Scaling—a Plenitude of Power Laws

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

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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

Frame 1/117

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Allometry

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

References

Outline

All about scaling:

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

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Frame 4/117

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Definitions

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

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

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

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Definitions
Examples

History: Metabolism

Measuring exponents
History: River networks

Earlier theories

Geometric argument

Blood networks

River networks

Reference

Frame 5/117

Definitions

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

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

▶ Using [·] to indicate dimension, then

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

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

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Looking at data

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

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

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

with slope equal to α , the scaling exponent.

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

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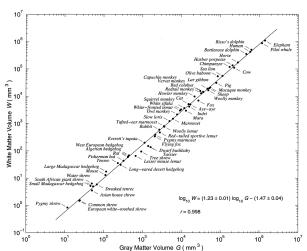
Scaling-at-large

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

References

Frame 7/117

A beautiful, heart-warming example:



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

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Scaling-at-large

Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River network
Earlier theories
Geometric argument

 $\alpha \simeq 1.23$

'computing elements'

gray matter:

white

matter:

'wiring'

References

Frame 8/117



Why is $\alpha \simeq 1.23$?

Quantities (following Zhang and Sejnowski):

- ► *G* = Volume of gray matter (cortex/processors)
- ightharpoonup W =Volume of white matter (wiring)
- ightharpoonup 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 $W \propto G^{4/3}/T$

Why is $\alpha \simeq 1.23$?

A rough understanding:

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

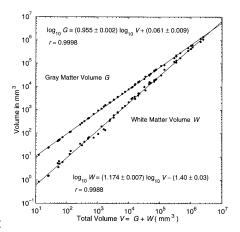
Scaling

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...

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Frame 9/117

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

References

Frame 11/117

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Good scaling:

General rules of thumb:

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

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

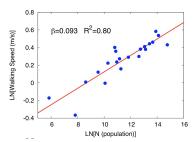
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Unconvincing scaling:

Average walking speed as a function of city population:



Two problems:

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

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

Definitions.

Power laws are the signature of scale invariance:

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

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

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Allometry

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

eferences

Frame 14/117



Scale invariance

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

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

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

•

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

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

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Frame 13/117

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Scaling-at-large

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Definitions
Examples
History: Metabolism
Measuring exponents
History: River networ
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.
- ightharpoonup \Rightarrow scale matters for the exponential.

Scaling

Scaling-at-large

Allometry
Definitions
Examples
History: Metabolism
Measuring exponente
History: River networ
Earlier theories
Geometric argument
Blood networks

References

Frame 16/117



Frame 15/117

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.
- ▶ ⇒ 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 (\boxplus) :

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

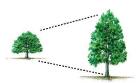


Definitions:

Isometry:

dimensions scale linearly with each other.





Allometry: dimensions scale nonlinearly.



Frame 17/117

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Definitions

Examples

History: Metabolism

Measuring exponents

History: River network

Earlier theories

Geometric argument

Blood networks

River networks

Conclusion

References

Frame 20/117

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

References

Frame 21/117



A wonderful treatise on scaling:

ON SIZE AND LIFE THOMAS A. McMAHON AND JOHN TYLER BONNER

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For the following slide:

The biggest living things (left). All the organisms are drawn to the same scale. 1, The largest flying bird (albatross); 2, the largest known animal (the blue whale), 3, the largest extinct land mammal (Baluchitherium) with a human figure shown for scale; 4, the tallest living land animal (giraffe); 5, Tyrannosaurus: 6. Diplodocus: 7, one of the largest flying reptiles (Pteranodon); 8, the largest extinct snake; 9, the length of the largest tapeworm found in man; 10, the largest living reptile (West African crocodile); 11, the largest extinct lizard; 12, the largest extinct bird (Aepyornis); 13, the largest jellyfish (Cyanea); 14, the largest living lizard (Komodo dragon); 15, sheep; 16, the largest bivalve mollusc (Tridacna); 17; the largest fish (whale shark); 18, horse; 19, the largest crustacean (Japanese spider crab); 20, the largest sea scorpion (Eurypterid); 21, large tarpon; 22, the largest lobster; 23, the largest mollusc (deep-water squid, Architeuthis); 24, ostrich; 25, the lower 105 feet of the largest organism (giant sequoia), with a 100-foot larch superposed.

p. 2, McMahon and Bonner [18]

Scaling-at-large Allometry Frame 24/117 母 りへで

The many scales of life:

McMahon and

Bonner, 1983^[18]





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).

