

Scaling—a Plenitude of Power Laws

Principles of Complex Systems
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Outline

Scaling-at-large

- Allometry
- Examples
- Metabolism and Truthicide
- Death by fractions
- Measuring allometric exponents
- River networks
- Earlier theories
- Geometric argument
- Blood networks
- River networks
- Conclusion

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Scalingarama

General observation:

Systems (complex or not)
that cross many spatial and temporal scales
often exhibit some form of **scaling**.

Outline—All about scaling:

- Definitions.
- Examples.
- How to measure your power-law relationship.
- Scaling in metabolism and river networks.
- The Unsolved Allometry Theoricides.

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A power law relates two variables x and y as follows:

$$y = cx^\alpha$$



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- c is the **scaling exponent** (or just exponent)
- (α can be any number in principle but we will find various restrictions.)
- c is the **prefactor** (which can be important!)



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- The **prefactor c** must balance dimensions.

- Imagine the height ℓ and volume v of a family of shapes are related as:

$$\ell = cv^{1/4}$$

- Using $[\cdot]$ to indicate dimension, then

$$[c] = [l]/[v^{1/4}] = L/L^{3/4} = L^{1/4}.$$



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Looking at data

- Power-law relationships are linear in log-log space:

$$y = cx^\alpha$$

$$\Rightarrow \log_b y = \alpha \log_b x + \log_b c$$

with slope equal to α , the scaling exponent.

- Much searching for straight lines on log-log or double-logarithmic plots.
- Good practice: **Always, always, always use base 10.**
- Talk only about orders of magnitude (powers of 10).

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Why is $\alpha \approx 1.23$?

A rough understanding:

- We are here: $W \propto G^{4/3}/T$
- Observe weak scaling $T \propto G^{0.10 \pm 0.02}$.
- (Implies $S \propto G^{0.9} \rightarrow$ convolutions fill space.)
- $\Rightarrow W \propto G^{4/3}/T \propto G^{1.23 \pm 0.02}$

Scaling

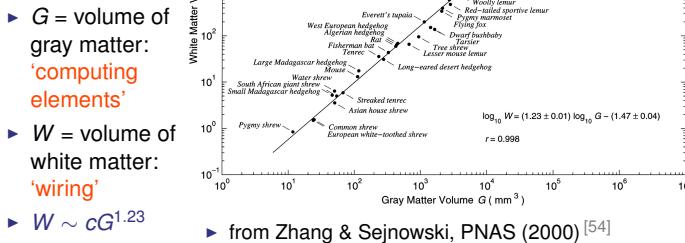
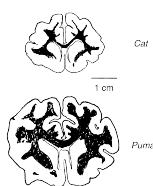
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A beautiful, heart-warming example:



Why is $\alpha \approx 1.23$?

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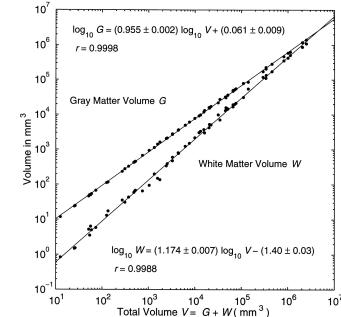
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Trickiness:



- With $V = G + W$, some power laws must be approximations.
- Measuring exponents is a hairy business...

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Good scaling:

General rules of thumb:

- High quality:** scaling persists over three or more orders of magnitude for each variable.
- Medium quality:** scaling persists over three or more orders of magnitude for only one variable and at least one for the other.
- Very dubious:** scaling 'persists' over less than an order of magnitude for both variables.

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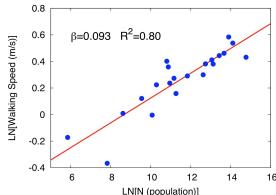
A rough understanding:

- $G \sim ST$ (convolutions are okay)
- $W \sim \frac{1}{2} pSL$
- $G \sim L^3 \leftarrow$ this is a little sketchy...
- Eliminate S and L to find $W \propto G^{4/3}/T$



Unconvincing scaling:

Average walking speed as a function of city population:



Two problems:

1. use of natural log, and
2. minute variation in dependent variable.

- ▶ from Bettencourt et al. (2007)^[4]; otherwise very interesting—see later.

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Scale invariance

Compare with $y = ce^{-\lambda x}$:

- ▶ If we rescale x as $x = rx'$, then

$$y = ce^{-\lambda rx'}$$

- ▶ Original form cannot be recovered.
- ▶ Scale matters for the exponential.

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Definitions

Power laws are the signature of scale invariance:

Scale invariant ‘objects’ look the ‘same’ when they are appropriately rescaled.

- ▶ Objects = geometric shapes, time series, functions, relationships, distributions,...
- ▶ ‘Same’ might be ‘statistically the same’
- ▶ To rescale means to change the units of measurement for the relevant variables

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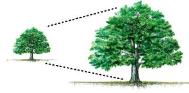
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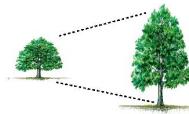
Definitions:

Isometry:



- ▶ Dimensions scale linearly with each other.

Allometry:



Dimensions scale nonlinearly.

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Scale invariance

Our friend $y = cx^\alpha$:

- ▶ If we rescale x as $x = rx'$ and y as $y = r^\alpha y'$, then

$$r^\alpha y' = c(rx')^\alpha$$

$$\Rightarrow y' = cr^\alpha x'^\alpha r^{-\alpha}$$

$$\Rightarrow y' = cx'^\alpha$$

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Definitions

Isometry versus Allometry:

- ▶ Iso-metry = ‘same measure’
- ▶ Allo-metry = ‘other measure’

Confusingly, we use allometric scaling to refer to both:

1. Nonlinear scaling of a dependent variable on an independent one (e.g., $y \propto x^{1/3}$)
2. The relative scaling of correlated measures (e.g., white and gray matter).

