = M^1$ and thus is
65 proportional (isometric, not allometric) to body size. As a consequence, since mass-
66 specific metabolism scales as $M^{-1/4}$, the lifetime metabolism of each gram of an
67 organism is independent of body size. Though frequently remarked upon, this

characteristic of the lifespan is usually considered an outcome of other scaling relationships (Brown et al. 2004; Lindstedt and Calder 1981) and has not been treated as a primary principle of scaling theory — although it has formed the basis of a theory of aging (Pearl 1928). To us, these observations suggest that, instead, the scaling of lifetimes may reflect a fundamental manner in which organisms of all body masses are ecologically and evolutionarily functionally similar. Thus, we would expect that adding time to scaling theory would simplify the theory with no loss of explanatory power.

Here we build forcefully on this suggestion by defending a simple proposition: it is productive to view organisms as four-dimensional objects with three spatial dimensions and one temporal dimension that is equal to the generation time. This *space-lifetime* hypothesis has immediate implications. Scaling now has to be thought of as simultaneous proportional change in all linear dimensions and in generation time. On this view, $\frac{3}{4}$ scaling of metabolism is not at all surprising since the exchange of energy with the environment takes place through a three-dimensional surface (two spatial and one temporal) and expenditures are correspondingly four dimensional (three spatial and one temporal). All the $\frac{1}{4}$-power allometries for linear dimensions and life history follow simultaneously from this simple view.

Blum (1977) reasoned similarly that if organisms were literally four-dimensional then the $\frac{3}{4}$ exponent follows easily, but he did not suggest what that fourth dimension should be. Time associated with physiological processes has been treated as an explicit dimension in some physiological models of metabolism (da Silva et al. 2006; Heusner 1982b) and of course plays a key role in many others (e.g., Banavar et al. 2002). However, in this paper we are concerned with ecological time, and specifically

generation times. Ecological time-related characters have been mentioned in the literature as candidates for a fourth dimension, but this topic has not been explored further (Calder 1984; Hainsworth 1981).

It is a straightforward observation that, to a first approximation, the power of unity in the lifetime metabolic-expenditure isometry ($M^{3/4} \times M^{1/4} = M^{1}$) is subdivided into approximately equal quarters among the four total temporal and spatial dimensions: lifespan scales as $M^{1/4}$ and metabolic rate per chronological unit of time as $M^{3/4}$. Purely equal subdivision among the dimensions does not have to occur, and in fact there may be many exceptions. For example, using the database of Froese and Pauly (2000) we determined (Ginzburg, unpublished ms.) that the slope of metabolic rate of fishes, after adjusting for temperature, is 0.84, higher than $3/4$. We found that at the same time fish generation time scales with the exponent of 0.16, so the lifetime metabolism scales again as power 1. In contrast, mammals show a more even distribution between temporal and spatial dimensions (Calder 1984).

Generation time as a dimension

Why should generation time be so significant that it forms a fourth dimension for organisms? Time units driven by astronomical events do not form a natural timescale for biology. Although organisms may respond to various astronomical cycles, the periodicity of such cycles depends upon accidental properties of the solar system and not the functional requirements of biological systems. When we adopt a timescale more suitable for organisms we would expect it to exhibit a clear relationship to processes important for organismic function and fitness.

