Scaling—a Plenitude of Power Laws

Principles of Complex Systems Course CSYS/MATH 300, Fall, 2009

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General observation:

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

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All about scaling:

- Definitions.
- Examples.
- ► How to measure your power-law relationship.
- Mechanisms giving rise to your power-laws.

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

$$y = cx^{\alpha}$$

- $ightharpoonup \alpha$ 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.

• eg., length ℓ and volume v of common nails are related as:

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

▶ Using [·] to indicate dimension, then

$$[c] = [I]/[V^{1/4}] = L/L^{3/4} = L^{1/4}$$

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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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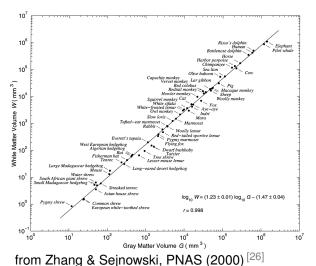
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A beautiful, heart-warming example:



 $\alpha \simeq 1.23$

gray matter: 'computing elements'

white matter: 'wiring' Scaling-at-large

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Quantities (following Zhang and Sejnowski)

- ► *G* = Volume of gray matter (cortex/processors)
- ► *W* = Volume of white matter (wiring)
- ► *T* = Cortical thickness (wiring)
- ► S = Cortical surface area
- ► L = Average length of white matter fibers
- p = density of axons on white matter/cortex interface

A rough understanding:

- ▶ G ~ ST (convolutions are okay)
- $ightharpoonup W \sim \frac{1}{2} pSL$
- ▶ G ~ L³
- lacktriangle Eliminate S and L to find $W \propto G^{4/3}/T$

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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 $W \propto G^{4/3}/T$

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A rough understanding:

- ▶ We are here: $W \propto G^{4/3}/T$
- Observe weak scaling $T \propto G^{0.10\pm0.02}$
- ▶ (Implies $S \propto G^{0.9} \rightarrow$ convolutions fill space.)
- $ightharpoonup \Rightarrow W \propto G^{4/3}/T \propto G^{1.23\pm0.02}$

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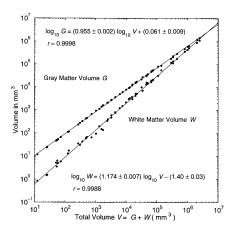
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Trickiness:

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

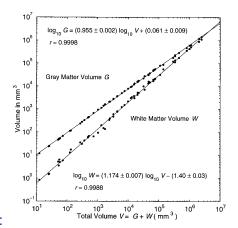
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Good scaling:

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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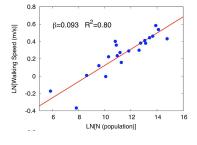
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Unconvincing scaling:

Average walking speed as a function of city population:



Two problems:

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

from Bettencourt et al. (2007) [3]; otherwise very interesting!

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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,
- 'Same' might be 'statistically the same'
- ▶ To rescale means to change the units of

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

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

If we rescale x as x = rx', then

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

- Original form cannot be recovered.
- ightharpoonup \Rightarrow scale matters for the exponential.

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More on $y = ce^{-\lambda x}$:

- ▶ Say $x_0 = 1/\lambda$ is the characteristic scale.
- ► For $x \gg x_0$, y is small, while for $x \ll x_0$, y is large.
- ▶ ⇒ More on this later with size distributions.

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Allometry (⊞):

[refers to] differential growth rates of the parts of a living organism's body part or process.

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Isometry:

dimensions scale linearly with each other.





Allometry: dimensions scale nonlinearly.

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Isometry versus Allometry:

- Isometry = 'same measure'
- Allometry = 'other measure'

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Isometry versus Allometry:

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Confusingly, we use allometric scaling to refer to both:

- 1. nonlinear scaling (e.g., $x \propto y^{1/3}$)
- and the relative scaling of different measures (e.g., resting heart rate as a function of body size)

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A wonderful treatise on scaling:

ON SIZE AND LIFE

THOMAS A MCMAHON AND JOHN TYLER BONNER

McMahon and Bonner, 1983^[18] Scaling-at-large

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For the following slide:

The biggest living things (left). All the organisms are drawn to the same scale. 1. The largest flying bird (albatross); 2, the largest known animal (the blue whale), 3, the largest extinct 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 extinct snake; 9, the length of 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, horse; 19, the largest crustacean (Japanese spider crab): 20, the largest sea scorpion (Eurypterid); 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.

