

Optimal Supply Networks II: Blood, Water, and Truthicide

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Principles of Complex Systems, Vols. 1 & 2
CSYS/MATH 300 and 303, 2021–2022 | @pocsvox

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Law and Order, Special Science Edition: Truthicide Department

“In the scientific integrity system known as peer review, the people are represented by two highly overlapping yet equally important groups: the independent scientists who review papers and the scientists who punish those who publish garbage. This is one of their stories.”

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What one might expect:

$\alpha = 2/3$ because ...

Dimensional analysis suggests an energy balance surface law:

$$P \propto S \propto V^{2/3} \propto M^{2/3}$$

Assumes isometric scaling (not quite the spherical cow).

Lognormal fluctuations:
Gaussian fluctuations in $\log_{10} P$ around $\log_{10} cM^\alpha$.

Stefan-Boltzmann law for radiated energy:

$$\frac{dE}{dt} = \sigma \epsilon S T^4 \propto S$$

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Outline

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Animal power

Fundamental biological and ecological constraint:

$$P = c M^\alpha$$

P = basal metabolic rate

M = organismal body mass



The prevailing belief of the Church of Quarterology:

$$\alpha = 3/4$$

$$P \propto M^{3/4}$$

Huh?

Stories—The Fraction Assassin:



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$$P = c M^\alpha$$

Prefactor c depends on **body plan** and **body temperature**:

Birds	39–41 °C
Eutherian Mammals	36–38 °C
Marsupials	34–36 °C
Monotremes	30–31 °C



The prevailing belief of the Church of Quarterology:

Most obvious concern:

$$3/4 - 2/3 = 1/12$$

An exponent higher than 2/3 points suggests a fundamental inefficiency in biology.

Organisms must somehow be running ‘hotter’ than they need to balance heat loss.



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Related putative scalings:

Wait! There's more!:

- 🌀 number of capillaries $\propto M^{3/4}$
- 🌀 time to reproductive maturity $\propto M^{1/4}$
- 🌀 heart rate $\propto M^{-1/4}$
- 🌀 cross-sectional area of aorta $\propto M^{3/4}$
- 🌀 population density $\propto M^{-3/4}$

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The great 'law' of heartbeats:

Assuming:

- 🌀 Average lifespan $\propto M^\beta$
- 🌀 Average heart rate $\propto M^{-\beta}$
- 🌀 Irrelevant but perhaps $\beta = 1/4$.

Then:

$$\begin{aligned} \text{Average number of heart beats in a lifespan} \\ \approx (\text{Average lifespan}) \times (\text{Average heart rate}) \\ \propto M^{\beta-\beta} \\ \propto M^0 \end{aligned}$$

- 🌀 Number of heartbeats per life time is independent of organism size!
- 🌀 ≈ 1.5 billion

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From PoCS, the Prequel to CocoNuTs:

"How fast do living organisms move:
Maximum speeds from bacteria to
elephants and whales"

Meyer-Vernet and Rospars,
American Journal of Physics, **83**, 719–722,
2015. [35]

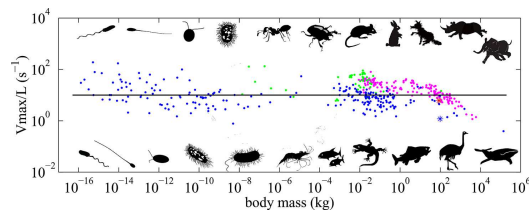


Fig. 1. Maximum relative speed versus body mass for 202 running species (157 mammals plotted in magenta and 45 non-mammals plotted in green), 127 swimming species and 91 micro-organisms (plotted in blue). The sources of the data are given in Ref. 16. The solid line is the maximum relative speed (Eq. (13)) estimated in Sec. III. The human world records are plotted as asterisks for running (upper) and for swimming (lower). Some examples of organisms of various masses are sketched in black (drawings by François Meyer).

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"A general scaling law reveals why the largest animals are not the fastest" [↗](#)
Hirt et al.,
Nature Ecology & Evolution, **1**, 1116, 2017. [23]

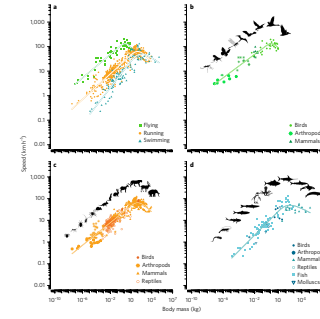


Figure 2 | Empirical data and time-dependent model fits for the allometric scaling of maximum speed. **a–d**, Comparison of scaling for the different locomotion modes (flying, running, swimming). **b–d**, Taxonomic differences are illustrated separately for flying ($n=55$), running ($n=64$) and swimming ($n=37$) animals. Overall model fit: $R^2=0.893$. The residual variation does not exhibit a signature of taxonomy (only a weak effect of thermoregulation, see Methods).

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A theory is born:

1840's: Sarrus and Rameaux^[44] first suggested $\alpha = 2/3$.



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A theory grows:

1883: Rubner^[42] found $\alpha \approx 2/3$.



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Theoretical story:

- 🌀 Maximum speed increases with size: $v_{\max} = aM^b$
- 🌀 Takes a while to get going: $v(t) = v_{\max}(1 - e^{-kt})$
- 🌀 $k \sim F_{\max}/M \sim cM^{d-1}$
Literature: $0.75 \lesssim d \lesssim 0.94$
- 🌀 Acceleration time = depletion time for anaerobic energy: $\tau \sim fM^g$ Literature: $0.76 \lesssim g \lesssim 1.27$
- 🌀 $v_{\max} = aM^b(1 - e^{-hM^i})$
- 🌀 $i = d - 1 + g$ and $h = cf$

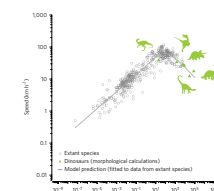


Figure 3 | Predicting the maximum speed of selected species with the time-dependent model. The model prediction (grey line) is fitted to data of extant species (grey circles) and extended to higher body masses. Speed data for dinosaurs (green triangles) come from detailed morphological model calculations (values in Table 1) and were not used to obtain model parameters.

- 🌀 Literature search for maximum speeds of running, flying and swimming animals.
- 🌀 Search terms: "maximum speed", "escape speed" and "sprint speed".

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Theory meets a different 'truth':

1930's: Brody, Benedict study mammals. [6]
Found $\alpha \approx 0.73$ (standard).



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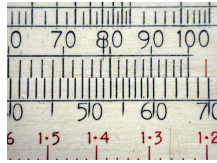
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Our hero faces a shadowy cabal:



- 1932: Kleiber analyzed 13 mammals. [25]
- Found $\alpha = 0.76$ and suggested $\alpha = 3/4$.
- Scaling law of Metabolism became known as [Kleiber's Law](#) (2011 Wikipedia entry is embarrassing).
- 1961 book: "The Fire of Life. An Introduction to Animal Energetics". [26]

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When a cult becomes a religion:

1950/1960: Hemmingsen [20, 21]
Extension to unicellular organisms.
 $\alpha = 3/4$ assumed true.



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Quarterology spreads throughout the land:

The Cabal assassinates 2/3-scaling:

- 1964: Troon, Scotland.
- 3rd Symposium on Energy Metabolism.
- $\alpha = 3/4$ made official ...



...29 to zip.

- But the Cabal slipped up by **publishing the conference proceedings** ...