113 Since populations of established species tend to be roughly stable over the long
114 run, the per-capita rate of survival to the next generation has to be approximately unity.
115 That is, one surviving daughter of a size equal to its mother has to replace each mother
116 per generation. This is a requirement for ecological and evolutionary success.
117 Constructing one viable and reproductively capable daughter requires a certain duration
118 (a generation time) that is conveniently viewed as an organism's fourth dimension. So, on
119 average, it takes a generation time of metabolism for a mother to guarantee the existence
120 of her replacement. On this basis we deduce that the generation-time (and correlated
121 lifetime) metabolism should be isometric to body size, as described above. Thus
122 generation time is a plausible constraint inseparably linked to the size dimensions of an
123 organism through metabolism. Generation time is the fundamental timescale in studies of
124 evolution and in much of population dynamics, because of the obvious importance of
125 reproductive rates (Ginzburg and Colyvan 2004).
126 It is the average metabolic rate under natural conditions — the field metabolic
127 rate (FMR) — that is most relevant to this four-dimensional view, since organisms do not
128 typically live their entire lives at basal or standard metabolic rates. However, our analyses
129 are necessarily restricted to using basal rates, since currently there are too few species for
130 which both published FMR and life history data are available (Anderson and Jetz 2005;
131 Nagy et al. 1999). In any case, FMR scales roughly parallel to basal rates in vertebrate
132 taxa, and is close to $^{3}/_{4}$ in placental mammals (Nagy 2005). We expect that the results of
133 using basal rates will thus be comparable to use of FMR directly.
134 We have further found that the residuals of the scaling of basal metabolism and
135 the scaling of maximum lifespan covary negatively (226 species shared by datasets of

Savage, et al. 2004 and Ernest 2003; correlation coefficient –0.25, $p < 0.0002$), although the scatter is large. That is, a species that is overmetabolic with respect to the metabolism line has a tendency to be below the line for generation-time allometry, and vice-versa.

We venture below to make some specific predictions based on our four-dimensional view. We have been able to test some of them with satisfactory results; others remain conjectures for future testing.

Predicted and actual allometries for subsets of reduced dimensionality

First, consider a set of organisms of different sizes that all share the same generation time. This means that one dimension out of four is fixed and the organisms differ only in three dimensions rather than four. Metabolism in a three-dimensional system would be expected to scale not as $^3/_4$, but as $^2/_3$, consistent with the reasoning of Rubner (1883) and other pre-Kleiber workers. However, from our four-dimensional view the reason that the slope will be different is simply that one dimension has been removed.

An important special case of such three-dimensional sets is that members of a single species have essentially the same generation time. Thus we would predict that intraspecific metabolism would scale with a lower exponent, ideally $^2/_3$. This prediction is in complete agreement with the well-known observation that intraspecific scaling exponents for metabolism are often different than interspecific exponents and tend to be closer to $^2/_3$ than to $^3/_4$ (Chown et al. 2007; Feldman and McMahon 1983; Glazier 2005).

Secondly, note that if, in a three-dimensional set of organisms, we standardize an additional dimension (for example, one of the three spatial dimensions, say, body length),

157 we effectively remove two of the four dimensions and, by the foregoing reasoning,
158 expect the slope to be $\frac{1}{2}$ (i.e., the remaining variability is two-dimensional).
159 Substantial data are available to test these predictions for *Homo sapiens.* As a
160 single species it is three-dimensional and thus should exhibit a metabolic scaling
161 exponent of $\frac{2}{3}$; in fact, the data we have analyzed show the exponent equal to 0.63 with
162 a 95% confidence interval of 0.59 to 0.67 (Fig. 1A). We can further reduce the
163 dimensionality by performing a multiple regression of metabolic rate on both mass and
164 height, in which case we would expect a value of $\frac{1}{2}$ for the partial regression coefficient
165 associated with mass. In agreement with the prediction the observed value is 0.47 (0.43 –
166 0.51; Fig. 1 B). If, equivalently, we bin the individuals into groups of equal heights (0.01
167 log height [cm]), the mean slope for the scaling of metabolism within groups gives the
168 same result: 0.47 (0.42 – 0.52). Standard textbook formulas used in human physiology
169 that regress surface area for humans on their height and weight have the exponents of
170 weight varying between 0.43 and 0.54, in agreement with our own estimate (Dubin and
171 Zietz 1996; Dubois and Dubois 1916; Verbraecken et al. 2006).
172 We can perform the same test on an interspecific scale across placental mammal
173 species, with some caveats. The mammal data certainly incorporate a wider range of
174 variation in ecological and physiological constraints than do intraspecific data. In
175 particular, it is known that metabolism in small mammals (< 50g) scales with a much
176 shallower slope than it does in large mammals (Glazier 2005; McNab 1988) — see
177 below. Accordingly, we will restrict our analysis to species > 100g in body mass, among
178 which the allometric relationship is relatively uniform. We have also perforce used
179 maximum recorded lifespan to represent generation time; though an imperfect proxy,