Scaling-at-large

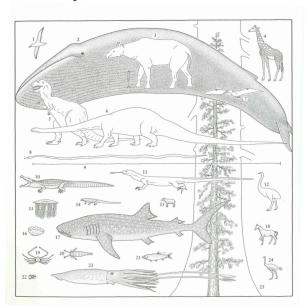
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The many scales of life:



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For the following slide:

Medium-sized creatures (above). 1, Dog; 2, common herring; 3, the largest egg (Aepyornis); 4, song thrush with egg; 5, the smallest bird (hummingbird) with egg; 6, queen bee; 7, common cockroach; 8, the largest stick insect; 9, the largest polyp (Branchiocerianthus); 10, the smallest mammal (flying shrew); 11, the smallest vertebrate (a tropical frog); 12, the largest frog (goliath frog); 13, common grass frog; 14, house mouse; 15, the largest land snail (Achatina) with egg; 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).

Scaling-at-large

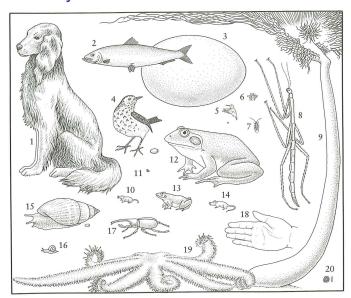
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The many scales of life:



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For the following slide:

Small, "naked-eye" creatures (lower left).

1, One of the smallest fishes (Trimmatom nanus); 2, common brown hydra, expanded; 3, housefly; 4, medium-sized ant; 5, the smallest vertebrate (a tropical frog, the same as the one numbered 11 in the figure above); 6, flea (Xenopsylla cheopis); 7, the smallest land snail; 8, common water flea (Daphnia).

The smallest "naked-eye" creatures and some large microscopic animals and cells (below right). 1, Vorticella, a ciliate; 2, the largest ciliate protozoan (Bursaria); 3, the smallest many-celled animal (a rotifer); 4, smallest flying insect (Elaphis); 5, another ciliate (Paramecium); 6, cheese mite; 7, human sperm; 8, human ovum; 9, dysentery amoeba; 10, human liver cell; 11, the foreleg of the flea (numbered 6 in the figure to the left).

Scaling-at-large

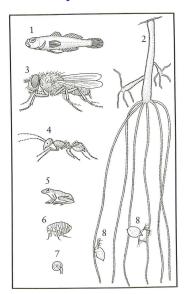
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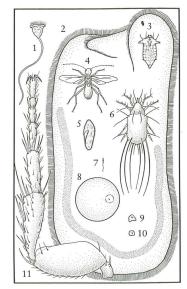
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The many scales of life:





Scaling-at-large

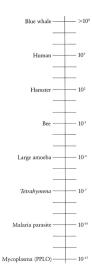
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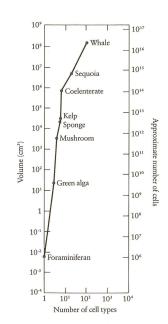
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Size range and cell differentiation:





Scaling-at-large

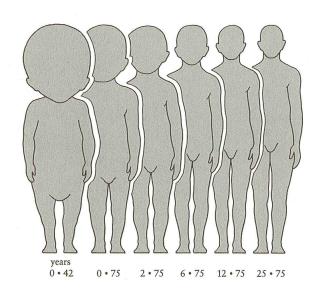
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Non-uniform growth:



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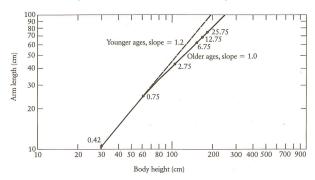
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Non-uniform growth—arm length versus height:

Good example of a break in scaling:



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

p. 32, McMahon and Bonner [18]