- "Energy Metabolism; Proceedings of the 3rd symposium held at Troon, Scotland, May 1964," Ed. Sir Kenneth Blaxter [4]

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An unsolved truthicide:

So many questions ...

- Did the truth kill a theory? Or did a theory kill the truth?
- Or was the truth killed by just a lone, lowly hypothesis?
- Does this go all the way to the top? To the National Academies of Science?
- Is 2/3-scaling really dead?
- Could 2/3-scaling have faked its own death?
- What kind of people would vote on scientific facts?

Modern Quarterology, Post Truthticide

- 3/4 is held by many to be the one true exponent.



In the Beat of a Heart: Life, Energy, and the Unity of Nature—by John Whitfield

- But: much controversy ...
- See 'Re-examination of the "3/4-law" of metabolism' by the Heretical Unbelievers Dodds, Rothman, and Weitz [14], and ensuing madness ...

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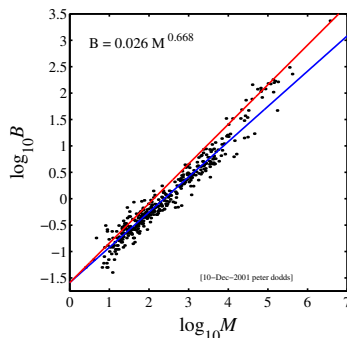
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Some data on metabolic rates

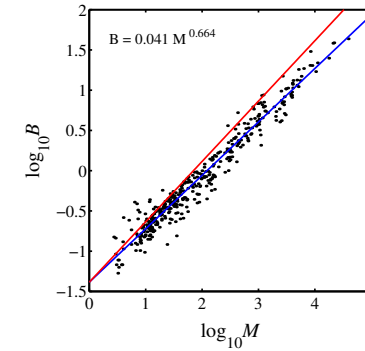


- Heusner's data (1991) [22]
- 391 Mammals
- blue line: 2/3
- red line: 3/4.
- ($B = P$)



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Some data on metabolic rates



- Bennett and Harvey's data (1987) [3]
- 398 birds
- blue line: 2/3
- red line: 3/4.
- ($B = P$)

- Passerine vs. non-passerine issue ...

Linear regression

Important:

- Ordinary Least Squares (OLS) Linear regression is only appropriate for analyzing a dataset $\{(x_i, y_i)\}$ when we know the x_i are measured without error.
- Here we assume that measurements of mass M have less error than measurements of metabolic rate B .
- Linear regression assumes Gaussian errors.

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Measuring exponents

More on regression:

If (a) we don't know what the errors of either variable are,
or (b) no variable can be considered independent,
then we need to use Standardized Major Axis Linear Regression. [43, 41]
(aka Reduced Major Axis = RMA.)

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Measuring exponents

For Standardized Major Axis Linear Regression:

$$\text{slope}_{\text{SMA}} = \frac{\text{standard deviation of } y \text{ data}}{\text{standard deviation of } x \text{ data}}$$

- Very simple!
- Minimization of sum of areas of triangles induced by vertical and horizontal residuals with best fit line.
- The only linear regression that is Scale invariant.
- Attributed to Nobel Laureate economist Paul Samuelson, but discovered independently by others.
- #somuchwin

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Measuring exponents

Relationship to ordinary least squares regression is simple:

$$\begin{aligned} \text{slope}_{\text{SMA}} &= r^{-1} \times \text{slope}_{\text{OLS } y \text{ on } x} \\ &= r \times \text{slope}_{\text{OLS } x \text{ on } y} \end{aligned}$$

where r = standard correlation coefficient:

$$r = \frac{\sum_{i=1}^n (x_i - \bar{x})(y_i - \bar{y})}{\sqrt{\sum_{i=1}^n (x_i - \bar{x})^2} \sqrt{\sum_{i=1}^n (y_i - \bar{y})^2}}$$

- Groovy upshot: If (1) a paper uses OLS regression when RMA would be appropriate, and (2) r is reported, we can figure out the RMA slope. [41, 29]

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Heusner's data, 1991 (391 Mammals)

range of M	N	$\hat{\alpha}$
≤ 0.1 kg	167	0.678 ± 0.038
≤ 1 kg	276	0.662 ± 0.032
≤ 10 kg	357	0.668 ± 0.019
≤ 25 kg	366	0.669 ± 0.018
≤ 35 kg	371	0.675 ± 0.018
≤ 350 kg	389	0.706 ± 0.016
≤ 3670 kg	391	0.710 ± 0.021

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Bennett and Harvey, 1987 (398 birds)

M_{max}	N	$\hat{\alpha}$
≤ 0.032	162	0.636 ± 0.103
≤ 0.1	236	0.602 ± 0.060
≤ 0.32	290	0.607 ± 0.039
≤ 1	334	0.652 ± 0.030
≤ 3.2	371	0.655 ± 0.023
≤ 10	391	0.664 ± 0.020
≤ 32	396	0.665 ± 0.019
≤ 100	398	0.664 ± 0.019

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Hypothesis testing

Test to see if α' is consistent with our data $\{(M_i, B_i)\}$:

$$H_0 : \alpha = \alpha' \text{ and } H_1 : \alpha \neq \alpha'$$

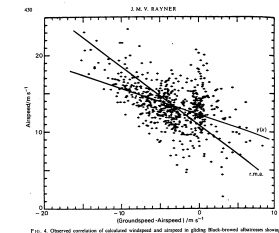
- Assume each B_i (now a random variable) is normally distributed about $\alpha' \log_{10} M_i + \log_{10} c$.
- Follows that the measured α for one realization of freedom is a t distribution with $N - 2$ degrees of freedom.
- Calculate a p -value: probability that the measured α is as least as different to our hypothesized α' as we observe.
- See, for example, DeGroot and Scherish, "Probability and Statistics."^[11]

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LINEAR RELATIONS IN BIOMECHANICS

TABLE II
Calculated Statistics of averaged V_x and winged V_x in the Black-throated bluebird *Dumetia melanogris* in gliding flight, after Pennycuik (1982)

number of data $n = 737$
mean $\bar{x}, \bar{y} = 31.4, 13.35$ mm^{-1}
variances $S_x^2, S_y^2 = 15.91, 8.218$ mm^{-2}
covariance $S_{xy} = -4.653$
correlation $\rho = -0.855$

model of speed correction: $V_x = a + \beta V_y$

model	intercept a	gradient β	range R^2
OLS regression	12.30	-0.334	-0.384 to -0.284
OLS regression	10.93	-0.769	-0.984 to -0.661
OLS regression	7.80	-1.766	-2.076 to -1.536
$\alpha = 1$	10.66	-0.855	-0.997 to -0.737
$\beta = 1$ or m.a.	11.59	-0.560	-0.648 to -0.479
$\beta = 2$	12.00	-0.431	-0.496 to -0.367

- Disparity between slopes for y on x and x on y regressions is a factor of r^2 (r^{-2})
- (Rayner uses ρ for r .)
- Here: $r^2 = .435^2 = 0.189$, and $r^{-2} = .435^{-2} = 2.29^2 = 5.285$.
- See also: LaBarbera [29] (who resigned ...)

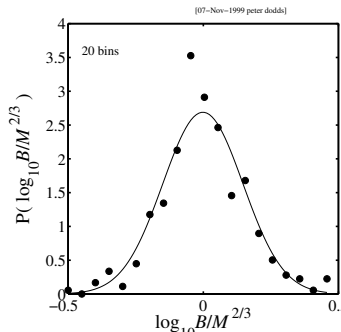
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Fluctuations—Things look normal ...



