

Scaling—a Plenitude of Power Laws

Principles of Complex Systems
Course 300, Fall, 2008

Prof. Peter Dodds

Department of Mathematics & Statistics
University of Vermont



Licensed under the *Creative Commons Attribution-NonCommercial-ShareAlike 3.0 License*.

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

River networks

Conclusion

References

Frame 1/114



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

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

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

- ▶ 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).

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

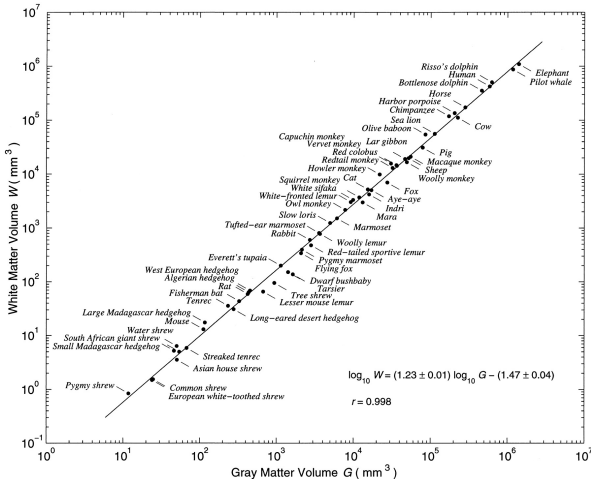
Blood networks

River networks

Conclusion

References

A beautiful, heart-warming example:



$$\alpha \approx 1.23$$

gray
matter:
'computing
elements'

white
matter:
'wiring'

from Zhang & Sejnowski, PNAS (2000) [26]

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blod networks

River networks

Conclusion

References

Frame 8/114

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)
- ▶ $W \sim \frac{1}{2}pSL$
- ▶ $G \sim L^3$ ← this is a little sketchy...
- ▶ Eliminate S and L to find $W \propto G^{4/3}/T$

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-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

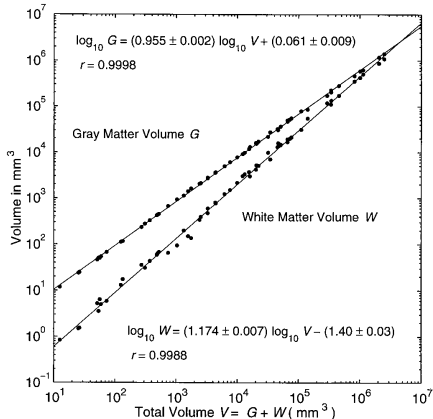
Blood networks

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-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-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

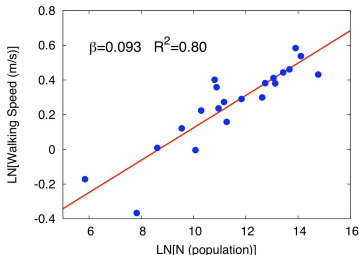
River networks

Conclusion

References

Unconvincing scaling:

Average walking speed as a function of city population:



Two problems:

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

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

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

River networks

Conclusion

References

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-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-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-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-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

River networks

Conclusion

References

Definitions

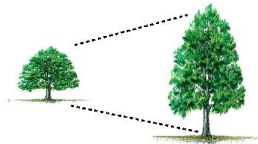
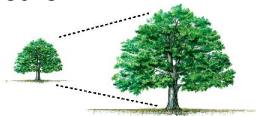
Allometry (田):

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

[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.

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

River networks

Conclusion

References

Frame 20/114

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)

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

River networks

Conclusion

References

A wonderful treatise on scaling:

ON SIZE AND LIFE

THOMAS A. McMAHON AND JOHN TYLER BONNER



Bonner and
McMahon, 1983 [6]