Scaling-at-large

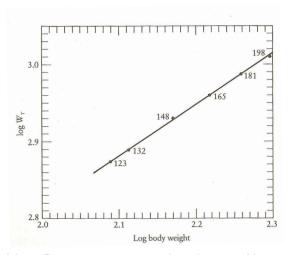
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Weightlifting: $M_{\text{worldrecord}} \propto M_{\text{lifter}}^{2/3}$



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

p. 53, McMahon and Bonner [18]

Scaling-at-large

Allometry Examples

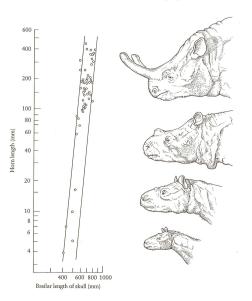
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Titanothere horns: $L_{ m horn} \sim L_{ m skull}^4$

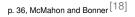


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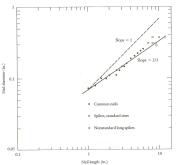
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The allometry of nails:





- ▶ Diameter

 ∠ Length^{2/3}

p. 58–59, McMahon and Bonner [18]

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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, resistive force \propto nail circumference = πd .
- ▶ Match forces independent of nail size: $d^4/\ell^2 \propto d$.
- ► Leads to $d \propto \ell^{2/3}$.

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- ► To drive nails in, resistive force \propto nail circumference = πd .
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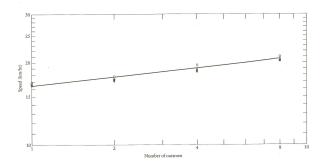
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Rowing: Speed \propto (number of rowers)^{1/9}

Shell dimensions and performances,

No. of oarsmen	Modifying description	Length, l	Beam, b (m)	1/6	Boat mass per oarsman (kg)	Time for 2000 m (min)			
						I	П	Ш	IV
8	Heavyweight	18.28	0.610	30.0	14.7	5.87	5.92	5.82	5,73
8	Lightweight	18.28	0.598	30.6	14.7				
4	With coxswain	12.80	0.574	22.3	18.1				
4	Without coxswain	11.75	0.574	21.0	18.1	6.33	6.42	6.48	6.13
2	Double scull	9.76	0.381	25.6	13.6				
2	Pair-oared shell	9.76	0.356	27.4	13.6	6.87	6.92	6.95	6.77
1	Single scull	7.93	0.293	27.0	16.3	7.16	7.25	7.28	7.17



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"Growth, innovation, scaling, and the pace of life in cities"

Bettencourt et al., PNAS, 2007. [3]

- Quantified levels of
 - Infrastructure
 - Wealth
 - Crime levels
 - Disease
 - Energy consumption

as a function of city size N (population).

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

Υ	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

 $Data \ sources \ are \ shown \ in \ \textit{SI Text}. \ CI, \ confidence \ interval; \ Adj-\textit{R}^2, \ adjusted \ \textit{R}^2; \ GDP, \ gross \ domestic \ product.$

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Intriguing findings:

- ▶ Global supply costs scale sublinearly with N (β < 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 (β > 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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Allegedly (data is messy):

▶ On islands: $\beta \approx 1/4$.

▶ On continuous land: $\beta \approx 1/8$.

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A focus:

- ▶ How much energy do organisms need to live?
- And how does this scale with organismal size?

Scaling-at-large

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A focus:

- ▶ How much energy do organisms need to live?
- And how does this scale with organismal size?

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Animal power

Fundamental biological and ecological constraint:

$$P = c M^{\alpha}$$

P =basal metabolic rate

M =organismal body mass





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Animal power

Fundamental biological and ecological constraint:

$$P = c M^{\alpha}$$

P =basal metabolic rate

M =organismal body mass







Scaling-at-large

History: Metabolism

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

History: Metabolism

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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*





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$$\alpha = 2/3$$

▶ Dimensional analysis suggests an energy balance surface law:

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

- ▶ Lognormal fluctuations: Gaussian fluctuations in log P around log cM^c
- ► Stefan-Boltzmann relation for radiated energy:

$$\frac{\mathrm{d}E}{\mathrm{d}t} = \sigma \varepsilon ST^4$$

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

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

- ► Lognormal fluctuations:

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- Stefan-Boltzmann relation for radiated energy:

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- Lognormal fluctuations:
 Gaussian fluctuations in $\log P$ around $\log cM^{\alpha}$.
- Stefan-Boltzmann relation for radiated energy:

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The prevailing belief of the church of quarterology

$$\alpha = 3/4$$

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

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The prevailing belief of the church of quarterology

$$\alpha = 3/4$$

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

Huh?

