Scaling—a Plenitude of Power Laws

Principles of Complex Systems
CSYS/MATH 300, Fall, 2010

Prof. Peter Dodds

Department of Mathematics & Statistics
Center for Complex Systems
Vermont Advanced Computing Center
University of Vermont

Outline

Scaling-at-large

Allometry
- Definitions
- Examples
- History: Metabolism
- Measuring exponents
- History: River networks
- Earlier theories
- Geometric argument
- Blood networks
- River networks
- Conclusion

References

Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

Definitions

General observation:

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

Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

Outline

All about scaling:

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

Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

Definitions

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

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

- α 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!)

Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

Definitions

- The prefactor c must balance dimensions.
- eg., length ℓ and volume v of common nails are related as:

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

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

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

Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

Looking at data

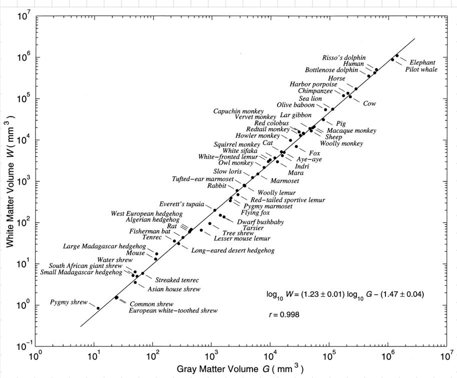
- Power-law relationships are linear in log-log space:

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

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

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).

A beautiful, heart-warming example:



from Zhang & Sejnowski, PNAS (2000) [41]

$\alpha \simeq 1.23$

gray matter: 'computing elements'

white matter: 'wiring'

Scaling

Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

Why is $\alpha \simeq 1.23$?

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:

- $G \sim ST$ (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 $W \propto G^{4/3}/T$

Scaling

Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

Why is $\alpha \simeq 1.23$?

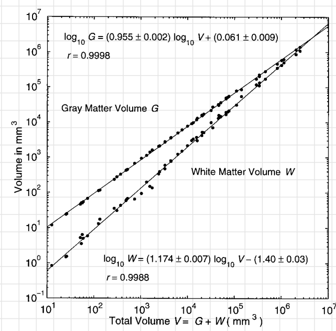
A rough understanding:

- 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

Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

Why is $\alpha \simeq 1.23$?



Trickiness:

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

Scaling

Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

Good scaling:

General rules of thumb:

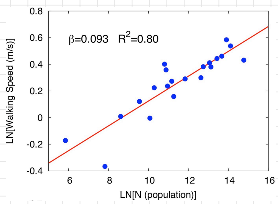
- *High quality:* scaling persists over three or more orders of magnitude for each variable.
- *Medium quality:* scaling persists over three or more orders of magnitude for only one variable and at least one for the other.
- *Very dubious:* scaling 'persists' over less than an order of magnitude for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

Scaling

Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

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) [4]; otherwise very interesting!

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

Scaling

Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

Scale invariance

Our friend $y = cx^{\alpha}$:

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

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

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

Scaling

Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

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.
- $\Rightarrow$ scale matters for the exponential.

Scaling

Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

Scale invariance

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.
- $\Rightarrow$ More on this later with size distributions.

Scaling

Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

Definitions

Allometry: (⊞)

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

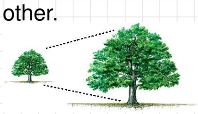
- First proposed by Huxley and Teissier, Nature, 1936 "Terminology of relative growth" [21]

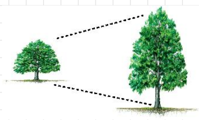
Scaling

Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

Definitions:

Isometry:
dimensions scale linearly with each other.





Allometry:
dimensions scale nonlinearly.

Definitions

Isometry versus Allometry:

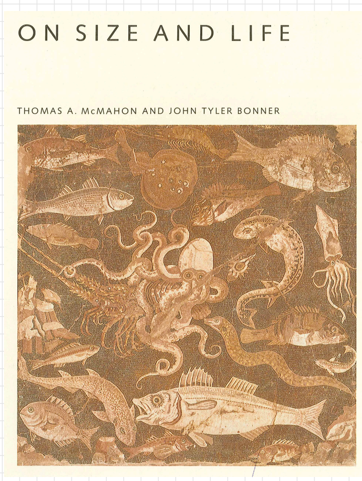
- Isometry = 'same measure'
- Allometry = 'other measure'

Confusingly, we use allometric scaling to refer to both:

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

A wonderful treatise on scaling:

McMahon and Bonner, 1983 [26]