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

River networks

Conclusion

References

Frame 23/114

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

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

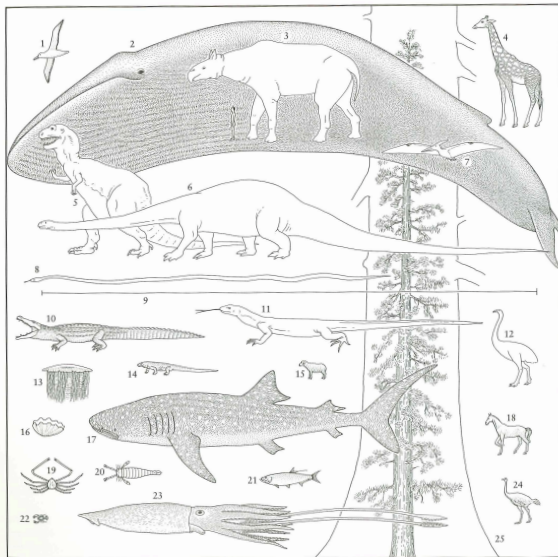
Blood networks

River networks

Conclusion

References

The many scales of life:



Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

River networks

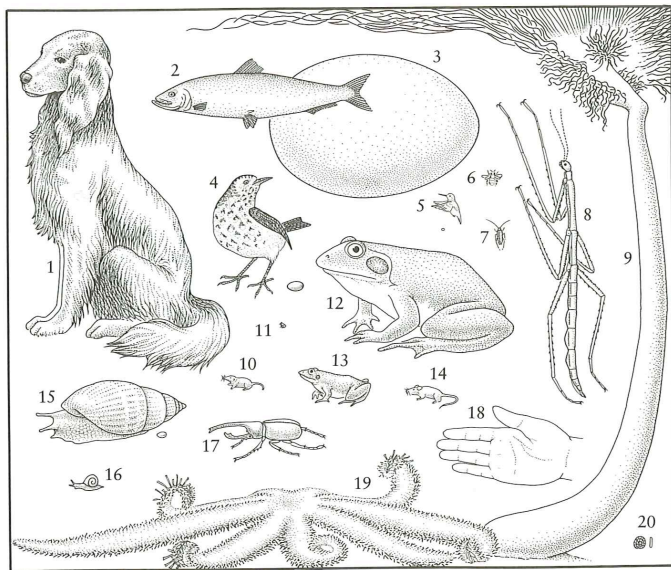
Conclusion

References

For the following slide:

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).

The many scales of life:



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).

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

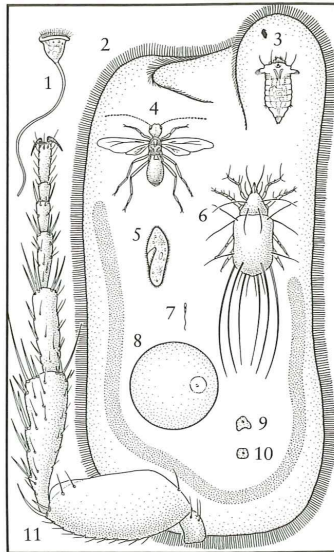
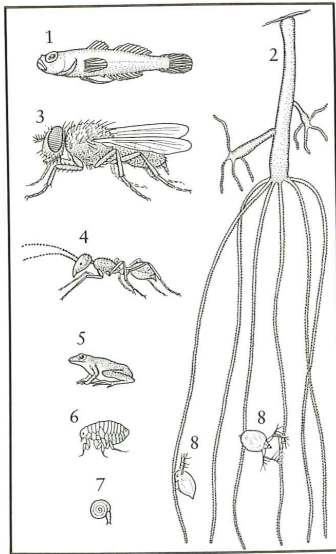
Blood networks

River networks

Conclusion

References

The many scales of life:



Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

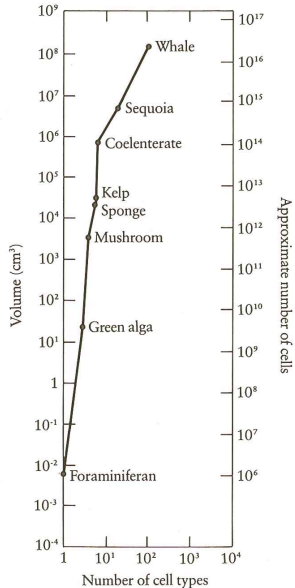
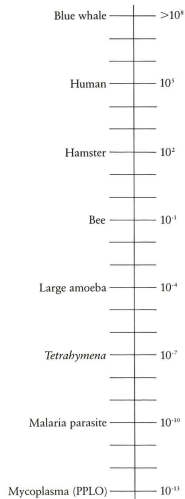
Blood networks