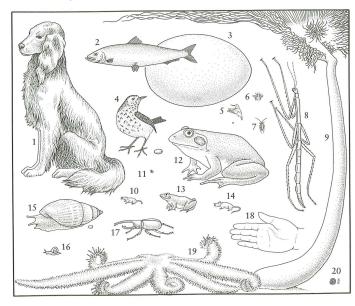


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p. 2, McMahon and Bonner [18]

p. 2, McMahon and Bonner [18]

The many scales of life:



p. 3, McMahon and Bonner [18]



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).

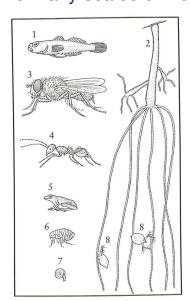
The smallest "naked-eye" creatures and some large microscopic animals and cells (below right). 1, Vorticella, a ciliate; 2, the largest ciliate protozoan (Bursaria); 3, the smallest many-celled animal (a rotifer); 4, smallest flying insect (Elaphis); 5, another ciliate (Paramecium); 6, cheese mite; 7, 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).

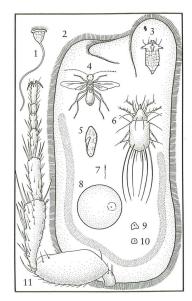
p. 2, McMahon and Bonner [18]

Scaling Scaling-at-large Allometry Frame 28/117

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The many scales of life:



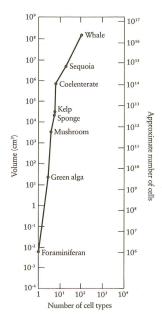




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Size range and cell differentiation:

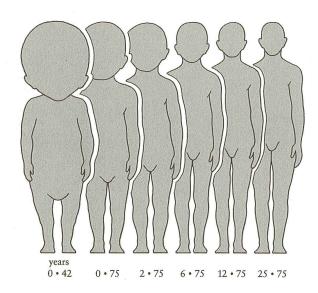






p. 3, McMahon and Bonner [18]

Non-uniform growth:



p. 32, McMahon and Bonner [18]

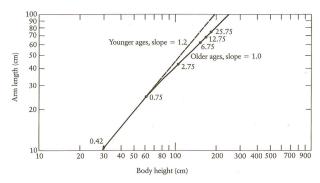
Scaling Scaling-at-large Allometry Definitions Examples History: Metabolism Measuring exponents History: River networks Earlier therories Geometric argument Blood networks River networks Conclusion References

Frame 31/117

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Non-uniform growth—arm length versus height:

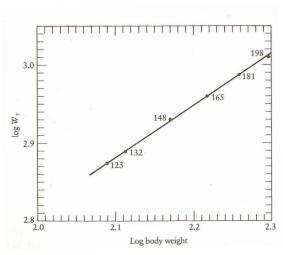
Good example of a break in scaling:



A crossover in scaling occurs around a height of 1 metre. p. 32, McMahon and Bonner [18]

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

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

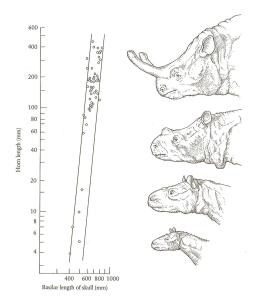


Idea: Power \sim cross-sectional area of isometric lifters.

p. 53, McMahon and Bonner [18]



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



p. 36, McMahon and Bonner [18]

Scaling
Scaling-at-large
Allometry

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

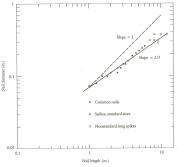
References

Frame 34/117

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The allometry of nails:





- ▶ Length $\propto \text{Mass}^{1/4}$
- ▶ Diameter

 ∠ Length^{2/3}

p. 58-59, McMahon and Bonner [18]