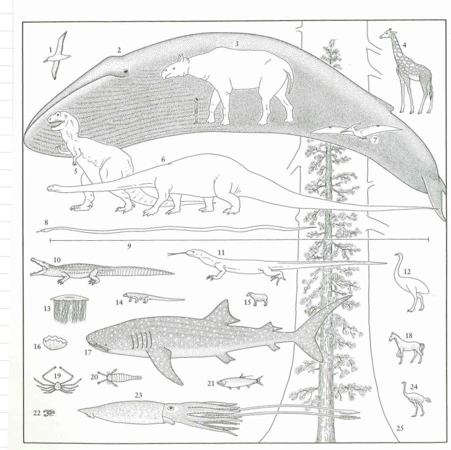


For the following slide:

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.

p. 2, McMahon and Bonner [26]

The many scales of life:



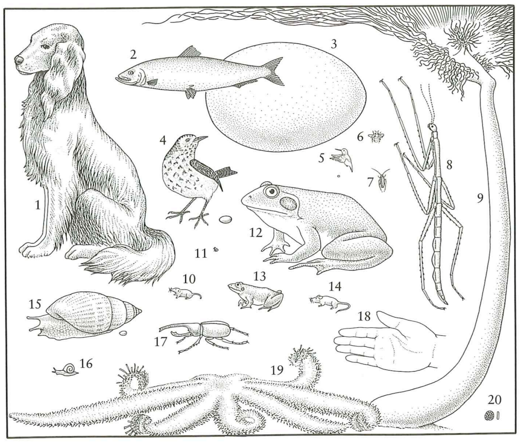
p. 2, McMahon and Bonner [26]

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).

p. 2, McMahon and Bonner [26]

The many scales of life:



p. 3, McMahon and Bonner [26]

Scaling

Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

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*).

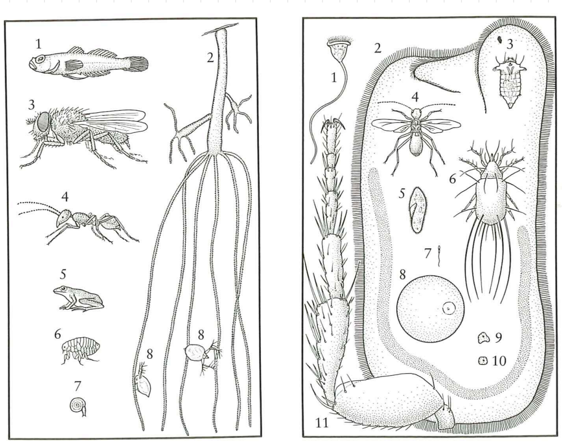
The smallest ''naked-eye'' creatures and some large microscopic animals and cells (*below right*). *1*, *Vorticella*, a ciliate; *2*, the largest ciliate protozoan (*Bursaria*); *3*, the smallest many-celled animal (a rotifer); *4*, smallest flying insect (*Elaphis*); *5*, another ciliate (*Paramecium*); *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*).

p. 2, McMahon and Bonner [26]

Scaling

Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

The many scales of life:

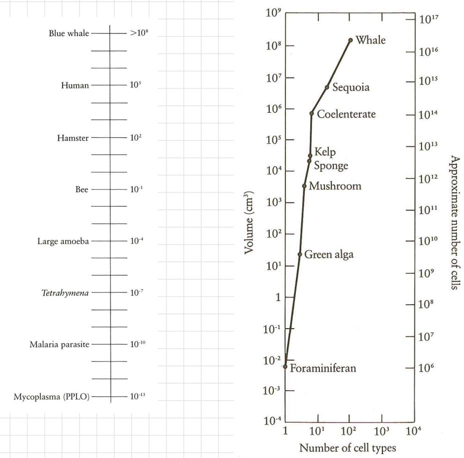


p. 3, McMahon and Bonner [26]

Scaling

Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

Size range and cell differentiation:

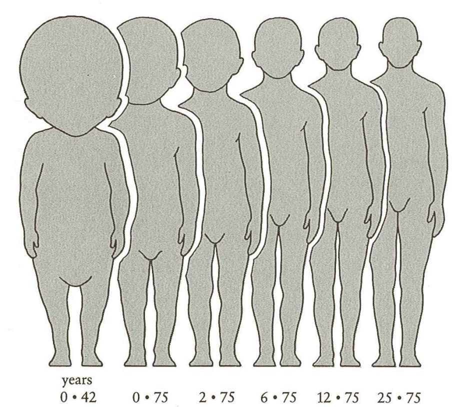


p. 3, McMahon and Bonner [26]