River networks

Conclusion

References

Size range and cell differentiation:



Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

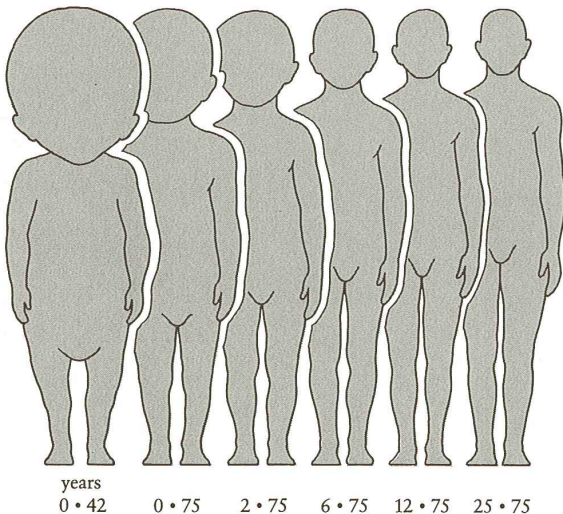
Blood networks

River networks

Conclusion

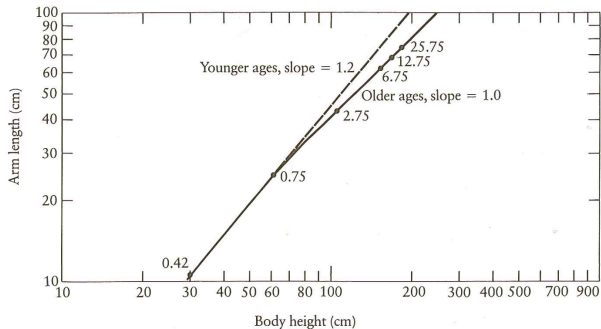
References

Non-uniform growth:



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, Bonner and McMahon [6]

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

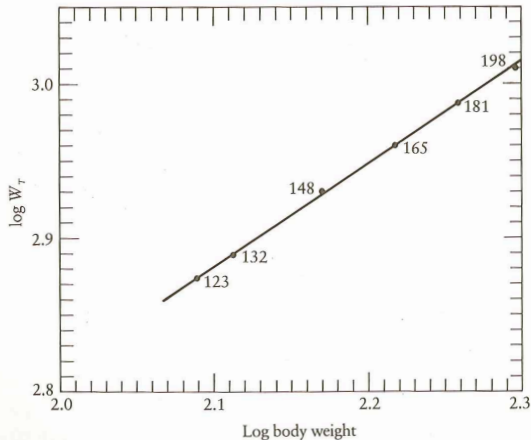
River networks

Conclusion

References

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

Scaling



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

p. 53, Bonner and McMahon [6]

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

River networks

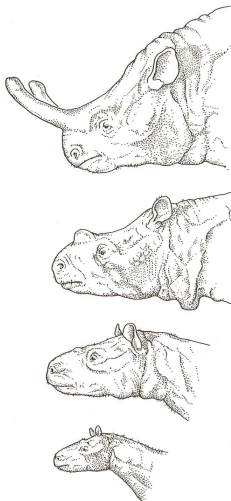
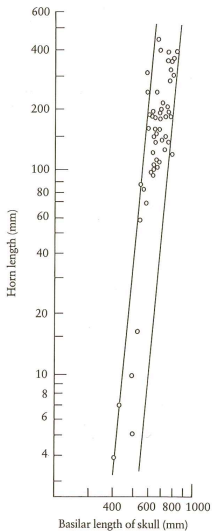
Conclusion

References

Frame 33/114



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



Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

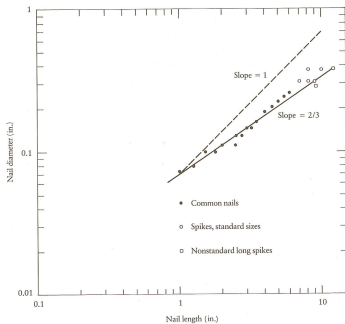
Blood networks

River networks

Conclusion

References

The allometry of nails:



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

p. 58–59, Bonner and McMahon [6]

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

River networks

Conclusion

References

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 $d \propto \ell^{2/3}$.