- $P(B|M) = 1/M^{2/3} f(B/M^{2/3})$
- Use a Kolmogorov-Smirnov test.

Revisiting the past—mammals

Full mass range:

	N	$\hat{\alpha}$	$p_{2/3}$	$p_{3/4}$
Kleiber	13	0.738	$< 10^{-6}$	0.11
Brody	35	0.718	$< 10^{-4}$	$< 10^{-2}$
Heusner	391	0.710	$< 10^{-6}$	$< 10^{-5}$
Bennett and Harvey	398	0.664	0.69	$< 10^{-15}$

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Revisiting the past—mammals

$M \leq 10$ kg:

	N	$\hat{\alpha}$	$p_{2/3}$	$p_{3/4}$
Kleiber	5	0.667	0.99	0.088
Brody	26	0.709	$< 10^{-3}$	$< 10^{-3}$
Heusner	357	0.668	0.91	$< 10^{-15}$

$M \geq 10$ kg:

	N	$\hat{\alpha}$	$p_{2/3}$	$p_{3/4}$
Kleiber	8	0.754	$< 10^{-4}$	0.66
Brody	9	0.760	$< 10^{-3}$	0.56
Heusner	34	0.877	$< 10^{-12}$	$< 10^{-7}$

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Analysis of residuals

1. Presume an exponent of your choice: 2/3 or 3/4.
2. Fit the prefactor ($\log_{10} c$) and then examine the residuals:

$$r_i = \log_{10} B_i - (\alpha' \log_{10} M_i - \log_{10} c).$$

3. H_0 : residuals are uncorrelated
 H_1 : residuals are correlated.
4. Measure the correlations in the residuals and compute a p -value.

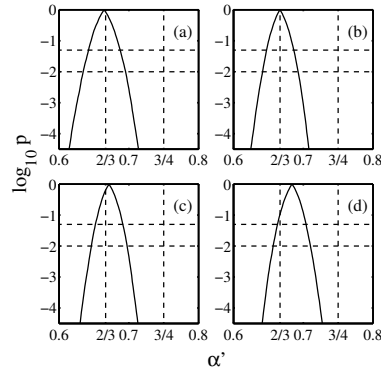
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Analysis of residuals—mammals



- $M < 3.2$ kg,
- $M < 10$ kg,
- $M < 32$ kg,
- all mammals.

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Impure scaling?:

- So: The exponent $\alpha = 2/3$ works for all birds and mammals up to 10–30 kg
- For mammals > 10–30 kg, maybe we have a new scaling regime
- Possible connection?: Economos (1983)—limb length break in scaling around 20 kg [15]
- But see later: non-isometric growth leads to lower metabolic scaling. Oops.

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Analysis of residuals

We use the spiffing Spearman Rank-Order Correlation Coefficient

Basic idea:

- Given $\{(x_i, y_i)\}$, rank the $\{x_i\}$ and $\{y_i\}$ separately from smallest to largest. Call these ranks R_i and S_i .

- Now calculate correlation coefficient for ranks, r_s :

$$r_s = \frac{\sum_{i=1}^n (R_i - \bar{R})(S_i - \bar{S})}{\sqrt{\sum_{i=1}^n (R_i - \bar{R})^2} \sqrt{\sum_{i=1}^n (S_i - \bar{S})^2}}$$

- Perfect correlation: x_i 's and y_i 's both increase monotonically.

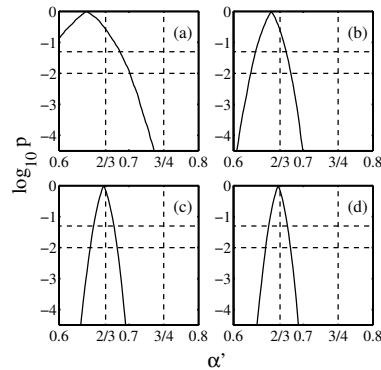
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Analysis of residuals—birds



- $M < 0.1$ kg,
- $M < 1$ kg,
- $M < 10$ kg,
- all birds.

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The widening gyre:

Now we're really confused (empirically):

- White and Seymour, 2005: unhappy with large herbivore measurements [56]. Pro 2/3: Find $\alpha \approx 0.686 \pm 0.014$.
- Glazier, BioScience (2006) [18]: "The 3/4-Power Law Is Not Universal: Evolution of Isometric, Ontogenetic Metabolic Scaling in Pelagic Animals."
- Glazier, Biol. Rev. (2005) [17]: "Beyond the 3/4-power law': variation in the intra- and interspecific scaling of metabolic rate in animals."
- Savage et al., PLoS Biology (2008) [45] "Sizing up allometric scaling theory" Pro 3/4: problems claimed to be finite-size scaling.

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Analysis of residuals

We assume all rank orderings are equally likely:

- r_s is distributed according to a Student's t -distribution with $N - 2$ degrees of freedom.
- Excellent feature: Non-parametric—real distribution of x 's and y 's doesn't matter.
- Bonus: works for non-linear monotonic relationships as well.
- See Numerical Recipes in C/Fortran which contains many good things. [39]

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Other approaches to measuring exponents:

- Clauset, Shalizi, Newman: "Power-law distributions in empirical data" [10] SIAM Review, 2009.
- See Clauset's page on measuring power law exponents (code, other goodies).
- See this collection of tweets for related amusement.

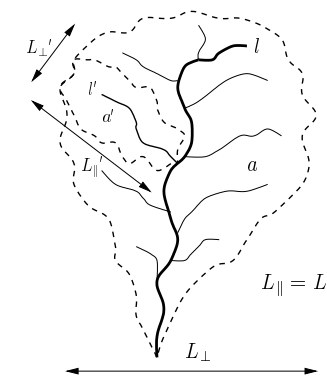
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Somehow, optimal river networks are connected:



- a = drainage basin area
- l = length of longest (main) stream
- $L = L_{||} =$ longitudinal length of basin

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Mysterious allometric scaling in river networks

1957: J. T. Hack [19]
 "Studies of Longitudinal Stream Profiles in Virginia and Maryland"

$$\ell \sim a^h$$

$$h \sim 0.6$$

- Anomalous scaling: we would expect $h = 1/2$...
- Subsequent studies: $0.5 \lesssim h \lesssim 0.6$
- Another quest to find **universality/god** ...
- A catch**: studies done on small scales.

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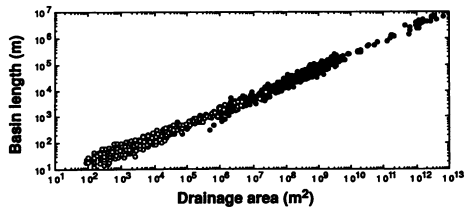
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Large-scale networks:

(1992) Montgomery and Dietrich [36]:



- Composite data set: includes everything from unchanneled valleys up to world's largest rivers.
- Estimated fit:

$$L \approx 1.78a^{0.49}$$

- Mixture of basin and main stream lengths.

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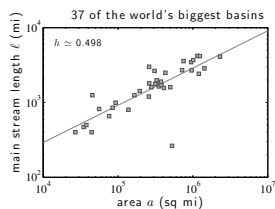
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World's largest rivers only:



- Data from Leopold (1994) [31, 13]
- Estimate of Hack exponent: $h = 0.50 \pm 0.06$

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Earlier theories (1973-):

Building on the surface area idea:

- McMahon (70's, 80's): Elastic Similarity [32, 34]
- Idea is that organismal shapes scale allometrically with 1/4 powers (like trees ...)
- Disastrously, cites Hemmingsen [21] for surface area data.
- Appears to be true for ungulate legs ... [33]
- Metabolism and shape never properly connected.