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llometry

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Related putative scalings:

- ▶ 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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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

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Assuming:

- ▶ Average lifespan $\propto M^{\beta}$
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Then:

Average number of heart beats in a lifespan

 ≃ (Average lifespan) × (Average heart rate)

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Assuming:

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

Then:

► Average number of heart beats in a lifespan \simeq (Average lifespan) \times (Average heart rate) $\propto M^{\beta-\beta}$

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Assuming:

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Then:

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

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Assuming:

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

Then:

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

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History

1840's: Sarrus and Rameaux [22] first suggested $\alpha = 2/3$.



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Frame 50/117



1883: Rubner^[21] found $\alpha \simeq 2/3$.



History: Metabolism

Frame 51/117





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



History: Metabolism

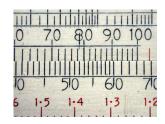
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1932: Kleiber analyzed 13 mammals. [15] Found $\alpha = 0.76$ and suggested $\alpha = 3/4$.



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1950/1960: Hemmingsen [12, 13] Extension to unicellular organisms. $\alpha = 3/4$ assumed true.



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1964: Troon, Scotland: [4] 3rd symposium on energy metabolism. $\alpha =$ 3/4 made official . . .



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1964: Troon, Scotland: [4] 3rd symposium on energy metabolism. $\alpha = 3/4$ made official . . .

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... 29 to zip.

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Today

▶ 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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Today

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But—much controversy...

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Today

▶ 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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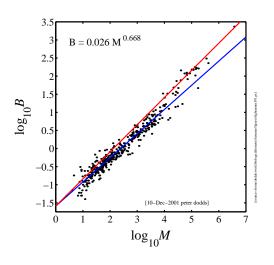
References

- ▶ But—much controversy...
- See 'Re-examination of the "3/4-law" of metabolism' Dodds, Rothman, and Weitz [9]

Frame 56/117



Some data on metabolic rates



- Heusner's data (1991) [14]
- ▶ 391 Mammals
- ▶ blue line: 2/3
- red line: 3/4.
- ► (*B* = *P*)

Scaling-at-large

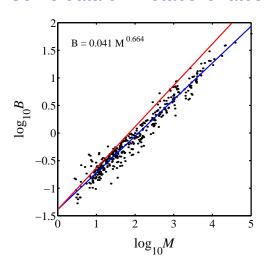
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Some data on metabolic rates



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

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Passerine vs. non-passerine...



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Frame 59/117





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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Linear regression

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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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More on regression:

If (a) we don't know what the errors of either variable are,

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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,

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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.

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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.

(aka Reduced Major Axis = RMA.)

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For Standardized Major Axis Linear Regression:

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

Very simple!

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Relationship to ordinary least squares regression is simple:

$$slope_{sma} = r^{-1} \times slope_{ols y on x}$$

= $r \times slope_{ols x on y}$

where r = standard correlation coefficient:

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

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Heusner's data, 1991 (391 Mammals)

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

Measuring exponents

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Bennett and Harvey, 1987 (398 birds)

<i>M</i> _{max}	N	\hat{lpha}		
≤ 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		
\leq 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		

Measuring exponents

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

$$H_0: \alpha = \alpha'$$
 and $H_1: \alpha \neq \alpha'$.