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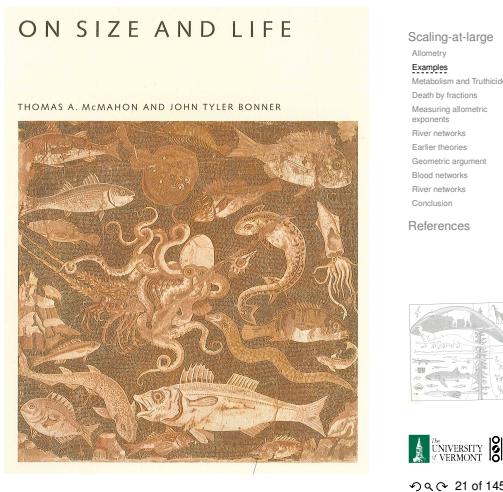
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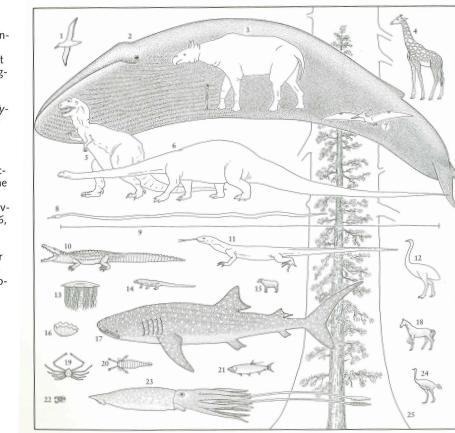
A wonderful treatise on scaling:

McMahon and Bonner, 1983^[31]



Scaling

The many scales of life:



The many scales of life:

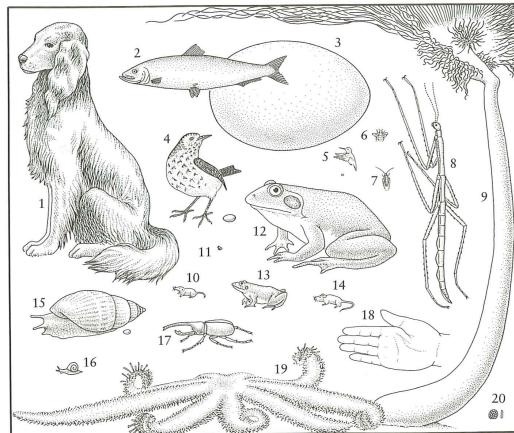
The biggest living things (left). All the organisms shown are larger than number 1. 1, the largest flying bird (albatross); 2, the largest known land mammal (*Baluchitherium*) with a human figure shown for scale; 4, the tallest living land animal (giraffe); 5, *Tyrannosaurus*; 6, *Diplodocus*; 7, one of the largest flying reptiles (*Pteranodon*); 8, the largest extant plesiosaur (*Melanostoma*); 9, the largest tapeworm found in man; 10, the largest living reptile (West African crocodile); 11, the largest extinct lizard; 12, the largest extinct bird (*Aepyornis*); 13, the largest jellyfish (*Cyanea*); 14, the largest living lizard (Komodo dragon); 15, sheep; 16, the largest bivalve mollusc (*Tridacna*); 17, the largest fish (whale shark); 18, the largest scorpion (Scorpio); 19, the largest oceanic spider crab; 20, the largest sea scorpion (Euryptenid); 21, large tarpon; 22, the largest lobster; 23, the largest mollusc (deep-water squid, *Architeuthis*); 24, ostrich; 25, the lower 105 feet of the largest organism (giant sequoia), with a 100-foot larch superposed.

p. 2, McMahon and Bonner^[31]

The many scales of life:

Medium-sized creatures (above). 1, Dog; 2, common herring; 3, the largest egg (*Aepyornis*); 4, house fly; 5, the smallest bird (hummingbird) with egg; 6, queen bee; 7, common cockroach; 8, the largest stick insect; 9, the largest polyp (*Briareum*); 10, the largest arthropod (mammal (flying shrew)); 11, the smallest vertebrate (tropical frog); 12, the largest frog (goliath frog); 13, common grasshopper; 14, house sparrow; 15, the largest land snail (*Achatina*) with shell; 16, common snail; 17, the largest beetle (goliath beetle); 18, human hand; 19, the largest starfish (*Luidia*); 20, the largest free-moving protozoan (an extinct nummulite).

p. 3, McMahon and Bonner^[31]



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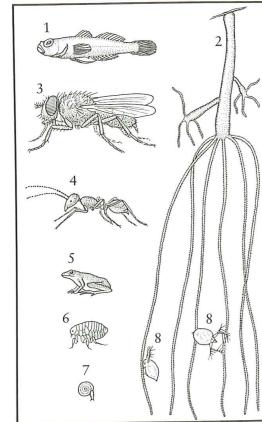
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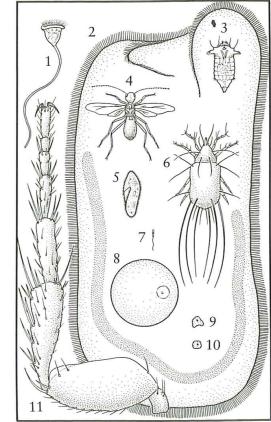


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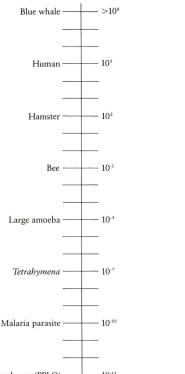
The many scales of life:



3, McMahon and Bonner^[31]



Size range (in grams) and cell differentiation:



10^{-13} to 10^8 , p.
3, McMahon and Bonner^[31]

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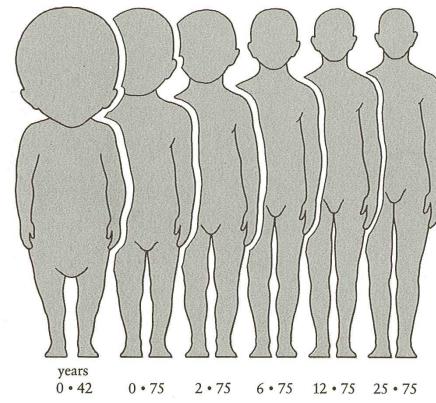
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Non-uniform growth:



p. 32, McMahon and Bonner^[31]