"Size and shape in biology" T. McMahon, Science, 179, 1201-1204, 1973. [32]

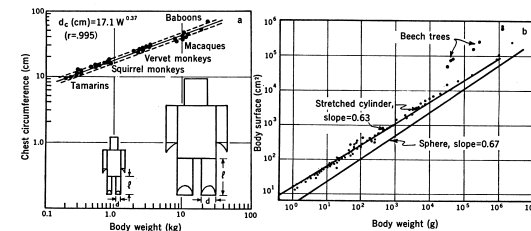
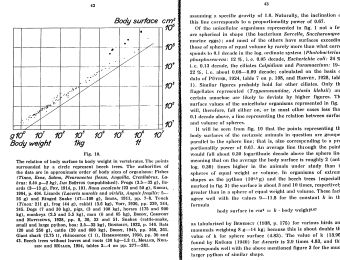


Fig. 3. (a) Chest circumference, d_c , plotted against body weight, W , for five species of primates. The broken lines represent the standard error in this least-squares fit (adapted from [27]). The model proposed here, whereby each length, l , increases as the 3/4 power of diameter, d , is illustrated for two weights differing by a factor of 16. (b) Body surface area plotted against weight for vertebrates. The animal data are reasonably well fitted by the stretched cylinder model (adapted from [46]).



- Hemmingsen's "fit" is for a 2/3 power, notes possible 10 kg transition. [7]
- p 46: "The energy metabolism thus definitely varies interspecifically over similar wide weight ranges with a higher power of the body weight than the body surface."

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Earlier theories (1977):

Building on the surface area idea ...

- Blum (1977) [5] speculates on four-dimensional biology: $P \propto M^{(d-1)/d}$
- $d = 3$ gives $\alpha = 2/3$
- $d = 4$ gives $\alpha = 3/4$
- So we need another dimension ...
- Obviously, a bit silly... [46]

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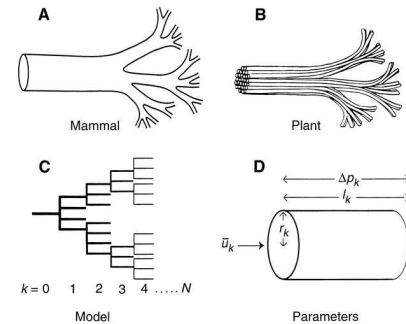
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Nutrient delivering networks:

- 1960's: Rashevsky considers blood networks and finds a 2/3 scaling.
- 1997: West *et al.* [53] use a network story to find 3/4 scaling.



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Nutrient delivering networks:

West *et al.*'s assumptions:

- hierarchical network
- capillaries (delivery units) invariant
- network impedance is minimized via evolution

Claims:

- $P \propto M^{3/4}$
- networks are fractal
- quarter powers everywhere

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Impedance measures:

☞ Poiseuille flow (outer branches):

$$Z = \frac{8\mu}{\pi} \sum_{k=0}^N \frac{\ell_k}{r_k^4 N_k}$$

☞ Pulsatile flow (main branches):

$$Z \propto \sum_{k=0}^N \frac{h_k^{1/2}}{r_k^{5/2} N_k}$$

☞ Wheel out Lagrange multipliers ...

☞ Poiseuille gives $P \propto M^1$ with a logarithmic correction.

☞ Pulsatile calculation explodes into flames.



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Data from real networks:

Network	R_n	R_r	R_ℓ	$-\frac{\ln R_n}{\ln R_n}$	$-\frac{\ln R_\ell}{\ln R_n}$	α
West <i>et al.</i>	-	-	-	1/2	1/3	3/4
rat (PAT)	2.76	1.58	1.60	0.45	0.46	0.73
cat (PAT) (Turcotte <i>et al.</i> [50])	3.67	1.71	1.78	0.41	0.44	0.79
dog (PAT)	3.69	1.67	1.52	0.39	0.32	0.90
pig (LCX)	3.57	1.89	2.20	0.50	0.62	0.62
pig (RCA)	3.50	1.81	2.12	0.47	0.60	0.65
pig (LAD)	3.51	1.84	2.02	0.49	0.56	0.65
human (PAT)	3.03	1.60	1.49	0.42	0.36	0.83
human (PAT)	3.36	1.56	1.49	0.37	0.33	0.94



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Not so fast ...

Actually, model shows:

☞ $P \propto M^{3/4}$ does not follow for pulsatile flow
☞ networks are not necessarily fractal.

Do find:

☞ Murray's cube law (1927) for outer branches: [37]

$$r_0^3 = r_1^3 + r_2^3$$

☞ Impedance is distributed evenly.

☞ Can still assume networks are fractal.



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Attempts to look at actual networks:



"Testing foundations of biological scaling theory using automated measurements of vascular networks"
Newberry, Newberry, and Newberry,
PLoS Comput Biol, **11**, e1004455, 2015. [38]



Newberry *et al.*,
PLoS Comput Biol, **11**, e1004455, . [7]



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Connecting network structure to α

1. Ratios of network parameters:

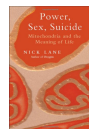
$$R_n = \frac{n_{k+1}}{n_k}, R_\ell = \frac{\ell_{k+1}}{\ell_k}, R_r = \frac{r_{k+1}}{r_k}$$

2. Number of capillaries $\propto P \propto M^\alpha$.

$$\Rightarrow \alpha = -\frac{\ln R_n}{\ln R_r^2 R_\ell}$$

(also problematic due to prefactor issues)

Some people understand it's truly a disaster:



"Power, Sex, Suicide: Mitochondria and the Meaning of Life"
by Nick Lane (2005). [30]

"As so often happens in science, the apparently solid foundations of a field turned to rubble on closer inspection."



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Let's never talk about this again:



"The fourth dimension of life: Fractal geometry and allometric scaling of organisms"
West, Brown, and Enquist,
Science, **284**, 1677-1679, 1999. [54]

☞ No networks: Scaling argument for energy exchange area a .

☞ Distinguish between biological and physical length scales (distance between mitochondria versus cell radius).

☞ Buckingham π action. [9]

☞ Arrive at $a \propto M^{D/D+1}$ and $\ell \propto M^{1/D}$.

☞ New disaster: after going on about fractality of a , then state $v \propto a^\ell$ in general.



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"It was the epoch of belief, it was the epoch of incredulity"



"A General Model for the Origin of Allometric Scaling Laws in Biology"
West, Brown, and Enquist,
Science, **276**, 122-126, 1997. [53]



"Nature"
West, Brown, and Enquist,
Nature, **400**, 664-667, 1999. [55]



"The fourth dimension of life: Fractal geometry and allometric scaling of organisms"
West, Brown, and Enquist,
Science, **284**, 1677-1679, 1999. [54]



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Really, quite confused:

Whole 2004 issue of Functional Ecology addresses the problem:

☞ J. Kozłowski, M. Konrzewski. "Is West, Brown and Enquist's model of allometric scaling mathematically correct and biologically relevant?" Functional Ecology 18: 283-9, 2004. [28]

☞ J. H. Brown, G. B. West, and B. J. Enquist. "Yes, West, Brown and Enquist's model of allometric scaling is both mathematically correct and biologically relevant." Functional Ecology 19: 735-738, 2005. [7]

☞ J. Kozłowski, M. Konrzewski. "West, Brown and Enquist's model of allometric scaling again: the same questions remain." Functional Ecology 19: 739-743, 2005.