Scaling

Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

Non-uniform growth:



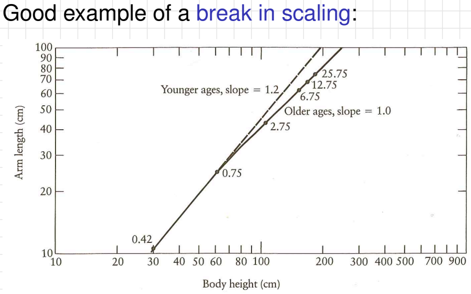
p. 32, McMahon and Bonner [26]

Scaling

Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

Non-uniform growth—arm length versus height:

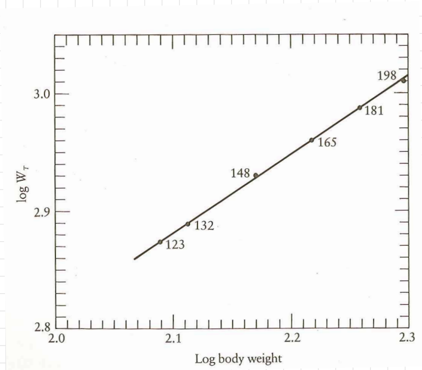
Good example of a break in scaling:



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

p. 32, McMahon and Bonner [26]

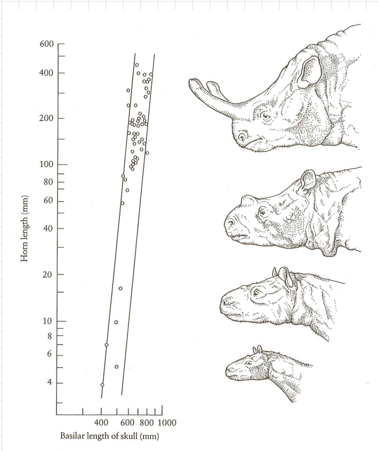
Weightlifting: $M_{\text{worldrecord}} \propto M_{\text{lifter}}^{2/3}$



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

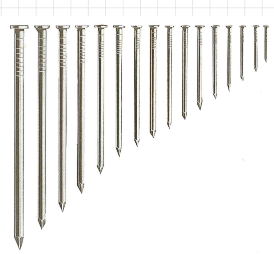
p. 53, McMahon and Bonner [26]

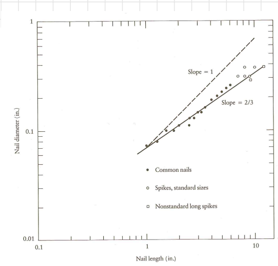
Titanothere horns: $L_{\text{horn}} \sim L_{\text{skull}}^{4}$



p. 36, McMahon and Bonner [26]

The allometry of nails:





- Diameter $\propto$ Mass$^{3/8}$
- Length $\propto$ Mass$^{1/4}$
- Diameter $\propto$ Length$^{2/3}$

p. 58–59, McMahon and Bonner [26]

The allometry of nails:

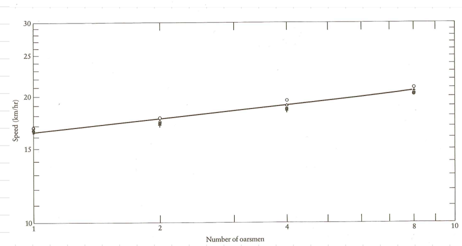
A buckling instability?:

- Physics/Engineering result: Columns buckle under a load which depends on d^4/ℓ^2.
- To drive nails in, resistive force $\propto$ nail circumference $= \pi d$.
- Match forces independent of nail size: $d^4/\ell^2 \propto d$.
- Leads to $d \propto \ell^{2/3}$.
- Argument made by Galileo [13] in 1638 in "Discourses on Two New Sciences." (⊞) [pdf] Also, see here (⊞).
- Also see McMahon, "Size and Shape in Biology," Science, 1973. [24]

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

Shell dimensions and performances.

No. of oarsmen	Modifying description	Length, l (m)	Beam, b (m)	l/b	Boat mass per oarsman (kg)	Time for 2000 m (min) I	II	III	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



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).

Scaling in Cities:

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-R^2, adjusted R^2; GDP, gross domestic product.

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.