lifespan does scale similarly to the other life history characters that jointly determine actual generation times (Lindstedt and Calder 1981). Finally, we have not investigated whether phylogenetic non-independence affects our estimates of slopes. Our interest here is in a direct comparison with the human data for which no comparable genealogical information is available. Moreover, published phylogenetically-based and non-phylogenetic studies tend to yield similar exponents for the relevant allometries in mammals, though some life history traits may be exceptions (Duncan et al. 2007; Martin et al. 2005; Nagy 2005). We expect that the results of a phylogenetically-based analysis would be qualitatively the same as ours, but an exploration of this additional complexity is beyond the scope of the present work.

Table 1 shows that the results for mammals are similar to those for humans. In the four-dimensional (unconstrained) case, the metabolic exponent is not different from $\frac{3}{4}$ and the 95% confidence interval does not include $\frac{2}{3}$. In the three-dimensional case (controlling for lifespan), the exponent is lower, but variation is such that it is consistent with either $\frac{2}{3}$ or $\frac{3}{4}$. In the two-dimensional case (controlling for both lifespan and length), the exponent is 0.46, not significantly different from $\frac{1}{2}$ and almost exactly the value that we obtained in the intraspecific case.

The focal values of $\frac{3}{4}$, $\frac{2}{3}$ and $\frac{1}{2}$ correspond to integer reductions in dimensionality, and they seem to represent the modal values seen widely in metabolic scaling (Glazier 2005). However, we can easily imagine fractional dimension reduction, which would produce metabolic scaling exponents of various intermediate values. For example, mammals are not perfect cubes, and the slope of the regression of body mass to length tends to be slightly larger (up to 3.6) than the expected 3.0 in most orders (Damuth

1990; Silva 1998). The same exponent is closer to 2.8 for fishes (this paper) and for mammalian carnivores (Van Valkenburgh 1990). Thus, constraining by body length would be expected to have different effects in different groups, because slightly more or slightly less than a full spatial dimension contributing to body mass is being standardized.

Actual morphological, developmental, or temporal constraints (as opposed to those imposed statistically by the investigator) may also cause observed metabolic allometries with powers outside of this simple set of $\frac{n-1}{n}$ fractions or with powers unexpected from the apparent dimensionality of the system. For example, the low exponents for metabolic scaling observed in small (< 50g) mammals ($\frac{1}{2}$ or even $\frac{1}{3}$; ref. (Glazier 2005) immediately suggest to us that small mammal species form effectively at most a two-dimensional set. We conjecture that small mammals experience constraints in *both* spatial and temporal dimensions. At present we have no suggestions for the source of the apparent reduction by an additional dimension. Nevertheless, the four-dimensional view allows us to frame a novel question about the system that may lead to further understanding. Likewise, some researchers argue that true basal metabolic rates of birds and mammals scale with an exponent near $\frac{2}{3}$ (Glazier 2005; Heusner 1982a; White and Seymour 2003). Should this turn out to be the case, it would suggest to us that under basal conditions mammals experience some constraints that have the effect of reducing the dimensionality by approximately one, in contrast to the $\frac{3}{4}$ scaling observed for FMR and predicted by our four-dimensional perspective.