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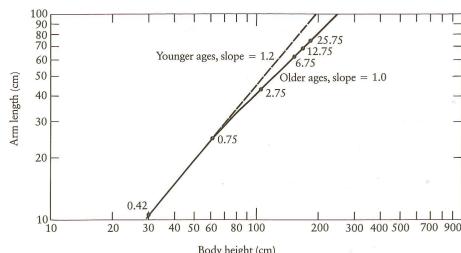
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Non-uniform growth—arm length versus height:

Good example of a **break in scaling**:



A **crossover** in scaling occurs around a height of 1 metre.

p. 32, McMahon and Bonner [31]

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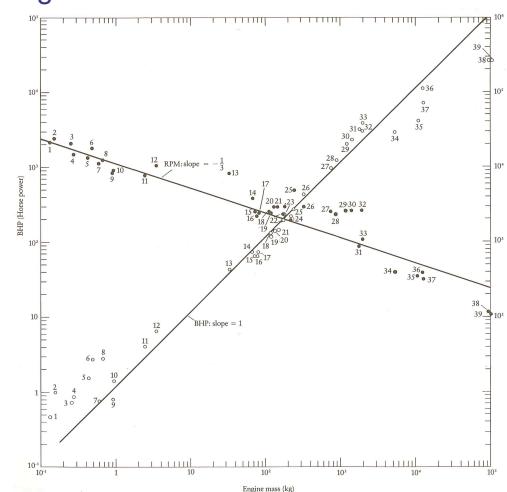
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Engines:



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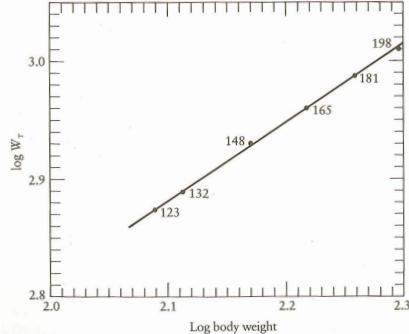


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The allometry of nails:

Observed: Diameter \propto Length $^{2/3}$ or $d \propto \ell^{2/3}$.

Weightlifting: $M_{\text{worldrecord}} \propto M_{\text{lifter}}^{2/3}$



Idea: Power \sim cross-sectional area of isometric lifters.

p. 53, McMahon and Bonner [31]

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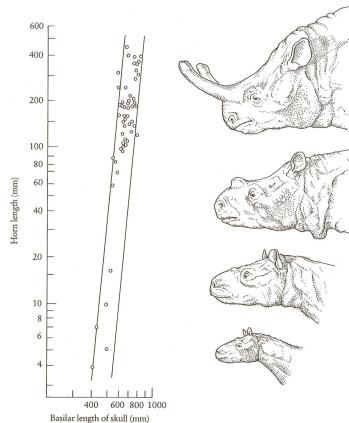
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Since $\ell d^2 \propto$ Volume v :

- Diameter \propto Mass $^{2/7}$ or $d \propto v^{2/7}$.
- Length \propto Mass $^{3/7}$ or $\ell \propto v^{3/7}$.
- Nails lengthen faster than they broaden (c.f. trees).

p. 58–59, McMahon and Bonner [31]

Titanotheres horns: $L_{\text{horn}} \sim L_{\text{skull}}^4$



p. 36, McMahon and Bonner [31]; a bit dubious.

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The allometry of nails:

A buckling instability?:

- Physics/Engineering result (): Columns buckle under a load which depends on d^4/ℓ^2 .
- To drive nails in, posit resistive force \propto nail circumference $= \pi d$.
- Match forces independent of nail size: $d^4/\ell^2 \propto d$.
- Leads to $d \propto \ell^{2/3}$.
- Argument made by Galileo [15] in 1638 in “Discourses on Two New Sciences.” () Also, see here. ()
- Euler, 1757. ()
- Also see McMahon, “Size and Shape in Biology,” Science, 1973. [29]

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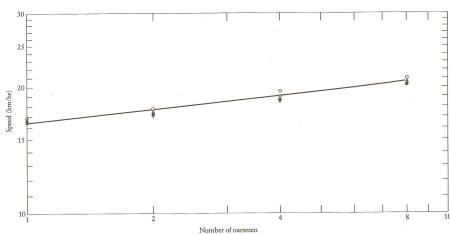


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Rowing: Speed \propto (number of rowers) $^{1/9}$

Shell dimensions and performances.

No. of oarsmen	Modifying description	Length, L (m)	Beam, b (m)	n/b	Boat mass per oarsman (kg)	Time for 2000 m (min)
8	Heavyweight	18.28	0.610	30.0	14.7	5.87
8	Lightweight	18.28	0.598	30.6	14.7	5.92
4	With coxswain	11.70	0.774	15.1	18.1	5.82
4	Without coxswain	11.75	0.574	21.0	18.1	6.13
2	Double scull	9.75	0.513	18.6	6.33	6.42
2	Pair-oared shell	9.76	0.556	27.4	13.6	6.87
1	Single scull	7.93	0.293	27.0	16.3	7.16
						7.23
						7.17



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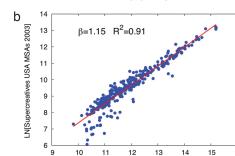
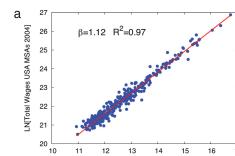


Fig. 1. Examples of scaling relationships. (a) Total wages per MSA in 2004 for the U.S. (blue points) vs. metropolitan population. (b) Supercreative employment per MSA in 2003, for the U.S. (blue points) vs. metropolitan population. Best-fit scaling relations are shown as solid lines.

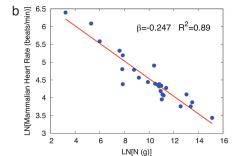
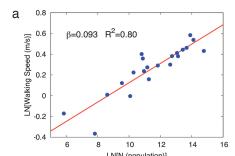


Fig. 2. The pace of urban life increases with city size in contrast to the pace of biological life, which decreases with organism size. (a) Walking speed vs. population for cities around the world. (b) Heart rate vs. the size (mass) of organisms.