Ecology—Species-area law: $N_{\text{species}} \propto A^{\beta}$

Allegedly (data is messy):

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

A focus:

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

Animal power

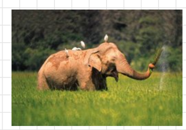
Fundamental biological and ecological constraint:

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

P = basal metabolic rate

M = organismal body mass

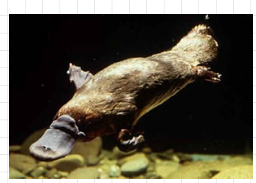




$P = c\,M^{\alpha}$

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




What one might expect:

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

- Dimensional analysis suggests an energy balance surface law:

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

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

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

The prevailing belief of the church of quarterology

$$\boxed{\alpha = 3/4}$$

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

Huh?

Scaling
Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

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

Scaling
Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

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

Scaling
Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

History

1840's: Sarrus and Rameaux [33] first suggested $\alpha = 2/3$.

Scaling
Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

History

1883: Rubner [31] found $\alpha \simeq 2/3$.

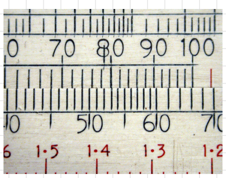
Scaling
Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

History

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

History

1932: Kleiber analyzed 13 mammals.[22]
Found $\alpha = 0.76$ and suggested $\alpha = 3/4$.



Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

History

1950/1960: Hemmingsen[18, 19]
Extension to unicellular organisms.
$\alpha = 3/4$ assumed true.

Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

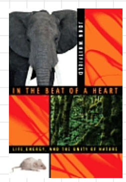
History

1964: Troon, Scotland:[5]
3rd symposium on energy metabolism.
$\alpha = 3/4$ made official . . . . . . 29 to zip.

Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

Today

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

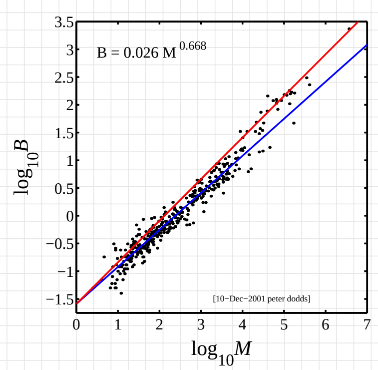


In the Beat of a Heart: Life, Energy, and the Unity of Nature—by John Whitfield

- But—much controversy...
- See 'Re-examination of the "3/4-law" of metabolism' Dodds, Rothman, and Weitz[11] and ensuing madness...

Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

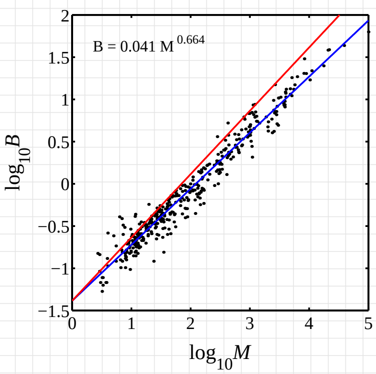
Some data on metabolic rates



- Heusner's data (1991)[20]
- 391 Mammals
- blue line: 2/3
- red line: 3/4.
- ($B = P$)

Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

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...

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.

Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

Measuring exponents

More on regression:

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

or (b) no variable can be considered independent,

then we need to use
Standardized Major Axis Linear Regression. [32, 30]

(aka Reduced Major Axis = RMA.)

Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

Measuring exponents

For Standardized Major Axis Linear Regression:

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

- Very simple!
- Scale invariant.

Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

Measuring exponents

Relationship to ordinary least squares regression is simple:

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

where r = standard correlation coefficient:

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

Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

Heusner's data, 1991 (391 Mammals)

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

Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

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

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 $\mathbf{B}_i$ (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." [8]

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	$< 10^{-15}$

Revisiting the past—mammals

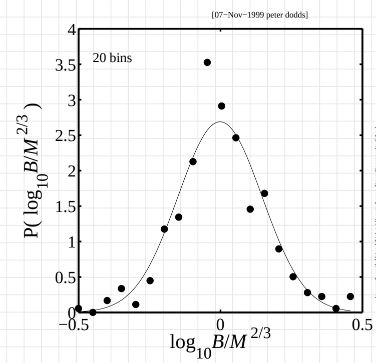
$M \leq 10$ kg:

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

$M \geq 10$ kg:

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

Fluctuations—Things look normal...



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

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.

Analysis of residuals

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.