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

River networks

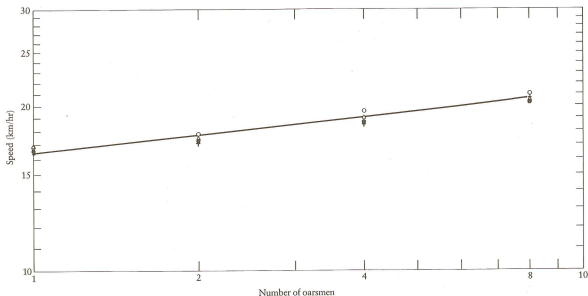
Conclusion

References

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				
8	Lightweight	18.28	0.598	30.6	14.7	5.87	5.92	5.82	5.73
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-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

River networks

Conclusion

References

Scaling in Cities:

- ▶ “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).

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

River networks

Conclusion

References

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-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

River networks

Conclusion

References

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.

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

River networks

Conclusion

References

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

Allegedly (data is messy):

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

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

River networks

Conclusion

References

A focus:

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

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

River networks

Conclusion

References

Fundamental biological and ecological constraint:

$$P = c M^\alpha$$

P = basal metabolic rate

M = organismal body mass



Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

River networks

Conclusion

References

$$P = c M^\alpha$$

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



Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

River networks

Conclusion

References

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 relation for radiated energy:

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

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

River networks

Conclusion

References

The prevailing belief of the church of quarterology

$$\alpha = 3/4$$

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

Huh?

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

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

River networks

Conclusion

References

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



Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

River networks

Conclusion

References

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



Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

River networks

Conclusion

References

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



Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

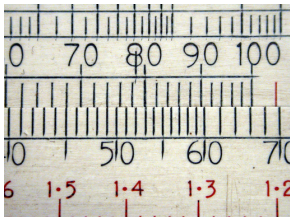
River networks

Conclusion

References

History

1932: Kleiber analyzed 13 mammals. [16]
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 [13, 14]
Extension to unicellular organisms.
 $\alpha = 3/4$ assumed true.



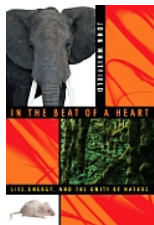
History

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



... 29 to zip.

- ▶ $3/4$ 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^[10]

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

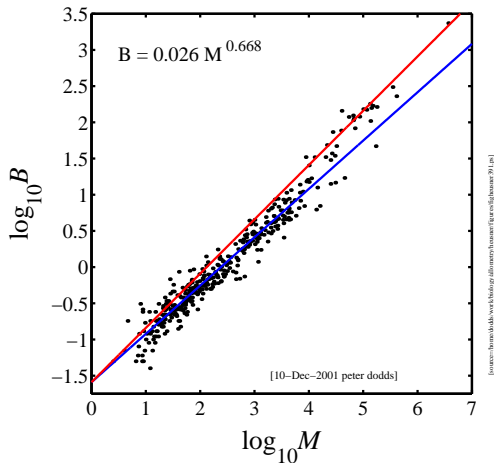
Blood networks

River networks

Conclusion

References

Some data on metabolic rates



- ▶ Heusner's data (1991) ^[15]
- ▶ 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

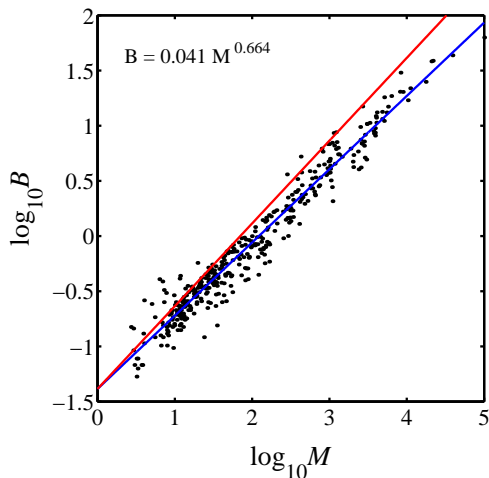
Blood networks

River networks

Conclusion

References

Some data on metabolic rates



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

Passerine vs. non-passerine...