- Assume each \mathbf{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 as least as different to our hypothesized α' as we observe.
- ► (see, for example, DeGroot and Scherish, "Probability and Statistics" [7])

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Revisiting the past—mammals

Full mass range:

	N	\hat{lpha}	$p_{2/3}$	$p_{3/4}$
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

$M \le 10 \text{ kg}$:					
	Ν	\hat{lpha}	$p_{2/3}$	$p_{3/4}$	
Kleiber	5	0.667	0.99	0.088	
Brody	26	0.709	$< 10^{-3}$	$< 10^{-3}$	
Heusner	357	0.668	0.91	$< 10^{-15}$	
$M \ge 10 \text{ kg}$:					
	Ν	\hat{lpha}	$p_{2/3}$	$p_{3/4}$	
Kleiber	8	0.754	$< 10^{-4}$	0.66	
Brody	9	0.760	$< 10^{-3}$	0.56	
Heusner	34	0.877	$< 10^{-12}$	$< 10^{-7}$	

Scaling-at-large

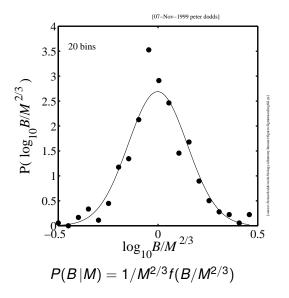
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Fluctuations—Kolmogorov-Smirnov test



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1. Presume an exponent of your choice: 2/3 or 3/4.

 Fit the prefactor (log₁₀ 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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We use the spiffing Spearman Rank-Order Correlation Cofficient.

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

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We assume all rank orderings are equally likely:

- ► r_s is distributed according to a Student's 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. [20]

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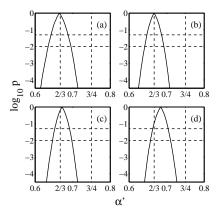
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Analysis of residuals—mammals



(a) M < 3.2 kg, (b) M < 10 kg, (c) M < 32 kg, (d) all mammals.

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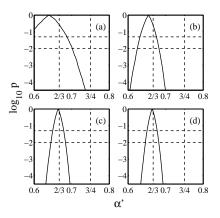
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Analysis of residuals—birds



(a) M < .1 kg, (b) M < 1 kg, (c) M < 10 kg, (d) all birds.

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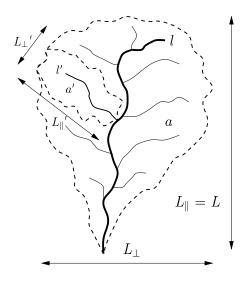
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Basic basin quantities: a, l, L_{\parallel} , L_{\perp} :



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

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1957: J. T. Hack [11] "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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$$\ell \sim a^h$$

$$h \sim 0.6$$

- ▶ Anomalous scaling: we would expect h = 1/2...
- Another quest to find universality/god...
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1957: J. T. Hack [11] "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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Scaling-at-large

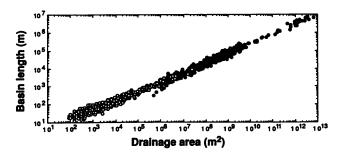
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Large-scale networks

(1992) Montgomery and Dietrich [19]:



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

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

Mixture of basin and main stream lengths.

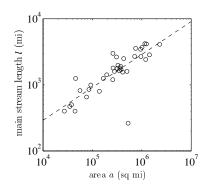
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World's largest rivers only:



- ▶ Data from Leopold (1994) [16, 8]
- ▶ Estimate of Hack exponent: $h = 0.50 \pm 0.06$

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Building on the surface area idea...

▶ Blum (1977) [5] speculates on four-dimensional biology:

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

- \triangleright d = 3 gives $\alpha = 2/3$
- \rightarrow d = 4 gives $\alpha = 3/4$
- So we need another dimension...
- Obviously, a bit silly.

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Allometry Farlier theories

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Building on the surface area idea:

- ► McMahon (70's, 80's): Elastic Similarity [17, 18]
- ► Idea is that organismal shapes scale allometrically with 1/4 powers (like nails and trees...)
- Appears to be true for ungulate legs.
- Metabolism and shape never properly connected.

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- 1960's: Rashevsky considers blood networks and finds a 2/3 scaling.
- ▶ 1997: West *et al.* [25] use a network story to find 3/4 scaling.