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From further back:

- Zipf action [55, 56] (we've been here already)
 - Survey by Naroll and von Bertalanffy [36]
- "The principle of allometry in biology and the social sciences"

General Systems, Vol 1, 1956.

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Scaling in Cities:

Scaling

Table 1. Scaling exponents for urban indicators vs. city size

Y	β	95% CI	Adj-R ²	Observations	Country-year
New patents	1.27	[1.25, 1.29]	0.72	331	U.S. 2001
Inventors	1.25	[1.22, 1.27]	0.76	331	U.S. 2001
Private R&D employment	1.34	[1.29, 1.39]	0.92	266	U.S. 2002
"Supercreative" employment	1.15	[1.11, 1.18]	0.89	287	U.S. 2003
R&D establishments	1.19	[1.14, 1.22]	0.77	287	U.S. 1997
R&D employment	1.26	[1.18, 1.43]	0.93	295	China 2002
Total wages	1.12	[1.09, 1.13]	0.96	361	U.S. 2002
Total bank deposits	1.08	[1.03, 1.11]	0.91	267	U.S. 1996
GDP	1.15	[1.06, 1.23]	0.96	295	China 2002
GDP	1.26	[1.09, 1.46]	0.64	196	EU 1999–2003
GDP	1.13	[1.03, 1.23]	0.94	37	Germany 2003
Total electrical consumption	1.07	[1.03, 1.11]	0.88	392	Germany 2002
New AIDS cases	1.23	[1.18, 1.29]	0.76	93	U.S. 2002–2003
Serious crimes	1.16	[1.11, 1.18]	0.89	287	U.S. 2003
Total housing	1.00	[0.99, 1.01]	0.99	316	U.S. 1990
Total employment	1.01	[0.99, 1.02]	0.98	331	U.S. 2001
Household electrical consumption	1.00	[0.94, 1.06]	0.88	377	Germany 2002
Household electrical consumption	1.05	[0.89, 1.22]	0.91	295	China 2002
Household water consumption	1.01	[0.89, 1.11]	0.96	295	China 2002
Gasoline stations	0.77	[0.74, 0.81]	0.93	318	U.S. 2001
Gasoline sales	0.79	[0.73, 0.80]	0.94	318	U.S. 2001
Length of electrical cables	0.87	[0.82, 0.92]	0.75	380	Germany 2002
Road surface	0.83	[0.74, 0.92]	0.87	29	Germany 2002

Data sources are shown in SI Text. CI, confidence interval; Adj-R², adjusted R²; GDP, gross domestic product.

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Scaling in Cities:

- "Growth, innovation, scaling, and the pace of life in cities"
 - Bettencourt et al., PNAS, 2007. [4]
 - Quantified levels of
 - Infrastructure
 - Wealth
 - Crime levels
 - Disease
 - Energy consumption
- as a function of city size N (population).

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Scaling in Cities:

Intriguing findings:

- Global supply costs scale **sublinearly** with N ($\beta < 1$).
 - Returns to scale for infrastructure.
- Total individual costs scale **linearly** with N ($\beta = 1$)
 - Individuals consume similar amounts independent of city size.
- Social quantities scale **superlinearly** with N ($\beta > 1$)
 - Creativity (# patents), wealth, disease, crime, ...

Density doesn't seem to matter...

- Surprising given that across the world, we observe two orders of magnitude variation in area covered by agglomerations (■) of fixed populations.

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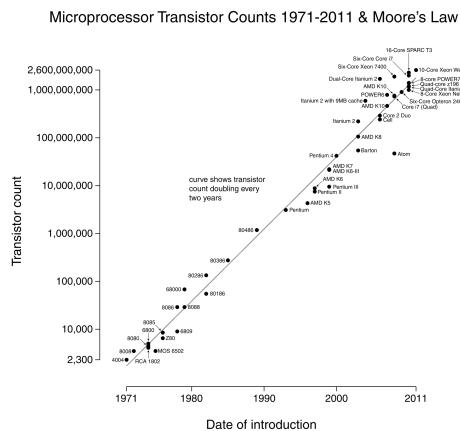
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Moore's Law: (田)



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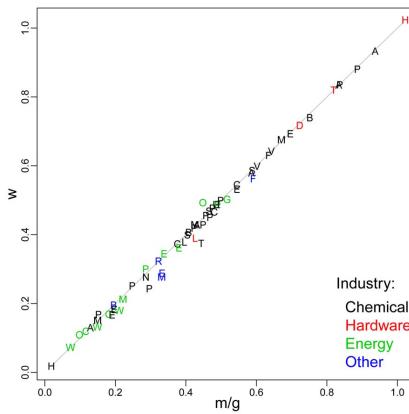


Figure 4. An illustration that the combination of exponentially increasing production and exponentially decreasing cost are equivalent to Wright's law. The value of the Wright parameter w is plotted against the prediction m/g based on the Sahal formula, where m is the exponent of cost reduction and g is the exponent of the increase in cumulative production.
doi:10.1371/journal.pone.0052669.g004

Scaling laws for technology production:

- "Statistical Basis for Predicting Technological Progress" [35] Nagy et al., PLoS ONE, 2013.
- y_t = stuff unit cost; x_t = total amount of stuff made.
- Wright's Law, cost decreases exponentially with total stuff made: [53]

$$y_t \propto x_t^{-w}.$$

- Moore's Law (田), framed as cost decrease connected with doubling of transistor density every two years: [33]

$$y_t \propto e^{-mt}.$$

- Sahal's observation that Moore's law gives rise to Wright's law if stuff production grows exponentially: [41]

$$x_t \propto e^{gt}.$$

- Sahal + Moore gives Wright with $w = m/g$.

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Scaling of Specialization:

- "Scaling of Differentiation in Networks: Nervous Systems, Organisms, Ant Colonies, Ecosystems, Businesses, Universities, Cities, Electronic Circuits, and Legos"
- M. A. Changizi, M. A. McDannald and D. Widders [8]
J. Theor. Biol., 2002.