The allometry of nails:

A buckling instability?:

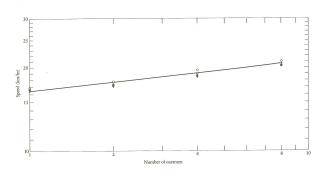
- ▶ Physics/Engineering result: Columns buckle under a load which depends on d^4/ℓ^2 .
- ► To drive nails in, resistive force \propto nail circumference = πd .
- ▶ Match forces independent of nail size: $d^4/\ell^2 \propto d$.
- ▶ Leads to $d \propto \ell^{2/3}$.

Scaling Scaling-at-large Allometry Definitions Examples History: Metabolism Measuring exponents History: River networks Earlier theories Geometric argument Blood networks Conclusion References Frame 36/117

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

Shell dimensions and performances.

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



Scalin

Frame 35/117

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Scaling-at-large

Definitions

Examples

History: Metabolism

Measuring exponents

History: River network

Earlier theories

Geometric argument

Blood networks

References

Frame 37/117

回 りゅつ

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

Scaling-at-large

Allometry
Definitions
Examples
History: Metabolism
Measuring exponent
History: River netwo

Conclusion

Frame 38/117



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-R², adjusted R²; GDP, gross domestic product.



Scaling in Cities:

Intriguing findings:

- ▶ Global supply costs scale sublinearly with N (β < 1).
 - ► Returns to scale for infrastructure.
- ▶ Total individual costs scale linearly with N ($\beta = 1$)
 - Individuals consume similar amounts independent of city size.
- ▶ Social quantities scale superlinearly with N ($\beta > 1$)
 - ► 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: $N_{ m species} \propto A^{\beta}$

Allegedly (data is messy):

▶ On islands: $\beta \approx 1/4$.

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

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

Frame 39/117

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A focus:

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



Frame 42/117

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Frame 41/117



Animal power

Fundamental biological and ecological constraint:

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

P = basal metabolic rate

M =organismal body mass







History: Metabolism

 $P = c M^{\alpha}$

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

References

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What one might expect:

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

► Dimensional analysis suggests an energy balance surface law:

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

► Lognormal fluctuations:

Gaussian fluctuations in $\log P$ around $\log cM^{\alpha}$.

Stefan-Boltzmann relation for radiated energy:

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

Frame 44/117

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Allometry

Frame 46/117

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The prevailing belief of the church of quarterology

$$\alpha = 3/4$$

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

Huh?

Scaling

Scaling-at-large

Allometry

Frame 47/117

回 り900

Related putative scalings:

- ▶ number of capillaries $\propto M^{3/4}$
- ▶ time to reproductive maturity $\propto M^{1/4}$
- ▶ heart rate $\propto M^{-1/4}$
- ightharpoonup 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

Frame 48/117

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The great 'law' of heartbeats:

Assuming:

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

Then:

- Average number of heart beats in a lifespan \simeq (Average lifespan) \times (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 Scaling-at-large Allometry Definitions Examples History: Metabolism Measuring exponents History: River networks Earlier theories Geometric argument Blood networks Conclusion References

History

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





Frame 50/117

母 りへで

History

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



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Scaling-at-large

Allometry
Definitions
Examples
History: Metabolism
Measuring exponent
History: River netwo
Earlier theories
Geometric argument
Blood networks
River networks

References

Frame 51/117

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History

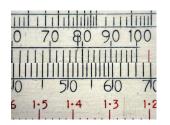
1930's: Brody, Benedict study mammals. [6] Found $\alpha \simeq 0.73$ (standard).



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

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



Scaling

Scaling-at-large

Examples
History: Metabolis
Measuring expone

History: River networks
Earlier theories
Geometric argumer
Blood networks
River networks

References

Frame 53/117



History

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



Scaling

Frame 52/117

回 り900

Scaling-at-large

Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networ
Earlier theories

References

History

1964: Troon, Scotland: [4]
3rd symposium on energy metabolism.

 $\alpha =$ 3/4 made official . . .

...29 to zip.