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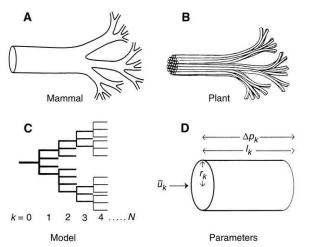
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West et al.'s assumptions:

- 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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West et al.'s assumptions:

- hierarchical network
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Claims:

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

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Allometry **Farlier theories**

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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):

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

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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

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

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

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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 $\propto P \propto M^{\alpha}$.

Soldiering on, assert:

- area-preservingness: $R_r = R_n^{-1/2}$
- ▶ space-fillingness: $R_{\ell} = R_n^{-1/3}$

 $\Rightarrow \alpha = 3/4$

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(also problematic due to prefactor issues)

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Data from real networks

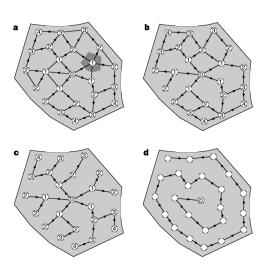
Network	R _n	R_r^{-1}	R_ℓ^{-1}	$-\frac{\ln R_r}{\ln R_n}$	$-rac{\ln R_\ell}{\ln R_n}$	α
West et al.	_	_	_	1/2	1/3	3/4
rat (PAT)	2.76	1.58	1.60	0.45	0.46	0.73
cat (PAT) (Turcotte <i>et al.</i> [24])	3.67	1.71	1.78	0.41	0.44	0.79
dog (PAT)	3.69	1.67	1.52	0.39	0.32	0.90
pig (LCX) pig (RCA) pig (LAD)	3.57 3.50 3.51	1.89 1.81 1.84	2.20 2.12 2.02	0.50 0.47 0.49	0.62 0.60 0.56	0.62 0.65 0.65
human (PAT) human (PAT)	3.03 3.36	1.60 1.56	1.49 1.49	0.42 0.37	0.36 0.33	0.83 0.94

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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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Banavar et al. find 'most efficient' networks with

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

▶ ... but also find

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

 \rightarrow d = 3:

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

- ► Consider a 3 g shrew with $V_{\text{blood}} = 0.1 V_{\text{body}}$
- ightharpoonup \Rightarrow 3000 kg elephant with $V_{
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- ► Consider a 3 g shrew with $V_{blood} = 0.1 V_{body}$
- ▶ \Rightarrow 3000 kg elephant with $V_{\text{blood}} = 10 V_{\text{body}}$
- Such a pachyderm would be rather miserable.

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

- \triangleright Q: how does the number of sustainable sinks $N_{\rm sinks}$
- ▶ Or: what is the highest α for $N_{\text{sinks}} \propto V^{\alpha}$?

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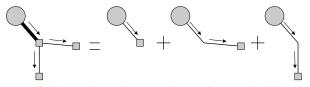
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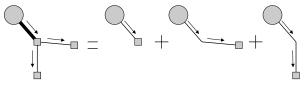
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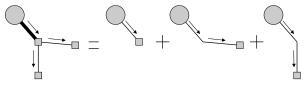
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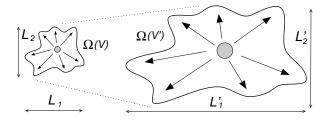
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Allometrically growing regions:



Have d length scales which scale as

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

- ▶ For isometric growth, $\gamma_i = 1/d$.
- For allometric growth, we must have at least two of the $\{\gamma_i\}$ being different

Scaling-at-large

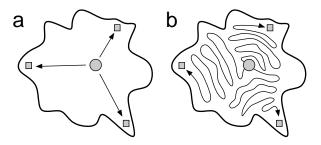
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Best and worst configurations (Banavar et al.)



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

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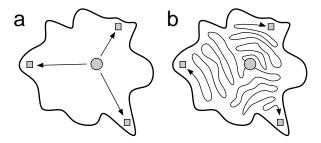
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Best and worst configurations (Banavar et al.)