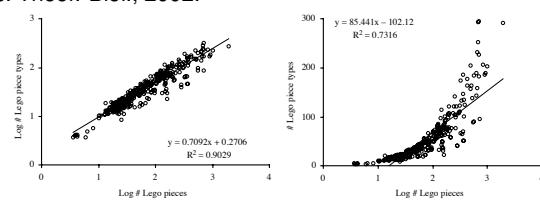


Fig. 3. Log-log (base 10) (left) and semi-log (right) plots of the number of Lego piece types vs. the total number of parts in Lego structures ($n = 391$). To help to distinguish the data points, logarithmic values were perturbed by adding a random number in the interval $[-0.05, 0.05]$, and non-logarithmic values were perturbed by adding a random number in the interval $[-1, 1]$.

- Nice 2012 wired.com write-up (田)

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$$C \sim N^{1/d}, d \geq 1:$$

- C = network differentiation = # node types.
- N = network size = # nodes.
- d = combinatorial degree.
- Low d : strongly specialized parts.
- High d : strongly combinatorial in nature, parts are reused.
- Claim: Natural selection produces high d systems.
- Claim: Engineering/brains produces low d systems.

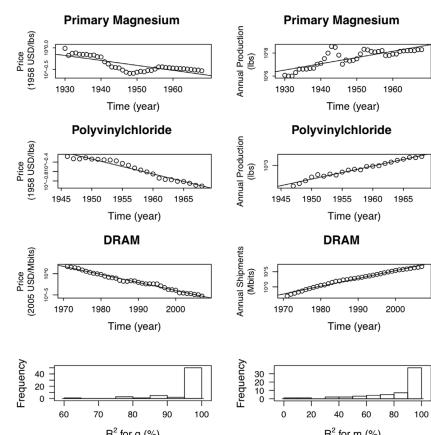


Figure 3. Three examples showing the logarithm of price as a function of time in the left column and the logarithm of production as a function of time in the right column, based on industry-wide data. We have chosen these examples to be representative. The top row contains examples with intermediate fits, the second row an example with an intermediate goodness of fit, and the third row one of the best examples. The fourth row of the figure show histograms of R^2 -values for fitting g and m for the 62 datasets.
doi:10.1371/journal.pone.0052669.g003

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Animal power

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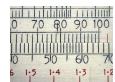
Fundamental biological and ecological constraint:

$$P = c M^\alpha$$

P = basal metabolic rate

M = organismal body mass

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$$P = c M^\alpha$$

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

Birds $39\text{--}41^\circ\text{C}$

Eutherian Mammals $36\text{--}38^\circ\text{C}$

Marsupials $34\text{--}36^\circ\text{C}$

Monotremes $30\text{--}31^\circ\text{C}$

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What one might expect:

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$\alpha = 2/3$ 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 $\log P$ around $\log cM^\alpha$.

- Stefan-Boltzmann law (田) for radiated energy:

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

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Ecology—Species-area law: (田)

Allegedly (data is messy): [52, 28]

$$N_{\text{species}} \propto A^\beta$$

- On islands: $\beta \approx 1/4$.
- On continuous land: $\beta \approx 1/8$.

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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TABLE I Summary of results*											
Network	Node	No. data points	Range of log N	Log-log R^2	Semi-log R^2	$P_{\text{power}}/P_{\text{log}}$	Relationship between C and N	Comb. degree	Exponent α for type-net	Figure in text	
Selected networks											
Electronic circuits	Component	373	2.12	0.747	0.602	0.054e-5	Power law	2.29	0.92	2	
Legos**	Piece	391	2.65	0.903	0.732	0.091e-7	Power law	1.41	—	3	
Businesses											
military vessels	Employee	13	1.88	0.971	0.832	0.053e-3	Power law	1.60	—	4	
military offices	Employee	8	1.59	0.964	0.789	0.16e-16	Increasing	1.13	—	4	
universities	Employee	9	1.55	0.766	0.749	0.27e-27	Increasing	1.37	—	4	
insurance co.	Employee	52	2.30	0.748	0.685	0.11e-10	Increasing	1.04	—	4	
Universities across schools history of Duke	Faculty	112	2.72	0.695	0.549	0.09e-01	Power law	1.81	—	5	
Faculty	46	0.94	0.921	0.892	0.09e-05	Increasing	2.07	—	5		
Ant colonies	size-type	Ant	46	6.00	0.481	0.454	0.11e-04	Power law	8.16	—	6
size-range-type	Ant	22	5.24	0.658	0.548	0.17e-04	Power law	8.00	—	6	
Organizations	Cell	134	12.40	0.249	0.165	0.08e-02	Power law	17.73	—	7	
Neurotubes	Neuron	10	0.85	0.520	0.584	0.16e-16	Increasing	4.56	—	9	
Competitive networks											
Books	Organism	—	—	—	—	—	Power law	~3	0.3 to 1.0	—	
Clinics	Business	82	2.44	0.905	0.832	0.08e-8.8	Power law	1.56	—	10	

* (1) The kind of network, (2) what the nodes are within that kind of network, (3) the number of data points, (4) the logarithmic range of network size, (5) the log-log correlation, (6) the semi-log correlation, (7) the size-dependence probabilities under, respectively, power-law and logarithmic models, (8) the empirically determined body-size relationship between differentiation C and organization size N if one of the two models can be refuted with $p < 0.05$; otherwise we just write "Increasing" to denote that neither model can be rejected, (9) the combinatorial degree (i.e. the inverse of the basal slope of a log-log plot of C versus N), (10) the scaling exponent for how quickly the degree α scales with type-network size C (in those cases for which data exist). (11) figure in this text where the plots are presented. Values for α below represent the broad trend from the literature.

** (1) The kind of network, (2) what the nodes are within that kind of network, (3) the number of data points, (4) the logarithmic range of network size, (5) the log-log correlation, (6) the semi-log correlation, (7) the size-dependence probabilities under, respectively, power-law and logarithmic models, (8) the empirically determined body-size relationship between differentiation C and organization size N if one of the two models can be refuted with $p < 0.05$; otherwise we just write "Increasing" to denote that neither model can be rejected, (9) the combinatorial degree (i.e. the inverse of the basal slope of a log-log plot of C versus N), (10) the scaling exponent for how quickly the degree α scales with type-network size C (in those cases for which data exist). (11) figure in this text where the plots are presented. Values for α below represent the broad trend from the literature.