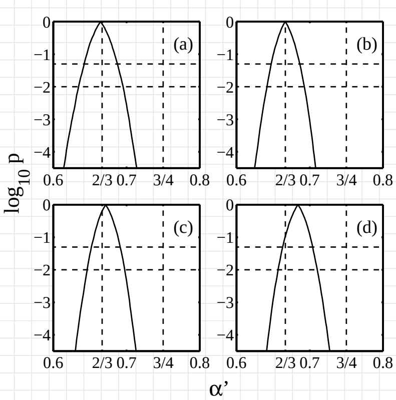
Analysis of residuals

We assume all rank orderings are equally likely:

- r_s is distributed according to a Student's t-distribution (⊞) with $N-2$ degrees of freedom.
- Excellent feature: Non-parametric—real distribution of x's and y's doesn't matter.
- Bonus: works for non-linear monotonic relationships as well.
- See Numerical Recipes in C/Fortran (⊞) which contains many good things.[29]

Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

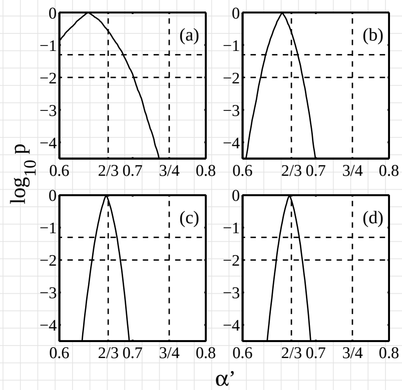
Analysis of residuals—mammals



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

Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

Analysis of residuals—birds



(a) $M < 0.1$ kg,
(b) $M < 1$ kg,
(c) $M < 10$ kg,
(d) all birds.

Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

Other approaches to measuring exponents:

For distributions with power law tails:

- Clauset et al..
-

Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

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[12]
- But see later: non-isometric growth leads to lower metabolic scaling. Oops.

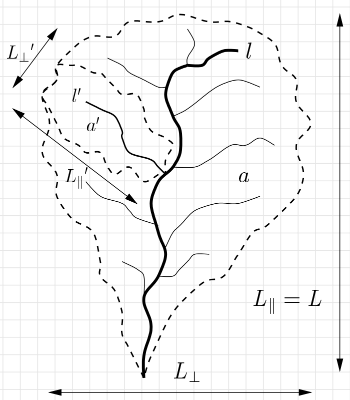
Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

The widening gyre:

Now we're really confused (empirically):

- White and Seymour, 2005: unhappy with large herbivore measurements [40]. Pro 2/3: Find $\alpha \simeq 0.686 \pm 0.014$.
- White ... [39]
- Glazier, BioScience (2006) [16]: "The 3/4-Power Law Is Not Universal: Evolution of Isometric, Ontogenetic Metabolic Scaling in Pelagic Animals."
- Glazier, Biol. Rev. (2005) [15]: "Beyond the 3/4-power law': variation in the intra- and interspecific scaling of metabolic rate in animals."
- Savage et al., PLoS Biology (2008) [34] "Sizing up allometric scaling theory" Pro 3/4: problems claimed to be finite-size scaling.
- Mori et al. [?]
- Add more.

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

River networks

- 1957: J. T. Hack [17]
  "Studies of Longitudinal Stream Profiles in Virginia and Maryland"

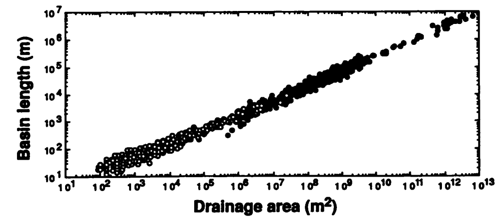
$$\ell \sim a^h$$

$$h \sim 0.6$$

- 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.

Large-scale networks:

(1992) Montgomery and Dietrich [27]:

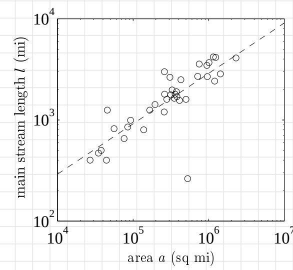


- Composite data set: includes everything from unchanneled valleys up to world's largest rivers.
- Estimated fit:

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

- Mixture of basin and main stream lengths.

World's largest rivers only:



- Data from Leopold (1994) [23, 10]
- Estimate of Hack exponent: $h = 0.50 \pm 0.06$

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... [35]

Earlier theories

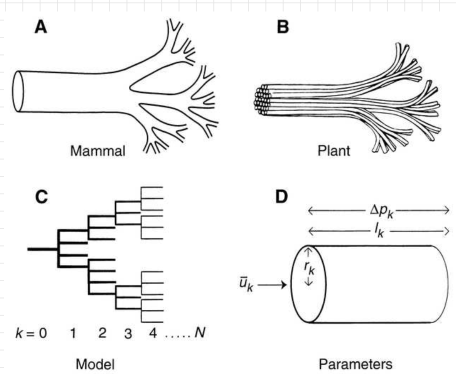
Building on the surface area idea:

- McMahon (70's, 80's): Elastic Similarity [24, 26]
- Idea is that organismal shapes scale allometrically with 1/4 powers (like nails and trees...)
- Appears to be true for ungulate legs... [25]
- Metabolism and shape never properly connected.