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Real supply networks are close to optimal:

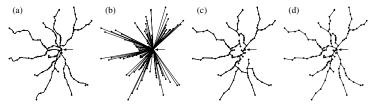


Figure 1. (a) Commuter rail network in the Boston area. The arrow marks the assumed root of the network. (b) Star graph. (c) Minimum spanning tree. (d) The model of equation (3) applied to the same set of stations.

(2006) Gastner and Newman [10]: "Shape and efficiency in spatial distribution networks"

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Approximate network volume by integral over region:

$$\min V_{\rm net} \propto \int_{\Omega_{\rm d},\rho(V)} \rho \, ||\vec{x}|| \, \mathrm{d}\vec{x}$$

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Approximate network volume by integral over region:

$$\min \textit{V}_{\rm net} \propto \int_{\Omega_{d,D}(\textit{V})} \rho \, ||\vec{\textit{x}}|| \, \mathrm{d}\vec{\textit{x}}$$

$$\to
ho V^{1+\gamma_{\max}} \int_{\Omega_{d,p}(c)} (c_1^2 u_1^2 + \ldots + c_k^2 u_k^2)^{1/2} d\vec{u}$$

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Approximate network volume by integral over region:

$$egin{aligned} \min m{V}_{
m net} &\propto \int_{\Omega_{d,D}(m{V})}
ho \, ||ec{x}|| \, \mathrm{d}ec{x} \ \ &
ightarrow
ho m{V}^{1+\gamma_{
m max}} \int_{\Omega_{d,D}(m{c})} (c_1^2 u_1^2 + \ldots + c_k^2 u_k^2)^{1/2} \mathrm{d}ec{u} \ & \propto
ho m{V}^{1+\gamma_{
m max}} \end{aligned}$$

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► General result:

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

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

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

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

$$\min V_{
m net/allo} \propto
ho V^{1+\gamma_{
m allo}}$$

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

$$rac{\min V_{
m net/iso}}{\min V_{
m net/allo}}
ightarrow 0 ext{ as } V
ightarrow \infty$$

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

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

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

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

$$rac{\min V_{
m net/iso}}{\min V_{
m net/allo}}
ightarrow 0 ext{ as } V
ightarrow \infty$$

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General result:

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

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

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▶ 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 [23], $V_{\rm net} \propto V$.
- Sink density must ∴ decrease as volume increases:

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

Density of suppliable sinks decreases with organism size.

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Density of suppliable sinks decreases with organism size.

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

$$P \propto \rho V$$

 \triangleright For d=3 dimensional organisms, we have

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

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▶ 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
- Economos: limb length break in scaling around 20 kg
- White and Seymour, 2005: unhappy with large herbivore measurements. Find $\alpha \simeq 0.686 \pm 0.014$

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Prefactor:

Stefan-Boltzmann law:

$$\frac{\mathrm{d}E}{\mathrm{d}t} = \sigma S T^4$$

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:

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

▶ Measured for $M \le 10$ kg:

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

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River networks

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

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

- Network volume grows faster than basin 'volume' (really area).
- ► It's all okay: Landscapes are d=2 surfaces living in D=3 dimension.
- Streams can grow not just in width but in depth...

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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

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

where h is Hack's exponent.

.: minimal volume calculations gives

$$h = 1/2$$

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- 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

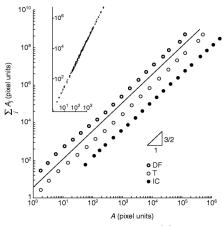
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From Banavar et al. (1999) [1]

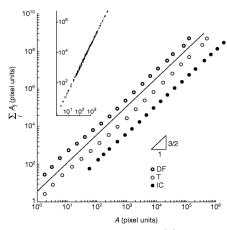
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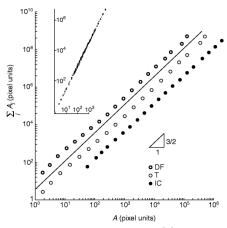
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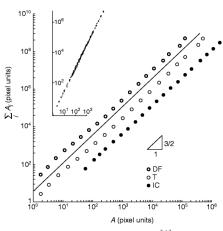
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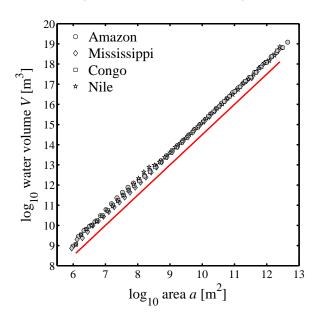
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Even better—prefactors match up:



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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.