The prevailing belief of the Church of Quarterology:

$$\alpha = 3/4$$

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

Huh?

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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:

- Average number of heart beats in a lifespan $\simeq (\text{Average lifespan}) \times (\text{Average heart rate})$
- $\propto M^{\beta-\beta}$
- $\propto M^0$
- Number of heartbeats per life time is independent of organism size!
- $\approx 1.5 \text{ billion....}$

Scaling

A theory is born:

1840's: Sarrus and Rameaux [43] first suggested $\alpha = 2/3$.



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Scaling

A theory grows:

1883: Rubner [40] found $\alpha \simeq 2/3$.



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Theory meets a different ‘truth’:

1930's: Brody, Benedict study mammals.^[7]
Found $\alpha \approx 0.73$ (standard).



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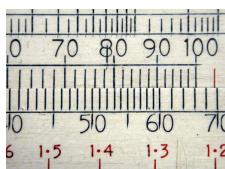


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Our hero faces a shadowy cabal:

- ▶ 1932: Kleiber analyzed 13 mammals.^[24]
- ▶ 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”.^[25]



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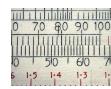
When a cult becomes a religion:

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.



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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?

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Modern Quarterology, Post Truthicide

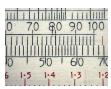
- ▶ 3/4 is held by many to be the one true exponent.



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

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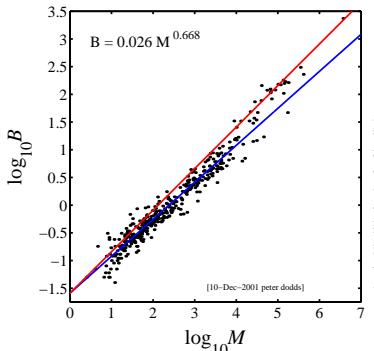


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- ▶ But: much controversy ...
- ▶ See ‘Re-examination of the “3/4-law” of metabolism’ by the Heretical Unbelievers Dodds, Rothman, and Weitz^[13], and ensuing madness...

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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Measuring exponents

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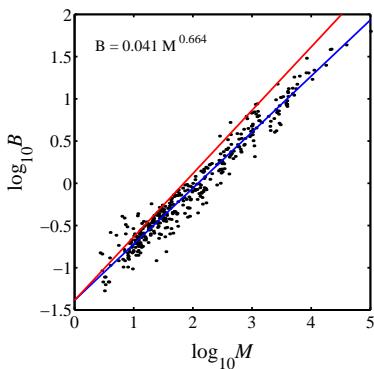
More on regression:

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. [42, 39] (aka Reduced Major Axis = RMA.)



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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...

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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!
- ▶ Scale invariant.



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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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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 $r = \text{standard correlation coefficient}$:



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



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Heusner's data, 1991 (391 Mammals)

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

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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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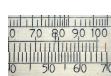
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Bennett and Harvey, 1987 (398 birds)

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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Revisiting the past—mammals

$M \leq 10 \text{ kg}:$

	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	$< 10^{-15}$

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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 obeys a t distribution with $N - 2$ degrees of freedom.
- Calculate a p -value: probability that the measured α is at least as different to our hypothesized α' as we observe.
- See, for example, DeGroot and Scherish, "Probability and Statistics."^[10]

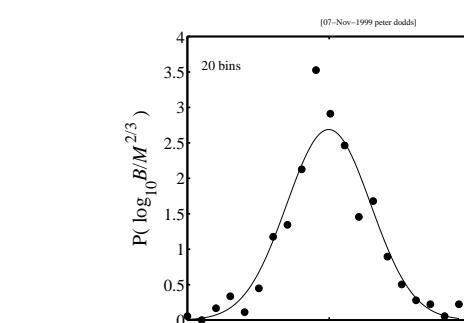
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Fluctuations—Things look normal...



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

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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.

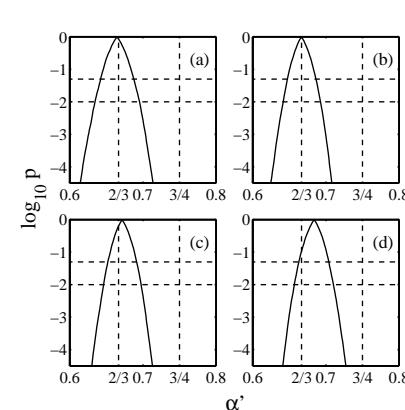
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Analysis of residuals—mammals



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Analysis of residuals

We use the spiffing Spearman Rank-Order Correlation Coefficient (田)

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.

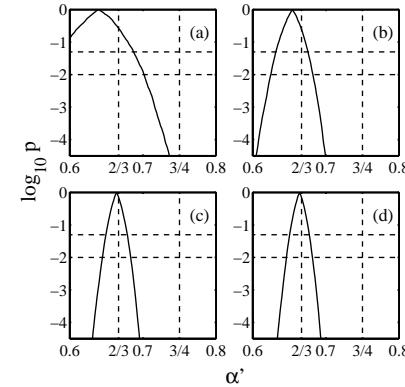
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Analysis of residuals—birds



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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 (田) 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 (田) which contains many good things. [37]

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Other approaches to measuring exponents:

- Clauset, Shalizi, Newman: "Power-law distributions in empirical data" [9] SIAM Review, 2009.
- See Clauset's page on measuring power law exponents (田) (code, other goodies).

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Recap:

- 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 [14]
- But see later: non-isometric growth leads to lower metabolic scaling. Oops.

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River networks

- 1957: J. T. Hack [19]

“Studies of Longitudinal Stream Profiles in Virginia and Maryland”

$$l \sim a^h$$

$$h \sim 0.6$$

- 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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The widening gyre:

Now we’re really confused (empirically):

- White and Seymour, 2005: unhappy with large herbivore measurements [51]. Pro 2/3: Find $\alpha \simeq 0.686 \pm 0.014$.
- 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) [44] “Sizing up allometric scaling theory” Pro 3/4: problems claimed to be finite-size scaling.