Nutrient delivering networks:

Scaling
Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

- 1960's: Rashevsky considers blood networks and finds a $2/3$ scaling.
- 1997: West *et al.* [38] use a network story to find $3/4$ scaling.



Nutrient delivering networks:

Scaling
Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

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

Impedance measures:

Scaling
Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

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):

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

Not so fast ...

Scaling
Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

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: [28]

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

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

Connecting network structure to α

Scaling
Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

1. Ratios of network parameters:

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

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

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

(also problematic due to prefactor issues)

Soldiering on, assert:

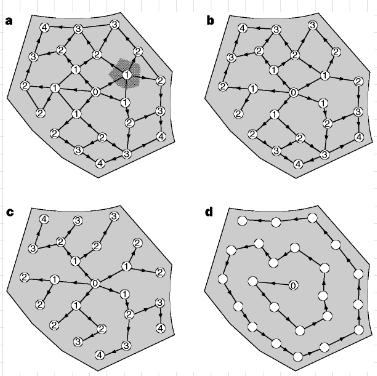
- area-preservingness: $R_r = R_n^{-1/2}$
- space-fillingness: $R_\ell = R_n^{-1/3}$
-

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

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 *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 *et al.*[37])	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., Nature, (1999) [1]
- Flow rate argument
- Ignore impedance
- Very general attempt to find most efficient transportation networks

Simple supply networks

- Banavar *et al.* find 'most efficient' networks with

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

- ... but also find

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

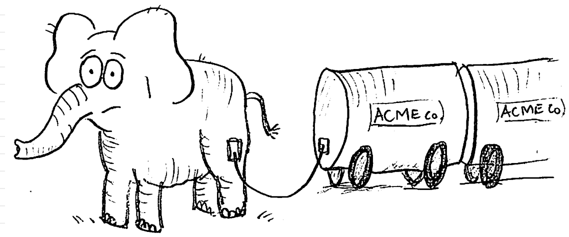
- $d = 3$:

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

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

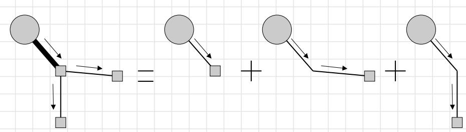
Simple supply networks

Such a pachyderm would be rather miserable:



Geometric argument

- "Optimal Form of Branching Supply and Collection Networks." Dodds, Phys. Rev. Lett., 2010. [9]
- 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:

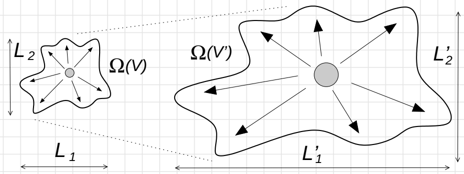


Geometric argument

- Q: how does the number of sustainable sinks N_{sinks} scale with volume V for the most efficient network design?
- Or: what is the highest α for $N_{\text{sinks}} \propto V^{\alpha}$?

Geometric argument

- Allometrically growing regions:



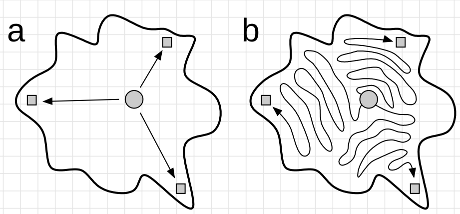
- Have d length scales which scale as

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

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

Geometric argument

- Best and worst configurations (Banavar et al.)



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

Minimal network volume:

Real supply networks are close to optimal:

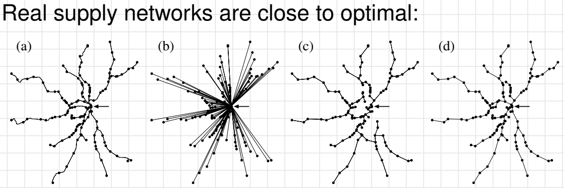


Figure 1. (a) Commuter rail network in the Boston area. The arrow marks the assumed root of the network. (b) Star graph. (c) Minimum spanning tree. (d) The model of equation (3) applied to the same set of stations.