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

River networks

Conclusion

References

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. 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

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

River networks

Conclusion

References

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!

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

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

River networks

Conclusion

References

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])

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

River networks

Conclusion

References

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	$< 10^{-15}$

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

River networks

Conclusion

References

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	$< 10^{-12}$	$< 10^{-7}$

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

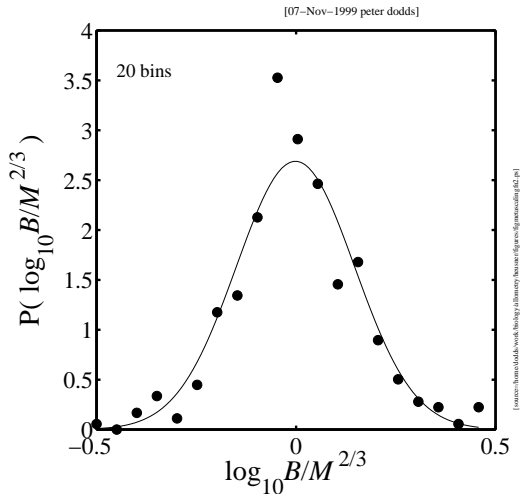
Blood networks

River networks

Conclusion

References

Fluctuations—Kolmogorov-Smirnov test



$$P(B|M) = 1/M^{2/3} f(B/M^{2/3})$$

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

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.

[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

We use the spiffing **Spearman Rank-Order Correlation Coefficient**.

Basic idea:

- ▶ Given $\{(x_i, y_i)\}$, rank the $\{x_i\}$ and $\{y_i\}$ separately from smallest to largest. Call these ranks R_i and S_i .
- ▶ Now calculate correlation coefficient for ranks, r_s :

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

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

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

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]

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

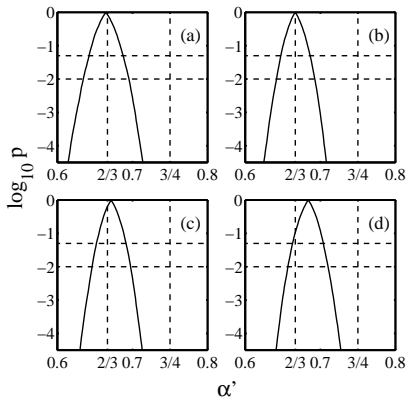
Blood networks

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

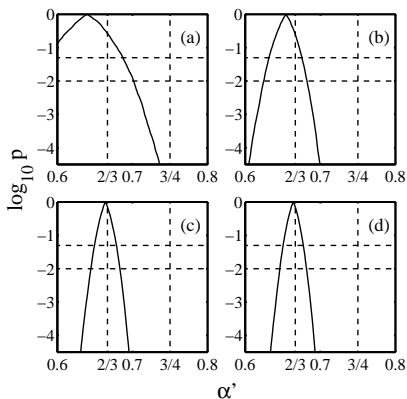
Blood networks

River networks

Conclusion

References

Analysis of residuals—birds



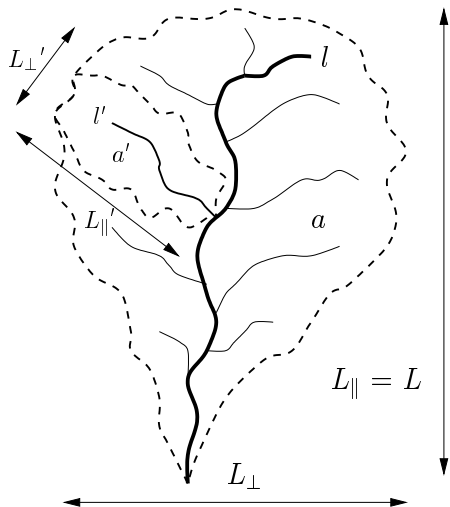
(a) $M < .1$ kg, (b) $M < 1$ kg, (c) $M < 10$ kg, (d) all birds.