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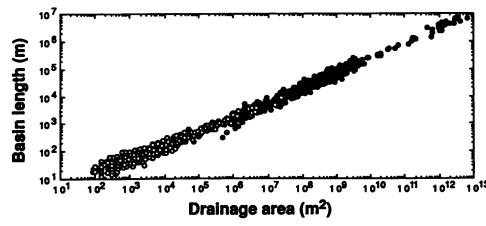
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Large-scale networks:

(1992) Montgomery and Dietrich [32]:



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

$$L \simeq 1.78a^{0.49}$$
- Mixture of basin and main stream lengths.

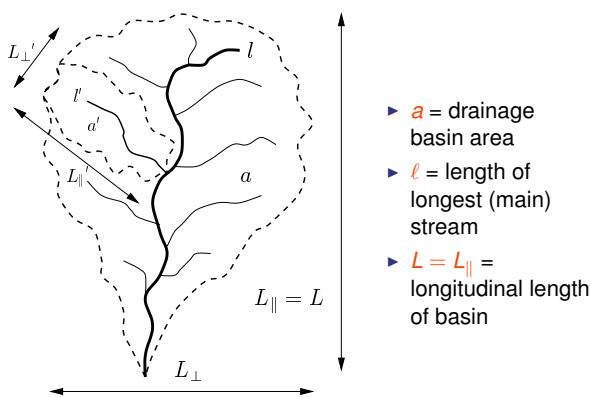
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Basic basin quantities: a , l , L_{\parallel} , L_{\perp} :



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

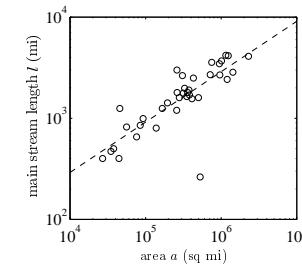
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World's largest rivers only:



- Data from Leopold (1994) [27, 12]
- Estimate of Hack exponent: $h = 0.50 \pm 0.06$

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Earlier theories

Building on the surface area idea...

- Blum (1977) [6] 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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'Tattooed Guy' Was Pivotal in Armstrong Case
 [nytimes] (田)



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- "... Leogrande's doping sparked a series of events ..."

Earlier theories

Building on the surface area idea:

- McMahon (70's, 80's): Elastic Similarity [29, 31]
- Idea is that organismal shapes scale allometrically with 1/4 powers (like trees...)
- Appears to be true for ungulate legs... [30]
- Metabolism and shape never properly connected.

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Nutrient delivering networks:

West et al.'s assumptions:

1. hierarchical network
2. capillaries (delivery units) invariant
3. network impedance is minimized via evolution

Claims:

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

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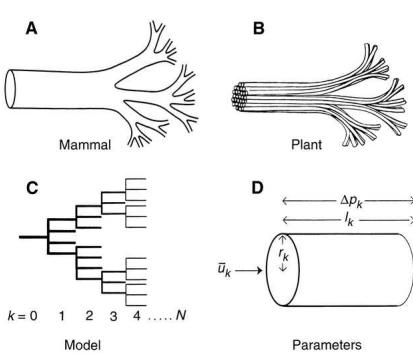


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Nutrient delivering networks:

- 1960's: Rashevsky considers blood networks and finds a 2/3 scaling.
- 1997: West et al. [50] use a network story to find 3/4 scaling.



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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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Not so fast ...

Actually, model shows:

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

Do find:

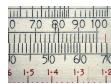
- Murray's cube law (1927) for outer branches:^[34]

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

- Impedance is distributed evenly.
- Can still assume networks are fractal.

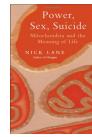
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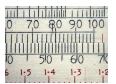
Some people understand it's truly a disaster:



"Power, Sex, Suicide: Mitochondria and the Meaning of Life" (田)
by Nick Lane (2005). [26]

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

Connecting network structure to α

1. Ratios of network parameters:

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

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)

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Really, quite confused:

Whole 2004 issue of Functional Ecology addresses the problem:

- J. Kozlowski, M. Konarzewski (2004). "Is West, Brown and Enquist's model of allometric scaling mathematically correct and biologically relevant?" *Functional Ecology* 18: 283–9, 2004.
- 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.
- J. Kozlowski, M. Konarzewski (2005). "West, Brown and Enquist's model of allometric scaling again: the same questions remain." *Functional Ecology* 19: 739–743, 2005.

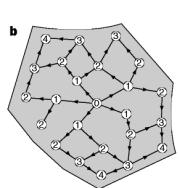
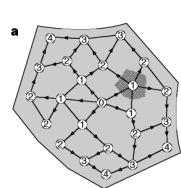
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Simple supply networks



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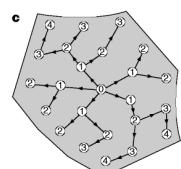
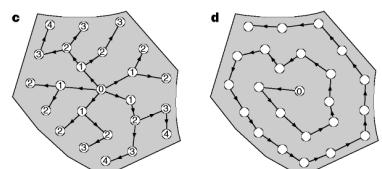
- Banavar et al., *Nature*, (1999) [1]
- Flow rate argument
- Ignore impedance
- Very general attempt to find most efficient transportation networks

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Data from real networks:

Network	R_n	R_r^{-1}	R_ℓ^{-1}	$-\frac{\ln R_r}{\ln R_n}$	$-\frac{\ln R_\ell}{\ln R_n}$	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> [49])	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

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 $V_{\text{blood}} = 0.1 V_{\text{body}}$
- ⇒ 3000 kg elephant with $V_{\text{blood}} = 10 V_{\text{body}}$

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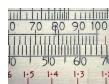
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- Q: how does the number of sustainable sinks N_{sinks} scale with volume V for the most efficient network design?