(2006) Gastner and Newman [14]: "Shape and efficiency in spatial distribution networks"

Minimal network volume:

Approximate network volume by integral over region:

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

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

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

Geometric argument

- General result:

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

- 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 $\gamma_{\max} = \gamma_{\text{allo}} > 1/d$: and

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

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

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

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 [36], $V_{\text{net}} \propto V$.
- Sink density must $\therefore$ decrease as volume increases:

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

- Density of suppliable sinks decreases with organism size.

Blood networks

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

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

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

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

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 $M \leq 10$ kg:

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

Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

River networks

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

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

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

Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

Hack's law

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

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

- Hack's law again:

$$\ell \sim a^h$$

- Can argue

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

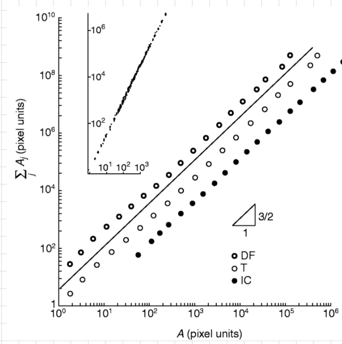
  where h is Hack's exponent.
- $\therefore$ minimal volume calculations gives

$$\boxed{h = 1/2}$$

Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

Real data:

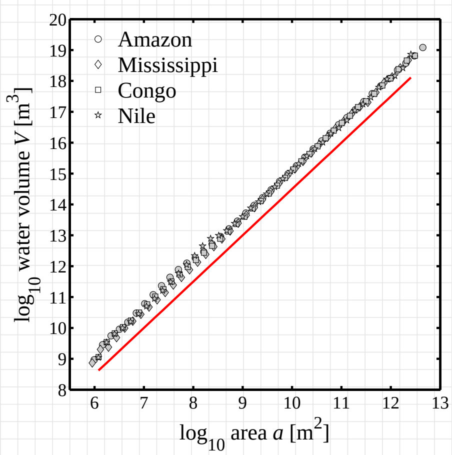
- Banavar et al.'s approach [1] is okay because ρ really is constant.
- The irony: shows optimal basins are isometric
- Optimal Hack's law: $\ell \sim a^h$ with $h = 1/2$
- (Zzzzz)



From Banavar et al. (1999) [1]

Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

Even better—prefactors match up:



Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

Yet more theoretical madness from the Quarterologists:

- 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.

Conclusion

- Supply network story consistent with dimensional analysis.
- Isometrically growing regions can be more efficiently supplied than allometrically growing ones.
- Ambient and region dimensions matter ($D = d$ versus $D > d$).
- Deviations from optimal scaling suggest inefficiency (e.g., gravity for organisms, geological boundaries).
- Actual details of branching networks not that important.
- Exact nature of self-similarity varies.

Scaling
Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

References I

[1] J. R. Banavar, A. Maritan, and A. Rinaldo.
Size and form in efficient transportation networks.
Nature, 399:130–132, 1999. pdf (⊞)

[2] J. R. Banavar, M. E. Moses, J. H. Brown, J. Damuth, A. Rinaldo, R. M. Sibly, and A. Maritan.
A general basis for quarter-power scaling in animals.
Proc. Natl. Acad. Sci., 107:15816–15820, 2010.
pdf (⊞)

[3] P. Bennett and P. Harvey.
Active and resting metabolism in birds—allometry, phylogeny and ecology.
J. Zool., 213:327–363, 1987. pdf (⊞)

References II

[4] 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.
pdf (⊞)

[5] K. L. Blaxter, editor.
Energy Metabolism; Proceedings of the 3rd symposium held at Troon, Scotland, May 1964.
Academic Press, New York, 1965.

[6] J. J. Blum.
On the geometry of four-dimensions and the relationship between metabolism and body mass.
J. Theor. Biol., 64:599–601, 1977.

References III

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

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

[9] P. S. Dodds.
Optimal form of branching supply and collection networks.
Phys. Rev. Lett., 104(4):048702, 2010. pdf (⊞)

[10] P. S. Dodds and D. H. Rothman.
Scaling, universality, and geomorphology.
Annu. Rev. Earth Planet. Sci., 28:571–610, 2000.
pdf (⊞)

References IV

[11] P. S. Dodds, D. H. Rothman, and J. S. Weitz.
Re-examination of the "3/4-law" of metabolism.
Journal of Theoretical Biology, 209:9–27, 2001.
pdf (⊞)

[12] A. E. Economos.
Elastic and/or geometric similarity in mammalian design.
Journal of Theoretical Biology, 103:167–172, 1983.
pdf (⊞)

[13] G. Galilei.
Dialogues Concerning Two New Sciences.
Kessinger Publishing, 2010.
Translated by Henry Crew and Alfonso De Salvio.