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Obliviously soldiering on, we could assert:

☞ area-preservingness:

$$R_r = R_n^{-1/2}$$

$$\Rightarrow \alpha = 3/4$$

☞ space-fillingness: $R_\ell = R_n^{-1/3}$



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“Curvature in metabolic scaling”
Kolokotronis, Savage, Deeds, and Fontana.
Nature, **464**, 753, 2010. [27]

Let's try a quadratic:

$$\log_{10} P \sim \log_{10} c + \alpha_1 \log_{10} M + \alpha_2 \log_{10} M^2$$

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Yah:

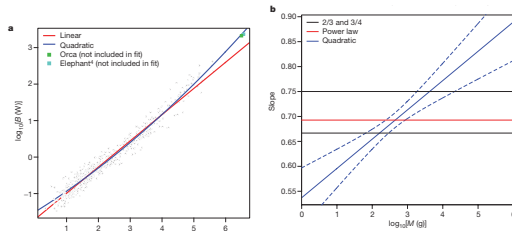


Figure 1 | Curvature in metabolic scaling. a. Linear (red) and quadratic (blue) fits (not including temperature) of $\log_{10}P$ versus $\log_{10}M$. The orca (green square) and Asian elephant (red square at larger mass) are not included in the fit, but are predicted well. Differences in the quality of fit are best seen in terms of the conditional mean of the error, estimated by the loess (locally-weighted scatterplot smoothing) fit of the residuals (Supplementary Information). See Table 1 for the values of the coefficients obtained from the fit. b. Slope of the quadratic fit (including temperature) with pointwise 90% confidence intervals (blue). The slope of the power law fit (red) and models with fixed 2/3 and 3/4 exponents (black) are included for comparison. This panel suggests that exponents estimated by assuming a power law will be highly sensitive to the mass range of the data set used, as shown in Fig. 2.



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“This raises the question of whether the theory can be adapted to agree with the data”¹

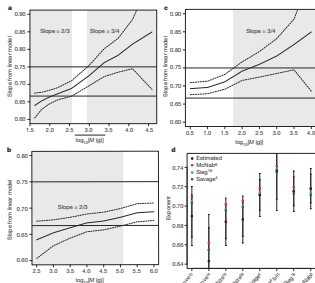
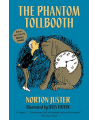


Figure 2 | Scaling exponent depends on mass range. a. Slope estimated by linear regression within a three log and mass range (smaller over the boundaries). Values on the absolute discrete axes are $\log_{10}M$ within the range. When the 90% confidence regions (dashed lines) include the 2/3 and 3/4 slopes, the local slope is consistent with a 2/3 or 3/4 exponent, respectively. These cases are indicated by the shaded regions (2/3 on the left and 3/4 on the right). b. Slope estimated by using all data points with $M < c$. The shaded region is consistent with 2/3 slope estimate. c. Slope estimated by using all data points with $M > c$. The shaded region is consistent with 3/4 slope estimate. d. Exponents estimated for eight historical data sets using linear regression (think *Bill* index). Legend: “Largest”, “Largest”, “Whale”, “Shrimp”, “Mammal”, and “Shrimp” using species average data (“Shrimp”) and historical data (“Shrimp”). Exponents predicted using coefficients from quadratic fits to MAMMs (red), Shrimp (green), or Savage’s (black) data and the three elements of log- M (Supplementary Information). Thick lines represent uncorrected 90% confidence intervals. Thin lines are multiplicity corrected intervals.



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Evolution has generally made things bigger¹



“The Phantom Tollbooth”
by Norton Juster (1961). [24]

- Regression starting at low M makes sense
- Regression starting at high M makes ...no sense

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Still going:



“A general model for metabolic scaling in self-similar asymmetric networks”
Brummer, Brummer, and Enquist,
PLoS Comput Biol, **13**, e1005394, 2017. [8]

Wut?:

“Most importantly, we show that the 3/4 metabolic scaling exponent from Kleiber’s Law can still be attained within many asymmetric networks.”

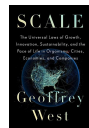
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Oh no:



“Scale: The Universal Laws of Growth, Innovation, Sustainability, and the Pace of Life in Organisms, Cities, Economies, and Companies”
by Geoffrey B. West (2017). [52]

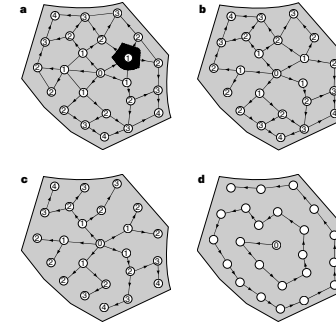
Amazon reviews excerpts (so, so not fair but ...):

- “Full of intriguing, big ideas but amazingly sloppy both in details and exposition, especially considering the author is a theoretical physicist.”
- “The beginning is terrible. He shows four graphs to illustrate scaling relationships, none of which have intelligible scales”
- “(he actually repeats several times that businesses can die but are not really an animal - O RLY?)”



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Simple supply networks:



- Banavar et al., Nature, (1999) [1].
- Flow rate argument.
- Ignore impedance.
- Very general attempt to find most efficient transportation networks.



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Simple supply networks

Banavar et al. find ‘most efficient’ networks with

$$P \propto M^{d/(d+1)}$$

...but also find

$$V_{\text{network}} \propto M^{(d+1)/d}$$

$d = 3$:

$$V_{\text{blood}} \propto M^{4/3}$$

- Consider a 3 g shrew with $V_{\text{blood}} = 0.1V_{\text{body}}$
- \Rightarrow 3000 kg elephant with $V_{\text{blood}} = 10V_{\text{body}}$

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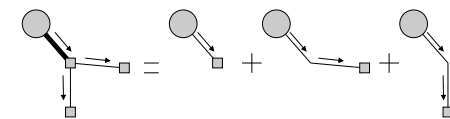
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Geometric argument



“Optimal Form of Branching Supply and Collection Networks”
Peter Sheridan Dodds,
Phys. Rev. Lett., **104**, 048702, 2010. [12]

- Consider one source supplying many sinks in a d -dim. volume in a D -dim. ambient space.
- Assume sinks are invariant.
- Assume sink density $\rho = \rho(V)$.
- Assume some cap on flow speed of material.
- See network as a bundle of virtual vessels:



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¹Already raised and fully established 9 years earlier. [14]

Geometric argument

Q: how does the number of sustainable sinks N_{sinks} scale with volume V for the most efficient network design?

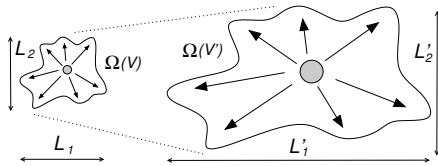
Or: what is the highest α for $N_{\text{sinks}} \propto V^\alpha$?



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Geometric argument

Allometrically growing regions:



Have d length scales which scale as

$$L_i \propto V^{\gamma_i} \text{ where } \gamma_1 + \gamma_2 + \dots + \gamma_d = 1.$$

For **isometric** growth, $\gamma_i = 1/d$.