Scaling

Scaling-at-large

Allometry
Definitions
Examples
History: Metabolism
Measuring exponent

History: River network Earlier theories Geometric argument Blood networks River networks

References

Frame 55/117

回 り900

Today

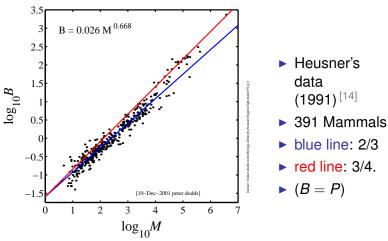
▶ 3/4 is held by many to be the one true exponent.



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 [9]

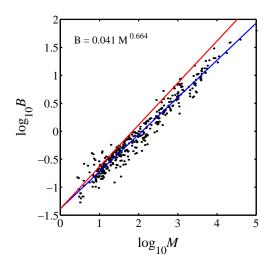
Some data on metabolic rates



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

母 りへで

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

Frame 56/117

母 りへで

Scaling-at-large

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

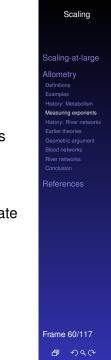
References

Frame 58/117

Important:

Linear regression

- ▶ 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.



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.)

Allometry

Measuring exponents

For Standardized Major Axis Linear Regression:

 $slope_{sma} = \frac{standard\ deviation\ of\ y\ data}{standard\ deviation\ of\ x\ data}$ Very simple!

Allometry

Frame 62/117



Measuring exponents

Relationship to ordinary least squares regression is simple:

$$slope_{SMA} = r^{-1} \times slope_{OLS y on x}$$

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

where r =standard correlation coefficient:

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

Scaling

Frame 61/117

母 りへで

Scaling-at-large

Allometry Measuring exponents

Heusner's data, 1991 (391 Mammals)

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

Scaling

Scaling-at-large

Allometry

Frame 64/117

母 りへで

Frame 63/117 母 りゅつ

Bennett and Harvey, 1987 (398 birds)

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

Hypothesis testing

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

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

- Assume each \mathbf{B}_i (now a random variable) is normally distributed about $\alpha' \log_{10} M_i + \log_{10} c$.
- ▶ Follows that the measured α for one realization obeys a t distribution with N-2 degrees of freedom.
- ▶ Calculate a *p*-value: probability that the measured α is as least as different to our hypothesized α' as we observe.
- ► (see, for example, DeGroot and Scherish, "Probability and Statistics" [7])

Scaling

Scaling-at-large

Allometry
Definitions
Examples
History: Metabolism
Measuring exponen
History: River netwo

Conclusion

Frame 66/117



Revisiting the past—mammals

Full mass range:

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

Scaling

Frame 65/117

回 りへで

Scaling

Scaling-at-large

Measuring exponents

Allometry

Scaling-at-large

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

References

Frame 67/117

母 りへで

Revisiting the past—mammals

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

	Ν	\hat{lpha}	$p_{2/3}$	$p_{3/4}$	
Kleiber	5	0.667	0.99	0.088	
Brody	26	0.709	$< 10^{-3}$	$< 10^{-3}$	
Heusner	357	0.668	0.91	$< 10^{-15}$	
$M \ge 10 \text{ kg}$:	N	\hat{lpha}	$p_{2/3}$	$p_{3/4}$	
Kleiber	8	0.754	$< 10^{-4}$	0.66	
Brody	9	0.760	$< 10^{-3}$	0.56	
Біоцу	9	0.700	< 10	0.00	

Scaling

Scaling-at-large

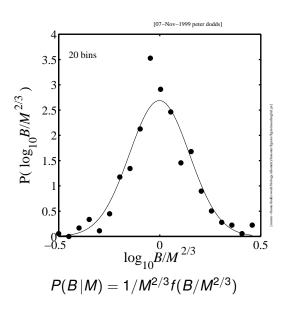
Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument

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Frame 68/117



Fluctuations—Kolmogorov-Smirnov test



Analysis of residuals

- 1. Presume an exponent of your choice: 2/3 or 3/4.
- 2. Fit the prefactor (log₁₀ c) and then examine the residuals:

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

- 3. *H*₀: residuals are uncorrelated *H*₁: residuals are correlated.
- 4. Measure the correlations in the residuals and compute a *p*-value.