References V

[14] M. T. Gastner and M. E. J. Newman.
Shape and efficiency in spatial distribution networks.
J. Stat. Mech.: Theor. & Exp., 1:P01015, 2006.
pdf (⊞)

[15] D. S. Glazier.
Beyond the ‘3/4-power law’: variation in the intra- and interspecific scaling of metabolic rate in animals.
Biol. Rev., 80:611–662, 2005. pdf (⊞)

[16] D. S. Glazier.
The 3/4-power law is not universal: Evolution of isometric, ontogenetic metabolic scaling in pelagic animals.
BioScience, 56:325–332, 2006. pdf (⊞)

References VI

[17] J. T. Hack.
Studies of longitudinal stream profiles in Virginia and Maryland.
United States Geological Survey Professional Paper, 294-B:45–97, 1957.

[18] A. Hemmingsen.
The relation of standard (basal) energy metabolism to total fresh weight of living organisms.
Rep. Steno Mem. Hosp., 4:1–58, 1950. pdf (⊞)

[19] A. Hemmingsen.
Energy metabolism as related to body size and respiratory surfaces, and its evolution.
Rep. Steno Mem. Hosp., 9:1–110, 1960. pdf (⊞)

Scaling
Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

References VII

[20] A. A. Heusner.
Size and power in mammals.
Journal of Experimental Biology, 160:25–54, 1991.
pdf (⊞)

[21] J. S. Huxley and G. Teissier.
Terminology of relative growth.
Nature, 137:780–781, 1936. pdf (⊞)

[22] M. Kleiber.
Body size and metabolism.
Hilgardia, 6:315–353, 1932. pdf (⊞)

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

Scaling
Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

References VIII

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

[25] T. A. McMahon.
Allometry and biomechanics: Limb bones in adult ungulates.
The American Naturalist, 109:547–563, 1975.
pdf (⊞)

[26] T. A. McMahon and J. T. Bonner.
On Size and Life.
Scientific American Library, New York, 1983.

[27] D. R. Montgomery and W. E. Dietrich.
Channel initiation and the problem of landscape scale.
Science, 255:826–30, 1992. pdf (⊞)

Scaling
Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

References IX

[28] C. D. Murray.
A relationship between circumference and weight in trees and its bearing on branching angles.
J. Gen. Physiol., 10:725–729, 1927. pdf (⊞)

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

[30] J. M. V. Rayner.
Linear relations in biomechanics: the statistics of scaling functions.
J. Zool. Lond. (A), 206:415–439, 1985.

Scaling
Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

References X

[31] M. Rubner.
Ueber den einfluss der körpergrösse auf stoffund kraftwechsel.
Z. Biol., 19:535–562, 1883. pdf (⊞)

[32] P. A. Samuelson.
A note on alternative regressions.
Econometrica, 10:80–83, 1942. pdf (⊞)

[33] Sarrus and Rameaux.
Rapport sur une mémoire adressé à l’Académie de Médecine.
Bull. Acad. R. Méd. (Paris), 3:1094–1100, 1838–39.

[34] V. M. Savage, E. J. Deeds, and W. Fontana.
Sizing up allometric scaling theory.
PLoS Computational Biology, 4:e1000171, 2008.
pdf (⊞)

Scaling
Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References

References XI

[35] J. Speakman.
On Blum's four-dimensional geometric explanation for the 0.75 exponent in metabolic allometry.
J. Theor. Biol., 144(1):139–141, 1990. pdf (⊞)

[36] W. R. Stahl.
Scaling of respiratory variables in mammals.
Journal of Applied Physiology, 22:453–460, 1967.

[37] D. L. Turcotte, J. D. Pelletier, and W. I. Newman.
Networks with side branching in biology.
Journal of Theoretical Biology, 193:577–592, 1998.
pdf (⊞)

[38] 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 (⊞)

References XII

[39] C. R. White, P. Cassey, and T. M. Blackburn.
Allometric exponents do not support a universal metabolic allometry.
Ecology, 88:315–323, 2007. pdf (⊞)

[40] C. R. White and R. S. Seymour.
Allometric scaling of mammalian metabolism.
J. Exp. Biol., 208:1611–1619, 2005. pdf (⊞)

[41] 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, 2000. pdf (⊞)

Scaling

Scaling-at-large
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion
References