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



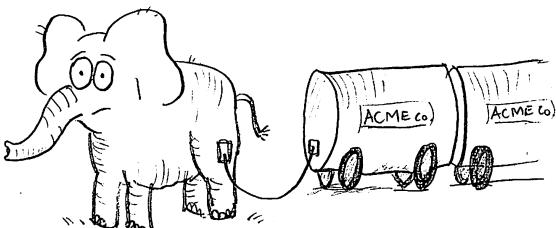
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Simple supply networks

Such a pachyderm would be rather miserable:



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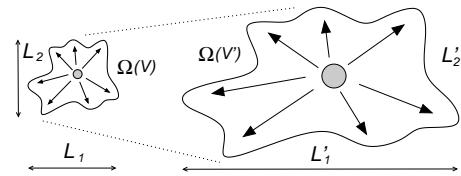
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- Allometrically growing regions:



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Geometric argument

- "Optimal Form of Branching Supply and Collection Networks." Dodds, Phys. Rev. Lett., 2010. [11]
- 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:

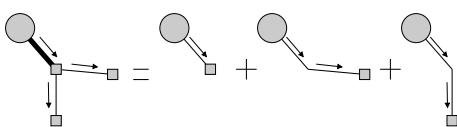
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Spherical cows and pancake cows:

- Question: How does the surface area S_{cow} of our two types of cows scale with cow volume V_{cow} ? Insert question from assignment 10 (田)
- Question: For general families of regions, how does surface area S scale with volume V ? Insert question from assignment 10 (田)



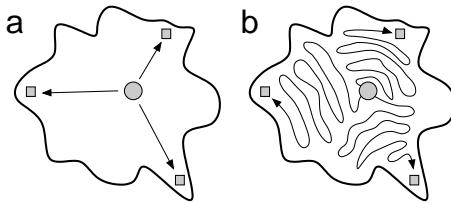
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Geometric argument

- 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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Geometric argument

- General result:

$$\min V_{\text{net}} \propto \rho V^{1+\gamma_{\max}}$$

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

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

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

$$\min V_{\text{net}/\text{allo}} \propto \rho V^{1+\gamma_{\text{allo}}}$$

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

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

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Minimal network volume:

Real supply networks are close to optimal:

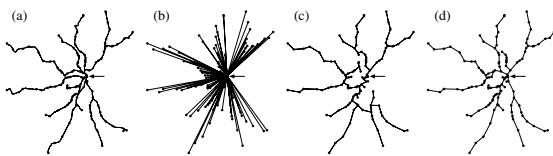


Figure 1. (a) Commuter rail network in the Boston area. The arrow marks the assumed root of the network. (b) Star graph. (c) Minimum spanning tree. (d) The model of equation (3) applied to the same set of stations.

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

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Blood networks

- 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.

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Minimal network volume:

Approximate network volume by integral over region:

$$\begin{aligned} \min V_{\text{net}} &\propto \int_{\Omega_{d,D}(V)} \rho ||\vec{x}|| d\vec{x} \\ &\rightarrow \rho V^{1+\gamma_{\max}} \int_{\Omega_{d,D}(c)} (c_1^2 u_1^2 + \dots + c_k^2 u_k^2)^{1/2} d\vec{u} \end{aligned}$$

Insert question from assignment 10 (田)

$$\propto \rho V^{1+\gamma_{\max}}$$

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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

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

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Prefactor:

Stefan-Boltzmann law: (□)

$$\frac{dE}{dt} = \sigma ST^4$$

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 :

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

- Measured for $M \leq 10$ kg:

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

Scaling

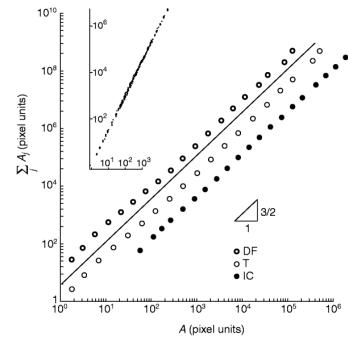
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Real data:

- 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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River networks

- View river networks as collection networks.
- Many sources and one sink.
- Assume ρ is constant over time:

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

- 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...

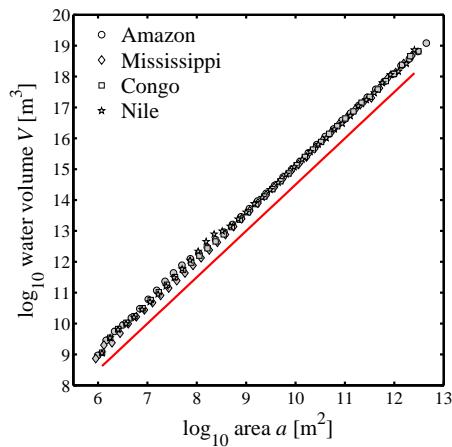
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Even better—prefactors match up:



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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.
- \therefore 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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Some people understand it's truly a disaster: (田)

Peter Sheridan Dodds, Theoretical Biologist's Buzzkill
By Mark Changizi | February 5th 2010 03:24 PM | 1 comment | Print | E-mail | Track Comments

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Mark Changizi
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There is an apocryphal story about a graduate mathematics student at the University of Virginia studying the properties of certain mathematical objects. In his fifth year some killjoy bastard elsewhere published a paper proving that there are no such mathematical objects. He dropped out of the program and I never did hear where he is today. He's probably making my cappuccino right now.

This week, a professor named Peter Sheridan Dodds published a new paper in *Physical Review Letters* further fleshing out a theory concerning why a 2/3 power law may apply for metabolic rate. The 2/3 law says that metabolic rate in animals rises as the 2/3 power of body mass. It was in a 2001 *Journal of Theoretical Biology* paper that he first argued that perhaps a 2/3 law applies, and that paper – along with others such as the one that just appeared – is what has put him in the Killjoy Hall of Fame. The University of Virginia's killjoy was a mere amateur.

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- 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.

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The unnecessary bafflement continues:

"Testing the metabolic theory of ecology" [38]

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



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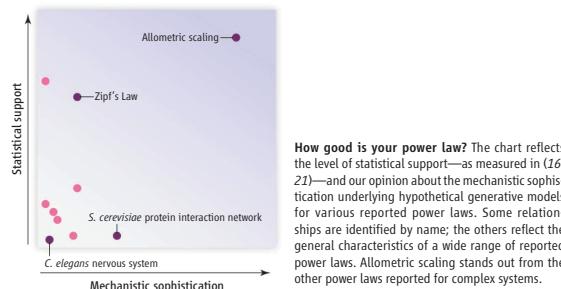
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Artisanal, handcrafted stupidity:

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



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

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