For **allometric** growth, we must have at least two of the $\{\gamma_i\}$ being different



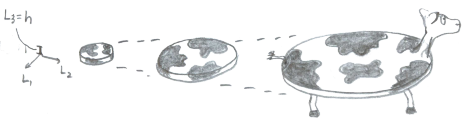
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Spherical cows and pancake cows:

Assume an isometrically scaling family of cows:



Extremes of allometry:
The pancake cows—



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Spherical cows and pancake cows:

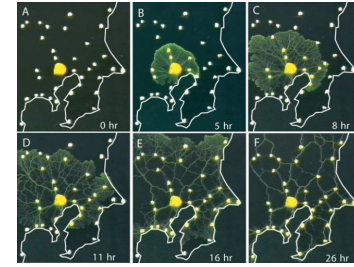
Question: How does the surface area S_{cow} of our two types of cows scale with cow volume V_{cow} ?
Insert question from assignment 4

Question: For general families of regions, how does surface area S scale with volume V ? Insert question from assignment 4



"Rules for Biologically Inspired Adaptive Network Design"

Tero et al.,
Science, **327**, 439-442, 2010. [49]



Urban deslime in action:

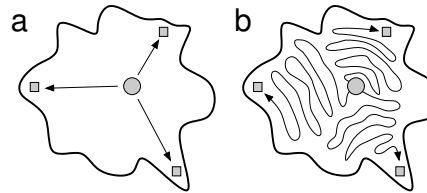
<https://www.youtube.com/watch?v=GwKuFREOgmo>



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Geometric argument

Best and worst configurations (Banavar et al.)



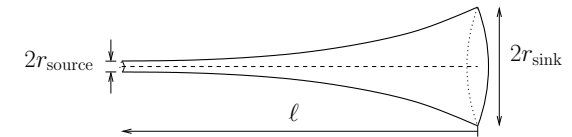
Rather obviously:
 $\min V_{\text{net}} \propto \sum \text{distances from source to sinks.}$



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Minimal network volume:

We add one more element:



Vessel cross-sectional area may vary with distance from the source.

Flow rate increases as cross-sectional area decreases.

e.g., a collection network may have vessels tapering as they approach the central sink.

Find that vessel volume v must scale with vessel length l to affect overall system scalings.



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Minimal network volume:

Real supply networks are close to optimal:

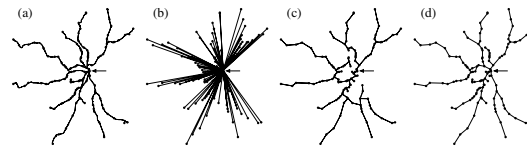


Figure 1. (a) Commuter rail network in the Boston area. The arrow marks the assumed root of the network. (b) Star graph. (c) Minimum spanning tree. (d) The model of equation (3) applied to the same set of stations.

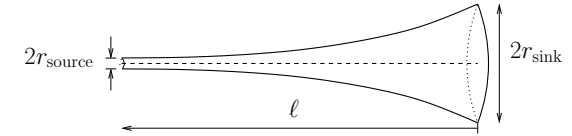
Gastner and Newman (2006): "Shape and efficiency in spatial distribution networks" [16]



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Minimal network volume:

Effecting scaling:



Consider vessel radius $r \propto (l + 1)^{-\epsilon}$, tapering from $r = r_{\text{max}}$ where $\epsilon \geq 0$.

Gives $v \propto l^{1-2\epsilon}$ if $\epsilon < 1/2$

Gives $v \propto 1 - l^{-(2\epsilon-1)} \rightarrow 1$ for large l if $\epsilon > 1/2$

Previously, we looked at $\epsilon = 0$ only.



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Minimal network volume:

For $0 \leq \epsilon < 1/2$, approximate network volume by integral over region:

$$\min V_{\text{net}} \propto \int_{\Omega_{d,D}(V)} \rho \|\vec{x}\|^{1-2\epsilon} d\vec{x}$$

Insert question from assignment 4 [↗](#)

$$\propto \rho V^{1+\gamma_{\max}(1-2\epsilon)} \text{ where } \gamma_{\max} = \max_i \gamma_i.$$

For $\epsilon > 1/2$, find simply that

$$\min V_{\text{net}} \propto \rho V$$

- So if supply lines can taper fast enough and without limit, minimum network volume can be made negligible.

For $0 \leq \epsilon < 1/2$:

$$\min V_{\text{net}} \propto \rho V^{1+\gamma_{\max}(1-2\epsilon)}$$

- If scaling is isometric, we have $\gamma_{\max} = 1/d$:

$$\min V_{\text{net/iso}} \propto \rho V^{1+(1-2\epsilon)/d}$$

- If scaling is allometric, we have $\gamma_{\max} = \gamma_{\text{allo}} > 1/d$: and

$$\min V_{\text{net/allo}} \propto \rho V^{1+(1-2\epsilon)\gamma_{\text{allo}}}$$

- Isometrically growing volumes **require less network volume** than allometrically growing volumes:

$$\frac{\min V_{\text{net/iso}}}{\min V_{\text{net/allo}}} \rightarrow 0 \text{ as } V \rightarrow \infty$$

For $\epsilon > 1/2$:

$$\min V_{\text{net}} \propto \rho V$$

- Network volume scaling is now independent of overall shape scaling.

Limits to scaling

- Can argue that ϵ must effectively be 0 for real networks over large enough scales.
- Limit to how fast material can move, and how small material packages can be.
- e.g., blood velocity and blood cell size.

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This
is a
really
clean
slide

Blood networks

- Velocity at capillaries and aorta approximately constant across body size [51]: $\epsilon = 0$.
- Material costly** \Rightarrow expect lower optimal bound of $V_{\text{net}} \propto \rho V^{(d+1)/d}$ to be followed closely.
- For cardiovascular networks, $d = D = 3$.
- Blood volume scales linearly with body volume [47], $V_{\text{net}} \propto V$.
- Sink density must \therefore decrease as volume increases:

$$\rho \propto V^{-1/d}.$$

- Density of suppliable sinks **decreases** with organism size.

Blood networks

- Then P , the rate of overall energy use in Ω , can at most scale with volume as

$$P \propto \rho V \propto \rho M \propto M^{(d-1)/d}$$

- For $d = 3$ dimensional organisms, we have

$$P \propto M^{2/3}$$

- Including other constraints may raise scaling exponent to a higher, less efficient value.



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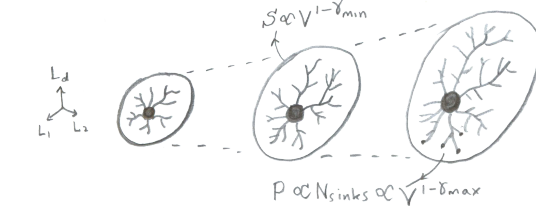
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- Exciting bonus:** Scaling obtained by the supply network story and the surface-area law **only match** for isometrically growing shapes. Insert question from assignment 4 [↗](#)

The surface area-supply network mismatch for allometrically growing shapes:



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Recall:

- The exponent $\alpha = 2/3$ works for all birds and mammals up to 10–30 kg
- For mammals $> 10\text{--}30$ kg, maybe we have a new scaling regime
- Economos: limb length break in scaling around 20 kg
- White and Seymour, 2005: unhappy with large herbivore measurements. Find $\alpha \approx 0.686 \pm 0.014$

Prefactor:

Stefan-Boltzmann law: [↗](#)

-

$$\frac{dE}{dt} = \sigma S T^4$$

where S is surface and T is temperature.