Scaling 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 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.

Scaling

Frame 69/117

Scaling-at-large

Scaling-at-large

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

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

Scaling-at-large

Allometry
Definitions
Examples
History: Metabolism

asuring exponents
tory: River network:
lier theories
ometric argument
od networks
er networks
nclusion

References

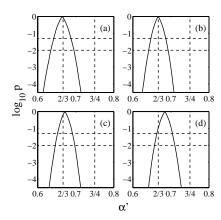
Frame 72/117



Frame 71/117

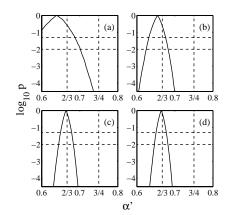


Analysis of residuals—mammals



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

Analysis of residuals—birds

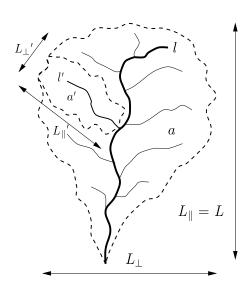


(a) M < .1 kg, (b) M < 1 kg, (c) M < 10 kg, (d) all birds.

Scaling Scaling-at-large Allometry Definitions Examples History: Metabolism Measuring exponents History: River networks Geometria regument Blood networks River networks Conclusion References

回 りへで

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



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

River networks

▶ 1957: J. T. Hack [11] "Studies of Longitudinal Stream Profiles in Virginia and Maryland" $\ell \sim a^h$

$$\ell \sim a'$$

$$h \sim 0.6$$

- ▶ 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

Scaling-at-large

Allometry

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

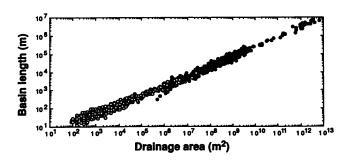
References

Allometry

Scaling-at-large

Large-scale networks

(1992) Montgomery and Dietrich [19]:

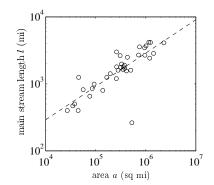


- ➤ Composite data set: includes everything from unchanneled valleys up to world's largest rivers.
- ► Estimated fit:

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

Mixture of basin and main stream lengths.

World's largest rivers only:



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

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

Frame 79/117

母 りへで

Scaling

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

Frame 78/117

母 りへで

Scaling-at-large

Illometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River network
Earlier theories
Geometric argument
Blood networks
River networks

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Frame 81/117

Earlier theories

Building on the surface area idea:

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

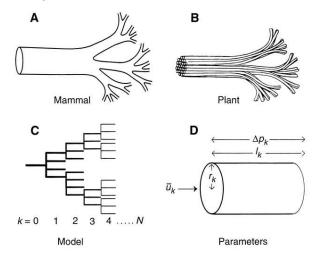
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Frame 82/117

回 りへで

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.





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



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):

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



母 りへで

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:

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

Scaling-at-large

Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networ
Earlier theories
Geometric argument

References

Frame 86/117





Connecting network structure to α

1. Ratios of network parameters:

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

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

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

(also problematic due to prefactor issues)

Soldiering on, assert:

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

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

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

Scaling

Scaling-at-large

Definitions
Examples
History: Metabolism

Measuring expon History: River net Earlier theories Geometric argum Blood networks River networks Conclusion

References

Data from real networks

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

Scaling

Scaling-at-large

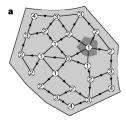
Definitions
Examples
History: Metabolism
Measuring exponen
History: River netwo
Earlier theories
Geometric argumer

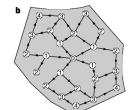
Conclusion

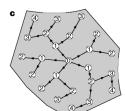
Frame 88/117

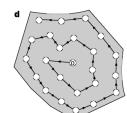


Simple supply networks









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

Scalir

Scaling-at-large

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

References

Frame 89/117

雪 りへで

Simple supply networks

▶ Banavar et al. find 'most efficient' networks with

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

▶ ... but also find

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

► *d* = 3:

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

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

Scaling

Scaling-at-large

Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River network
Earlier theories
Geometric argument

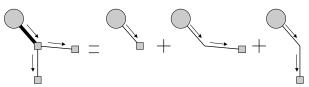
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Frame 90/117



Geometric argument

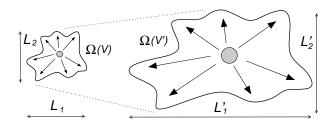
- ► Consider one source supplying many sinks in a *d*-dim. volume in a *D*-dim. ambient space.
- Assume sinks are invariant.
- ▶ Assume $\rho = \rho(V)$.
- ► Assume some cap on flow speed of material.
- See network as a bundle of virtual vessels:



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

Geometric argument

Allometrically growing regions:



▶ Have *d* length scales which scale as

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

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

Scaling

Scaling-at-large

Definitions
Examples
History: Metabolism
Measuring exponent
History: River networ
Earlier theories
Geometric argument
Blood networks

leferences

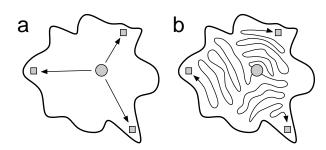
Frame 93/117



Scaling-at-large

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:

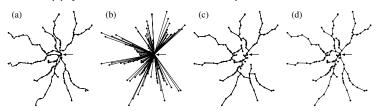


Figure 1. (a) Commuter rail network in the Boston area. The arrow marks the assumed root of the network. (b) Star graph. (c) Minimum spanning tree. (d) The model of equation (3) applied to the same set of stations.

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

Frame 95/117



Scaling

Frame 92/117

Scaling-at-large

Scaling-at-large

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

References

Frame 94/117

900

Minimal network volume:

Approximate network volume by integral over region:

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

Scaling

Scaling-at-large

Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River network
Earlier theories
Geometric argument

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Geometric argument

General result:

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

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

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

$$rac{\mathsf{min}\; V_{\mathrm{net/iso}}}{\mathsf{min}\; V_{\mathrm{net/allo}}}
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ightarrow \infty$$

Scalin

Scaling-at-large

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

eferences

Frame 97/117



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

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

Density of suppliable sinks decreases with organism size. Scaling

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

Scaling-at-large

Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River network
Earlier theories
Geometric argument

onclusion

Frame 100/117



Frame 99/117



Recap:

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

Scaling

Scaling-at-larg

Allometry
Definitions
Examples
History: Metabolism
Measuring exponents
History: River networ

River networks Conclusion

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:

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

▶ Measured for $M \le 10$ kg:

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

Scaling

Scaling-at-large

Definitions
Examples
History: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Rlood networks

eferences

Frame 102/117



River networks

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

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

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

Scaling

Frame 101/117

母 りへで

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

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

Hack's law again:

$$\ell \sim a^h$$

Can argue

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

where h is Hack's exponent.

▶ ∴ minimal volume calculations gives

$$h = 1/2$$

Scaling

Scaling-at-large

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

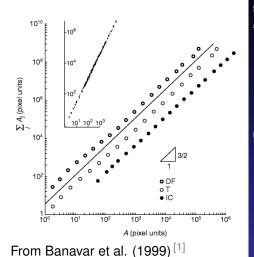
References

Frame 105/117

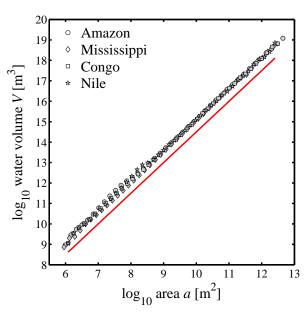


Real data:

- 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)



Even better—prefactors match up:





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

Frame 106/117

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

Frame 109/117

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Scaling

Scaling-at-large

Definitions

Examples

History: Metabolism

Measuring exponents

History: River network

Earlier theories

Geometric argument

Blood networks

References

Frame 110/117



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

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

References

Frame 113/117

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

References

Frame 11<u>4/11</u>7

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Scaling-at-large Allometry References Frame 115/117 母 りへで

Scaling

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