Scaling-at-large

Allometry

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

References

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

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

- ▶ 1957: J. T. Hack^[12]
 “Studies of Longitudinal Stream Profiles in Virginia and Maryland”

$$l \sim a^h$$

$$h \sim 0.6$$

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

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

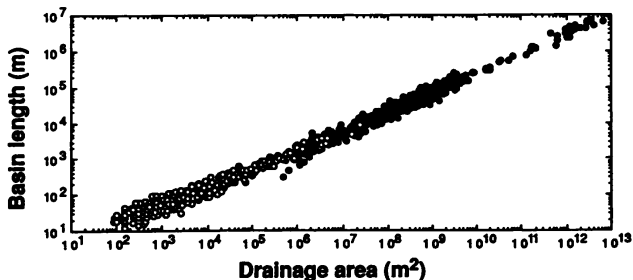
River networks

Conclusion

References

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.

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

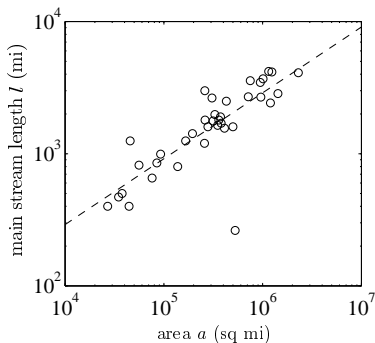
Blood networks

River networks

Conclusion

References

World's largest rivers only:



- ▶ Data from Leopold (1994) ^[17, 9]
- ▶ Estimate of Hack exponent: $h = 0.50 \pm 0.06$

Scaling-at-large

Allometry

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

References

Earlier theories

Building on the surface area idea...

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

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

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

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

River networks

Conclusion

References

Earlier theories

Building on the surface area idea:

- ▶ McMahon (70's, 80's): Elastic Similarity^[18, 6]
- ▶ 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.

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

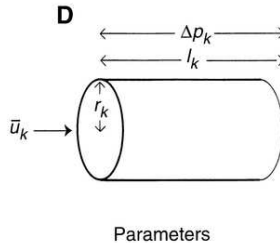
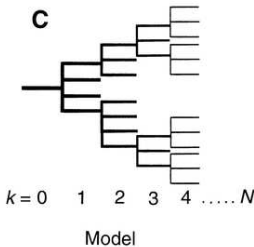
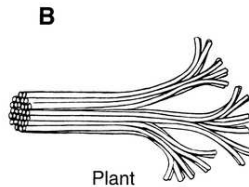
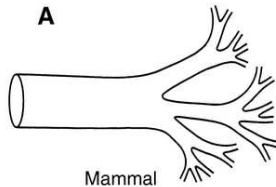
River networks

Conclusion

References

Nutrient delivering networks:

- ▶ 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.



Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

River networks

Conclusion

References

Nutrient delivering networks:

West et al.'s assumptions:

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

Claims:

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

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

River networks

Conclusion

References

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):

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

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

River networks

Conclusion

References

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.

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

River networks

Conclusion

References

Connecting network structure to α

1. Ratios of network parameters:

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

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

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

(also problematic due to prefactor issues)

Soldiering on, assert:

▶ area-preservingness: $R_r = R_n^{-1/2}$

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

▶

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

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

River networks

Conclusion

References

Data from real networks

Network	R_n	R_r^{-1}	R_ℓ^{-1}	$-\frac{\ln R_r}{\ln R_n}$	$-\frac{\ln R_\ell}{\ln R_n}$	α
West <i>et al.</i>	–	–	–	1/2	1/3	3/4
rat (PAT)	2.76	1.58	1.60	0.45	0.46	0.73
cat (PAT) (Turcotte <i>et al.</i> [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)	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