- Very rough estimate of prefactor based on scaling of normal mammalian body temperature and surface area S :

$$B \approx 10^5 M^{2/3} \text{ erg/sec.}$$

- Measured for $M \leq 10$ kg:

$$B = 2.57 \times 10^5 M^{2/3} \text{ erg/sec.}$$



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River networks

- View river networks as collection networks.
- Many sources and one sink.
- ϵ ?
- Assume ρ is constant over time and $\epsilon = 0$:

$$V_{\text{net}} \propto \rho V^{(d+1)/d} = \text{constant} \times V^{3/2}$$

- Network volume grows faster than basin 'volume' (really area).
- It's all okay:** Landscapes are $d=2$ surfaces living in $D=3$ dimensions.
- Streams can grow not just in width but in depth ...
- If $\epsilon > 0$, V_{net} will grow more slowly but $3/2$ appears to be confirmed from real data.

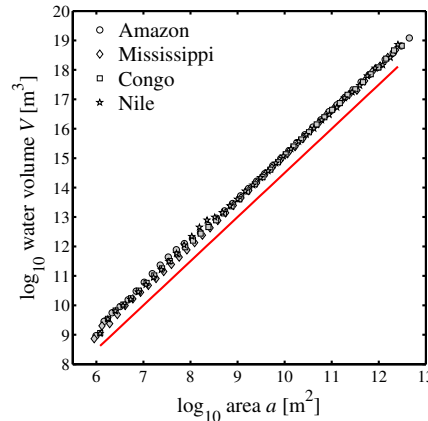
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Even better—prefactors match up:



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Some people understand it's truly a disaster:

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Hack's law

- Volume of water in river network can be calculated by adding up basin areas
- Flows sum in such a way that

$$V_{\text{net}} = \sum_{\text{all pixels}} a_{\text{pixel } i}$$

- Hack's law again:

$$\ell \sim a^h$$

- Can argue

$$V_{\text{net}} \propto V_{\text{basin}}^{1+h} = a_{\text{basin}}^{1+h}$$

where h is Hack's exponent.

- ∴ minimal volume calculations gives

$$h = 1/2$$

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The Cabal strikes back:

- Banavar et al., 2010, PNAS: "A general basis for quarter-power scaling in animals." [2]
- "It has been known for decades that the metabolic rate of animals scales with body mass with an exponent that is almost always < 1 , $> 2/3$, and often very close to $3/4$."
- Cough, cough, cough, hack, wheeze, cough.

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The unnecessary bafflement continues:

"Testing the metabolic theory of ecology" [40]

C. Price, J. S. Weitz, V. Savage, J. Stegen, A. Clarke, D. Coomes, P. S. Dodds, R. Etienne, A. Kerkhoff, K. McCulloh, K. Niklas, H. Olf, and N. Swenson
Ecology Letters, **15**, 1465–1474, 2012.

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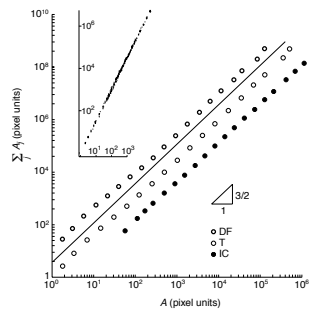
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Real data:

- Banavar et al.'s approach [1] is okay because ρ really is constant.
- The irony: shows optimal basins are isometric
- Optimal Hack's law: $\ell \sim a^h$ with $h = 1/2$
- (Zzzzz)



From Banavar et al. (1999) [1]

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Stories—Darth Quarter:



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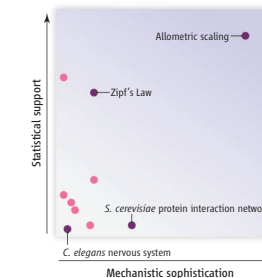
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Artisanal, handcrafted silliness:

"Critical truths about power laws" [48] Stumpf and Porter, Science, 2012



How good is your power law? The chart reflects the level of statistical support—as measured in (16, 21)—and our opinion about the mechanistic sophistication underlying hypothetical generative models for various reported power laws. Some relationships are identified by name; the others reflect the general characteristics of a wide range of reported power laws. Allometric scaling stands out from the other power laws reported for complex systems.

- Call generalization of Central Limit Theorem, stable distributions. Also: PLIPL0 action.
- Summary: Wow.

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Conclusion

- Supply network story consistent with dimensional analysis.
- Isometrically growing regions can be more efficiently supplied than allometrically growing ones.
- Ambient and region dimensions matter ($D = d$ versus $D > d$).
- Deviations from optimal scaling suggest inefficiency (e.g., gravity for organisms, geological boundaries).
- Actual details of branching networks not that important.
- Exact nature of self-similarity varies.
- 2/3-scaling lives on, largely in hiding.
- 3/4-scaling? Jury ruled a mistrial.
- The truth will out. Maybe.

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References I

- J. R. Banavar, A. Maritan, and A. Rinaldo. Size and form in efficient transportation networks. [Nature](#), 399:130–132, 1999. [pdf](#)
- J. R. Banavar, M. E. Moses, J. H. Brown, J. Damuth, A. Rinaldo, R. M. Sibly, and A. Maritan. A general basis for quarter-power scaling in animals. [Proc. Natl. Acad. Sci.](#), 107:15816–15820, 2010. [pdf](#)
- P. Bennett and P. Harvey. Active and resting metabolism in birds—allometry, phylogeny and ecology. [J. Zool.](#), 213:327–363, 1987. [pdf](#)

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References II

- K. L. Blaxter, editor. [Energy Metabolism; Proceedings of the 3rd symposium held at Troon, Scotland, May 1964.](#) Academic Press, New York, 1965.
- J. J. Blum. On the geometry of four-dimensions and the relationship between metabolism and body mass. [J. Theor. Biol.](#), 64:599–601, 1977. [pdf](#)
- S. Brody. [Bioenergetics and Growth.](#) Reinhold, New York, 1945. reprint, . [pdf](#)

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References III

- J. H. Brown, G. B. West, and B. J. Enquist. Yes, West, Brown and Enquist’s model of allometric scaling mathematically correct and biologically relevant? [Functional Ecology](#), 19:735–738, 2005. [pdf](#)
- A. B. Brummer, S. V. M., and B. J. Enquist. A general model for metabolic scaling in self-similar asymmetric networks. [PLoS Comput Biol](#), 13, 2017. [pdf](#)
- E. Buckingham. On physically similar systems: Illustrations of the use of dimensional equations. [Phys. Rev.](#), 4:345–376, 1914. [pdf](#)

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References IV

- A. Clauset, C. R. Shalizi, and M. E. J. Newman. Power-law distributions in empirical data. [SIAM Review](#), 51:661–703, 2009. [pdf](#)
- M. H. DeGroot. [Probability and Statistics.](#) Addison-Wesley, Reading, Massachusetts, 1975.
- P. S. Dodds. Optimal form of branching supply and collection networks. [Phys. Rev. Lett.](#), 104(4):048702, 2010. [pdf](#)
- P. S. Dodds and D. H. Rothman. Scaling, universality, and geomorphology. [Annu. Rev. Earth Planet. Sci.](#), 28:571–610, 2000. [pdf](#)

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References V

- P. S. Dodds, D. H. Rothman, and J. S. Weitz. Re-examination of the “3/4-law” of metabolism. [Journal of Theoretical Biology](#), 209:9–27, 2001. [pdf](#)
- A. E. Economos. Elastic and/or geometric similarity in mammalian design. [Journal of Theoretical Biology](#), 103:167–172, 1983. [pdf](#)
- M. T. Gastner and M. E. J. Newman. Shape and efficiency in spatial distribution networks. [J. Stat. Mech.: Theor. & Exp.](#), 1:P01015, 2006. [pdf](#)