Discussion

The space-lifetime view predicts the $\frac{3}{4}$ exponent for metabolic scaling across species. Significantly, it also successfully predicts the exponents of metabolic scaling in sets of organisms of progressively lower dimensionality, and further correctly predicts that intraspecific metabolic slopes will tend to be lower than interspecific slopes — and ordinarily closer to $\frac{2}{3}$. Considering these observations and other conjectures discussed above, we suggest that our proposed four-dimensional view of metabolic scaling is in many ways simpler than the conventional 3-D view but with a similar and, in some cases, superior predictive power.

We are aware that there are multiple explanations within the 3-D framework for many of the same patterns that we address (Glazier 2005). Perhaps surprisingly, we would argue that our theory is not likely to be a competing causal theory nor does it necessarily contradict existing 3-D theories. We rely, informally, on the concept of "duality" to suggest how this can be so.

Duality is a widely used concept in modern physics. The two dual theories describe the same facts in different ways, typically by differing by one dimension. In a sense they are the same theory, but distinct formulations that emphasize different aspects or package the ingredients differently (Randall 2005). Neither 3-D nor 4-D metabolic theory has yet been developed sufficiently to determine whether the theories are formally dual. But it is in the spirit of such a possible duality that we offer our 4-D view. The fact that we do not have a mechanistic 4-D model, yet see predictable relationships from that

244 perspective, strongly suggests duality with 3-D mechanistic theory rather than an
245 alternative or replacement.
246 We thus present our view at this time without a mechanistic underpinning.
247 Knowledge of regular patterns in nature without a concurrent understanding of their
248 underlying mechanisms is more common (and useful) in science than people often think
249 (Greene 2001). Darwin's lack of knowledge of the mechanisms of heredity (which we
250 now understand), or physics' lack of a mechanism for gravity (which we still do not
251 understand) are just two examples. Our presentation of a non-mechanistic framework
252 means only that this represents less of an intellectual advance than one would strive for. It
253 is in this spirit of stepwise progress that we offer our views.
254 When we add generation time to scaling theory as an organism's fourth
255 dimension, we see order involving metabolic exponents that was previously obscured.
256 The exponents depend in a simple way on the dimensionality of the set of organisms
257 being considered: $1/2$ for two dimensions, $2/3$ for three, $3/4$ for four. We believe that our
258 view can serve as a general organizing framework, within which various theories and
259 mechanisms may coexist peacefully, occupying their own (sub)space of correctly
260 identified dimensionality. Instead of expecting universal applicability of one of the
261 exponents (e.g., $3/4$, $2/3$ or $1/2$), we expect to see various exponents based on variation in
262 dimensionality. The four-dimensional view thus embraces network theory, aimed at
263 explaining the central tendencies of interspecific scaling, and simultaneously other
264 approaches, including those involving multiple constraints (e.g., Demetrius 2006; Glazier
265 2005; Kooijman 2000) that seek to explain much of the variation in metabolic scaling at
266 various scales and in particular groups. At the same time, the scaling patterns predicted

and successfully explained by the four-dimensional view offer a challenge to traditional theories, which must account for them.

Including the temporal dimension as an integral part of the organism's phenotype may have broader applications in ecology than just those involved with metabolism and scaling. If organisms are considered to occupy a 4-dimensional space, then time, like the dimensions of 3-D space, can be considered a resource. Where time for growth and reproduction is in short supply there are fewer resources to be divided, with implications for diversity, resource partitioning, and biogeography. Other ecological processes ultimately depending on reproductive rates (such as population fluctuations and local extinction probability) must depend partly on generation time. We speculate that an extended four-dimensional view, if confirmed by additional studies, may provide similar clarification of theoretical areas of ecology currently based in three dimensions.

Generation time has always been the fundamental unit of time for understanding evolution. Our suggested view of metabolic ecology is that a generational time scale is equally fundamental for ecology. A well-known metaphor by Hutchinson (1965) sets ecology as a theater and evolution as a play. We believe that the theatre's clock ticks at the same rate that the play is being performed. The coincidence of the basic time scale of ecology to that of evolution is another confirmation of the unity of the two fields of biology.

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