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

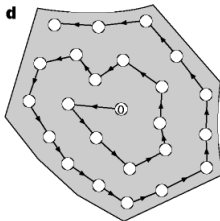
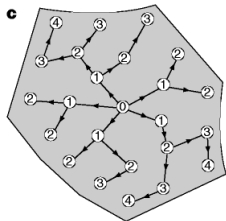
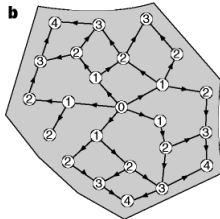
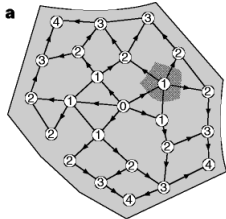
Blood networks

River networks

Conclusion

References

Simple supply networks



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

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

River networks

Conclusion

References

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 $V_{\text{blood}} = 10 V_{\text{body}}$
- ▶ Such a pachyderm would be rather miserable.

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

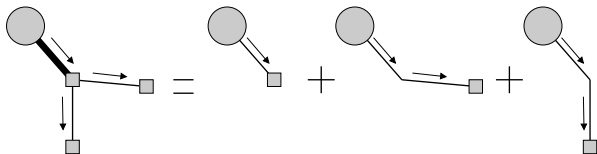
River networks

Conclusion

References

Geometric argument

- ▶ 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:



- ▶ **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 $N_{\text{sinks}} \propto V^\alpha$?

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

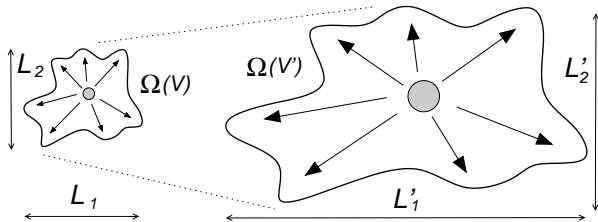
River networks

Conclusion

References

Geometric argument

- ▶ Allometrically growing regions:



- ▶ Have d length scales which scale as

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

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

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

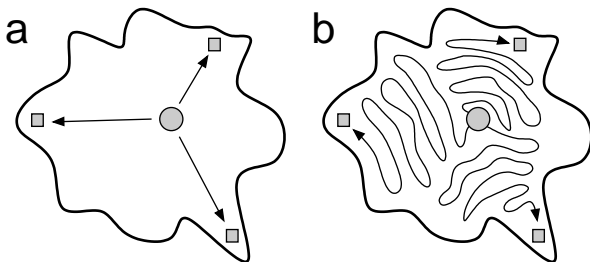
Blood networks

River networks

Conclusion

References

- ▶ Best and worst configurations (Banavar et al.)



- ▶ **Rather obviously:**

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

Minimal network volume:

Real supply networks are close to optimal:

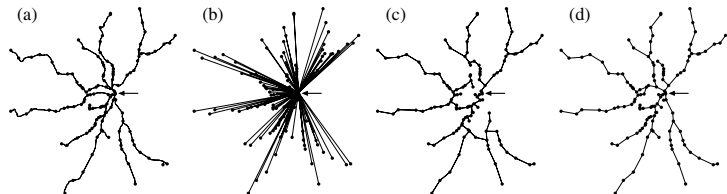


Figure 1. (a) Commuter rail network in the Boston area. The arrow marks the assumed root of the network. (b) Star graph. (c) Minimum spanning tree. (d) The model of equation (3) applied to the same set of stations.

(2006) Gastner and Newman^[11]: “Shape and efficiency in spatial distribution networks”

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

River networks

Conclusion

References

Minimal network volume:

Approximate network volume by integral over region:

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

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

River networks

Conclusion

References

Geometric argument

- ▶ General result:

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

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

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

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

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

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

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

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

River networks

Conclusion

References

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 blood volume ^[23], $V_{\text{net}} \propto V$.
- ▶ Sink density must \therefore decrease as volume increases:

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

- ▶ Density of supplyable sinks **decreases** with organism size.

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

River networks

Conclusion

References

Blood networks

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

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

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

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

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

Recap:

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

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

River networks

Conclusion

References

Prefactor:

Stefan-Boltzmann law:



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

where S is surface and T is temperature.