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References VI

- D. S. Glazier. Beyond the ‘3/4-power law’: variation in the intra- and interspecific scaling of metabolic rate in animals. [Biol. Rev.](#), 80:611–662, 2005. [pdf](#)
- D. S. Glazier. The 3/4-power law is not universal: Evolution of isometric, ontogenetic metabolic scaling in pelagic animals. [BioScience](#), 56:325–332, 2006. [pdf](#)
- J. T. Hack. Studies of longitudinal stream profiles in Virginia and Maryland. [United States Geological Survey Professional Paper](#), 294-B:45–97, 1957. [pdf](#)

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References VII

- A. Hemmingsen. The relation of standard (basal) energy metabolism to total fresh weight of living organisms. [Rep. Steno Mem. Hosp.](#), 4:1–58, 1950. [pdf](#)
- A. Hemmingsen. Energy metabolism as related to body size and respiratory surfaces, and its evolution. [Rep. Steno Mem. Hosp.](#), 9:1–110, 1960. [pdf](#)
- A. A. Heusner. Size and power in mammals. [Journal of Experimental Biology](#), 160:25–54, 1991. [pdf](#)

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References VIII

- M. R. Hirt, W. Jetz, B. C. Rall, and U. Brose. A general scaling law reveals why the largest animals are not the fastest. [Nature Ecology & Evolution](#), 1:1116, 2017. [pdf](#)
- N. Juster. [The Phantom Tollbooth.](#) Random House, 1961.
- M. Kleiber. Body size and metabolism. [Hilgardia](#), 6:315–353, 1932. [pdf](#)
- M. Kleiber. [The Fire of Life. An Introduction to Animal Energetics.](#) Wiley, New York, 1961.

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References IX

- [27] T. Kolokotronis, V. Savage, E. J. Deeds, and W. Fontana.
Curvature in metabolic scaling.
Nature, 464:753, 2010. [pdf](#)
- [28] J. Kozłowski and M. Konarzewski.
Is West, Brown and Enquist's model of allometric scaling mathematically correct and biologically relevant?
Functional Ecology, 18:283–289, 2004. [pdf](#)
- [29] P. La Barbera and R. Rosso.
On the fractal dimension of stream networks.
Water Resources Research, 25(4):735–741, 1989. [pdf](#)



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References X

- [30] N. Lane.
Power, Sex, Suicide: Mitochondria and the Meaning of Life.
Oxford University Press, Oxford, UK, 2005.
- [31] L. B. Leopold.
A View of the River.
Harvard University Press, Cambridge, MA, 1994.
- [32] T. McMahon.
Size and shape in biology.
Science, 179:1201–1204, 1973. [pdf](#)
- [33] T. A. McMahon.
Allometry and biomechanics: Limb bones in adult ungulates.
The American Naturalist, 109:547–563, 1975. [pdf](#)



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References XI

- [34] T. A. McMahon and J. T. Bonner.
On Size and Life.
Scientific American Library, New York, 1983.
- [35] N. Meyer-Vernet and J.-P. Rospars.
How fast do living organisms move: Maximum speeds from bacteria to elephants and whales.
American Journal of Physics, pages 719–722, 2015. [pdf](#)
- [36] D. R. Montgomery and W. E. Dietrich.
Channel initiation and the problem of landscape scale.
Science, 255:826–30, 1992. [pdf](#)



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References XII

- [37] C. D. Murray.
A relationship between circumference and weight in trees and its bearing on branching angles.
J. Gen. Physiol., 10:725–729, 1927. [pdf](#)
- [38] M. G. Newberry, E. D. B., and S. V. M.
Testing foundations of biological scaling theory using automated measurements of vascular networks.
PLoS Comput Biol, 11:e1004455, 2015. [pdf](#)
- [39] W. H. Press, S. A. Teukolsky, W. T. Vetterling, and B. P. Flannery.
Numerical Recipes in C.
Cambridge University Press, second edition, 1992.



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References XIII

- [40] C. Price, J. S. Weitz, V. Savage, S. Stegen, A. Clarke, D. Coomes, P. S. Dodds, R. Etienne, A. Kerkhoff, K. McCulloh, K. Niklas, H. Olff, and N. Swenson.
Testing the metabolic theory of ecology.
Ecology Letters, 15:1465–1474, 2012. [pdf](#)
- [41] J. M. V. Rayner.
Linear relations in biomechanics: the statistics of scaling functions.
J. Zool. Lond. (A), 206:415–439, 1985. [pdf](#)
- [42] M. Rubner.
Ueber den einfluss der körpergrösse auf stoffund kraftwechsel.
Z. Biol., 19:535–562, 1883. [pdf](#)



119 of 124

References XIV

- [43] P. A. Samuelson.
A note on alternative regressions.
Econometrica, 10:80–83, 1942. [pdf](#)
- [44] Sarrus and Rameaux.
Rapport sur une mémoire adressé à l'Académie de Médecine.
Bull. Acad. R. Méd. (Paris), 3:1094–1100, 1838–39.
- [45] V. M. Savage, E. J. Deeds, and W. Fontana.
Sizing up allometric scaling theory.
PLoS Computational Biology, 4:e1000171, 2008. [pdf](#)



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References XV

- [46] J. Speakman.
On Blum's four-dimensional geometric explanation for the 0.75 exponent in metabolic allometry.
J. Theor. Biol., 144(1):139–141, 1990. [pdf](#)
- [47] W. R. Stahl.
Scaling of respiratory variables in mammals.
Journal of Applied Physiology, 22:453–460, 1967.
- [48] M. P. H. Stumpf and M. A. Porter.
Critical truths about power laws.
Science, 335:665–666, 2012. [pdf](#)



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References XVI

- [49] A. Tero, S. Takagi, T. Saigusa, K. Ito, D. P. Bebbler, M. D. Fricker, K. Yumiki, R. Kobayashi, and T. Nakagaki.
Rules for biologically inspired adaptive network design.
Science, 327(5964):439–442, 2010. [pdf](#)
- [50] D. L. Turcotte, J. D. Pelletier, and W. I. Newman.
Networks with side branching in biology.
Journal of Theoretical Biology, 193:577–592, 1998. [pdf](#)
- [51] P. D. Weinberg and C. R. Ethier.
Twenty-fold difference in hemodynamic wall shear stress between murine and human aortas.
Journal of Biomechanics, 40(7):1594–1598, 2007. [pdf](#)



122 of 124

References XVII

- [52] G. B. West.
Scale: The Universal Laws of Growth, Innovation, Sustainability, and the Pace of Life in Organisms, Cities, Economies, and Companies.
Penguin Press, New York, 2017.
- [53] G. B. West, J. H. Brown, and B. J. Enquist.
A general model for the origin of allometric scaling laws in biology.
Science, 276:122–126, 1997. [pdf](#)
- [54] G. B. West, J. H. Brown, and J. Enquist.
The fourth dimension of life: Fractal geometry and allometric scaling of organisms.
Science, 284:1677–1679, 1999. [pdf](#)



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References XVIII

- [55] G. B. West, J. H. Brown, and J. Enquist. **Nature.** [Nature](#), 400:664–667, 1999. [pdf](#) 
- [56] C. R. White and R. S. Seymour. **Allometric scaling of mammalian metabolism.** [J. Exp. Biol.](#), 208:1611–1619, 2005. [pdf](#) 

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