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References I

 $pdf(\boxplus)$

- J. R. Banavar, A. Maritan, and A. Rinaldo. Size and form in efficient transportation networks. Nature, 399:130–132, 1999. pdf (⊞)
- P. Bennett and P. Harvey. Active and resting metabolism in birds—allometry, phylogeny and ecology. J. Zool., 213:327–363, 1987.
- L. M. A. Bettencourt, J. Lobo, D. Helbing, Kühnhert, and G. B. West.
 Growth, innovation, scaling, and the pace of life in cities.

 Proc. Natl. Acad. Sci., 104(17):7301–7306, 2007.

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Frame 110/117



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.

S. Brody. Bioenergetics and Growth. Reinhold, New York, 1945. reprint.

M. H. DeGroot.
 Probability and Statistics.
 Addison-Wesley, Reading, Massachusetts, 1975.

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Frame 111/117



References III

- P. S. Dodds and D. H. Rothman.
 Scaling, universality, and geomorphology.

 Annu. Rev. Earth Planet. Sci., 28:571–610, 2000.
 pdf (⊞)
- P. S. Dodds, D. H. Rothman, and J. S. Weitz. Re-examination of the "3/4-law" of metabolism. *Journal of Theoretical Biology*, 209(1):9–27, March 2001.
 - . $\underline{\mathsf{pdf}}\ (\boxplus)$
- M. T. Gastner and M. E. J. Newman. Shape and efficiency in spatial distribution networks. J. Stat. Mech.: Theor. & Exp., 1:01015–, 2006. pdf (H)

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References IV



J. T. Hack.

Studies of longitudinal stream profiles in Virginia and Maryland.

United States Geological Survey Professional Paper, 294-B:45-97, 1957.



A. Hemmingsen.

The relation of standard (basal) energy metabolism to total fresh weight of living organisms.

Rep. Steno Mem. Hosp., 4:1-58, 1950.



A. Hemmingsen.

Energy metabolism as related to body size and respiratory surfaces, and its evolution.

Rep. Steno Mem. Hosp., 9:1-110, 1960.

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References V

A. A. Heusner.
Size and power in mammals.

Journal of Experimental Biology, 160:25–54, 1991.

M. Kleiber.
Body size and metabolism.
Hilgardia, 6:315–353, 1932.

L. B. Leopold.A View of the River.Harvard University Press, Cambridge, MA, 1994.

T. McMahon.
Size and shape in biology.
Science, 179:1201–1204, 1973. pdf (⊞)

T. A. McMahon and J. T. Bonner. On Size and Life. Scientific American Library, New York, 1983. Scaling-at-large

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References VI

D. R. Montgomery and W. E. Dietrich. Channel initiation and the problem of landscape scale.

Science, 255:826–30, 1992. pdf (⊞)

W. H. Press, S. A. Teukolsky, W. T. Vetterling, and B. P. Flannery. Numerical Recipes in C. Cambridge University Press, second edition, 1992.

M. Rubner.

Ueber den einfluss der körpergrösse auf stoffund kraftwechsel.

Z. Biol., 19:535-562, 1883.

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References VII

Sarrus and Rameaux.

Rapport sur une mémoire adressé à l'Académie de Médecine.

Bull. Acad. R. Méd. (Paris), 3:1094-1100, 1838-39.

- W. R. Stahl.
 Scaling of respiratory variables in mammals.

 Journal of Applied Physiology, 22:453–460, 1967.
- D. L. Turcotte, J. D. Pelletier, and W. I. Newman. Networks with side branching in biology. Journal of Theoretical Biology, 193:577–592, 1998.
- 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 (⊞)

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References VIII



K. Zhang and T. J. Sejnowski.

A universal scaling law between gray matter and white matter of cerebral cortex.

Proceedings of the National Academy of Sciences, 97:5621-5626, May 2000. pdf (⊞)

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