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

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

- ▶ Measured for $M \leq 10$ kg:

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

Scaling-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:

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

- ▶ Network volume grows faster than basin 'volume' (really area).
- ▶ **It's all okay:**
Landscapes are $d=2$ surfaces living in $D=3$ 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

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

- ▶ Hack's law again:

$$l \sim a^h$$

- ▶ Can argue

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

where h is Hack's exponent.

- ▶ \therefore minimal volume calculations gives

$$h = 1/2$$

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

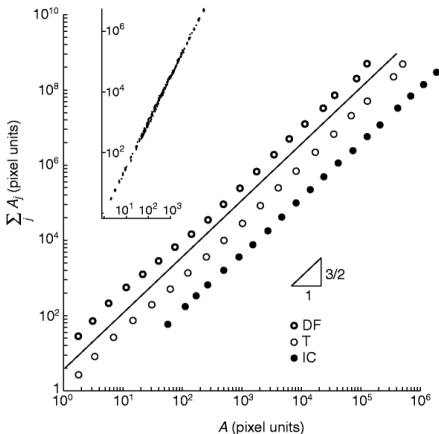
River networks

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: $a \sim \ell^h$ with $h = 1/2$
- ▶ (Zzzzz)



From Banavar et al. (1999) ^[1]

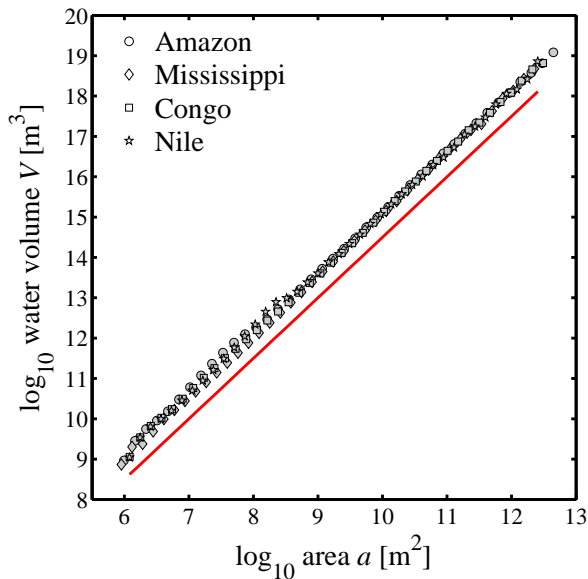
Scaling-at-large

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](#)

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-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

River networks

Conclusion

References

References I

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

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument





Blood networks

River networks

Conclusion

References

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.
-  J. T. Bonner and T. A. McMahon.
On Size and Life.
Scientific American Library, New York, 1983.
-  S. Brody.
Bioenergetics and Growth.
Reinhold, New York, 1945.
reprint, .

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument


Blood networks


River networks


Conclusion

References

References III

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

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

 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.
[. pdf](#) (田)

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks


River networks


Conclusion

References

References IV

 M. T. Gastner and M. E. J. Newman.
Shape and efficiency in spatial distribution networks.
J. Stat. Mech.: Theor. & Exp., 1:01015–, 2006.
[pdf](#) (⊞)

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

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

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument





Blood networks

River networks

Conclusion

References

References V

-  **A. Hemmingsen.**
Energy metabolism as related to body size and respiratory surfaces, and its evolution.
Rep. Steno Mem. Hosp., 9:1–110, 1960.
-  **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.

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks





River networks

Conclusion

References





Frame 114/114

References VI

-  T. McMahon.
Size and shape in biology.
Science, 179:1201–1204, 1973. [pdf](#) (田)
-  D. R. Montgomery and W. E. Dietrich.
Channel initiation and the problem of landscape scale.
Science, 255:826–30, 1992. [pdf](#) (田)
-  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.

[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

-  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](#) (田)

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

-  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](#) (田)

Scaling-at-large

Allometry

Definitions

Examples

History: Metabolism

Measuring exponents

History: River networks

Earlier theories

Geometric argument

Blood networks

River networks

Conclusion

References

Frame 117/114