

Optimal Supply Networks II: Blood, Water, and Truthicide

Last updated: 2023/01/30, 20:27:10 EST

Principles of Complex Systems, Vols. 1, 2, & 3D
CSYS/MATH 300, 303, & 394, 2022–2023 | @pocsvox

Prof. Peter Sheridan Dodds | @peterdodds

Computational Story Lab | Vermont Complex Systems Center
Santa Fe Institute | University of Vermont



Licensed under the [Creative Commons Attribution-NonCommercial-ShareAlike 3.0 License](https://creativecommons.org/licenses/by-nc-sa/3.0/).

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthicide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



1 of 124

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthicide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



2 of 124

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthicide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



3 of 124

Law and Order, Special Science Edition: Truthicide Department

“In the scientific integrity system known as peer review, the people are represented by two highly overlapping yet equally important groups: the independent scientists who review papers and the scientists who punish those who publish garbage. This is one of their stories.”

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthicide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



4 of 124

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthicide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



5 of 124

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthicide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



6 of 124

What one might expect:

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

Dimensional analysis suggests an energy balance surface law:

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

Assumes isometric scaling (not quite the spherical cow).

Lognormal fluctuations:
Gaussian fluctuations in $\log_{10} P$ around $\log_{10} cM^\alpha$.

Stefan-Boltzmann law for radiated energy:

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



4 of 124

PoCS
@pocsvox
Optimal Supply
Networks II

The prevailing belief of the Church of Quarterology:

$$\alpha = 3/4$$

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

Huh?

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthicide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



7 of 124

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthicide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



8 of 124

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthicide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



9 of 124

Outline

Metabolism and Truthicide

Death by fractions

Measuring exponents

River networks

Earlier theories

Geometric argument

Conclusion

References

Animal power

Fundamental biological and ecological constraint:

$$P = c M^\alpha$$

P = basal metabolic rate

M = organismal body mass



4 of 124

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthicide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



5 of 124

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthicide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



6 of 124

Stories—The Fraction Assassin:



2 of 124

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthicide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



3 of 124

$$P = c M^\alpha$$

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



4 of 124

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthicide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



5 of 124

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthicide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



6 of 124

The prevailing belief of the Church of Quarterology:

Most obvious concern:

$$3/4 - 2/3 = 1/12$$

An exponent higher than 2/3 points suggests a fundamental inefficiency in biology.

Organisms must somehow be running ‘hotter’ than they need to balance heat loss.



7 of 124

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthicide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



8 of 124

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthicide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



9 of 124

Related putative scalings:

Wait! There's more!:

- number of capillaries $\propto M^{3/4}$
- time to reproductive maturity $\propto M^{1/4}$
- heart rate $\propto M^{-1/4}$
- cross-sectional area of aorta $\propto M^{3/4}$
- population density $\propto M^{-3/4}$

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truticide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References

10 of 124

The great 'law' of heartbeats:

Assuming:

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

Then:

$$\begin{aligned} \text{Average number of heart beats in a lifespan} \\ \approx (\text{Average lifespan}) \times (\text{Average heart rate}) \\ \propto M^{\beta-\beta} \\ \propto M^0 \end{aligned}$$

- Number of heartbeats per life time is independent of organism size!
- ≈ 1.5 billion

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truticide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References

11 of 124

From PoCS, the Prequel to CocoNuTs:

"How fast do living organisms move:

Maximum speeds from bacteria to elephants and whales"

Meyer-Vernet and Rospars,
American Journal of Physics, **83**, 719–722,
2015. [35]

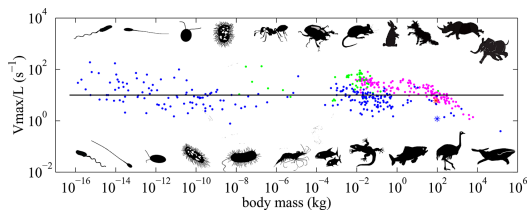


Fig. 1. Maximum relative speed versus body mass for 202 running species (157 mammals plotted in magenta and 45 non-mammals plotted in green), 127 swimming species and 91 micro-organisms (plotted in blue). The sources of the data are given in Ref. 16. The solid line is the maximum relative speed (Eq. (13)) estimated in Sec. III. The human world records are plotted as asterisks (upper for running and lower for swimming). Some examples of organisms of various masses are sketched in black (drawings by François Meyer).

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truticide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References

12 of 124

Theoretical story:

- Maximum speed increases with size: $v_{\max} = aM^b$
- Takes a while to get going: $v(t) = v_{\max}(1 - e^{-kt})$
- $k \sim F_{\max}/M \sim cM^{d-1}$
Literature: $0.75 \lesssim d \lesssim 0.94$
- Acceleration time = depletion time for anaerobic energy: $\tau \sim fM^g$ Literature: $0.76 \lesssim g \lesssim 1.27$
- $v_{\max} = aM^b(1 - e^{-hM^i})$
- $i = d - 1 + g$ and $h = cf$

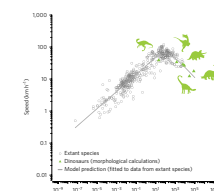


Figure 4. Predicting the maximum speed of selected species with the time-dependent model. The model prediction (grey line) is fitted to data of extant species (grey circles) and extended to higher body masses. Speed data for dinosaurs (green triangles) come from detailed morphological model calculations (values in Table 1) and were not used to obtain model parameters.

- Literature search for maximum speeds of running, flying and swimming animals.
- Search terms: "maximum speed", "escape speed" and "sprint speed".

12 of 124

"A general scaling law reveals why the largest animals are not the fastest"

Hirt et al.,
Nature Ecology & Evolution, **1**, 1116, 2017. [23]

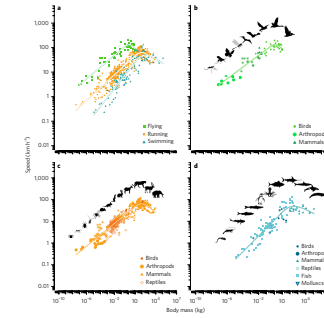


Figure 2. Empirical data and time-dependent model fits for the allometric scaling of maximum speed. a. Comparison of scaling for the different locomotion modes (flying, running, swimming). b–d. Taxonomic differences are illustrated separately for flying (n=55), running (n=45) and swimming (n=37) animals. Overall model fit: $R^2=0.893$. The residual variation does not exhibit a signature of taxonomy (only a weak effect of thermoregulation, see Methods).

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truticide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References

13 of 124

A theory is born:

1840's: Sarrus and Rameaux^[44] first suggested $\alpha = 2/3$.



PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truticide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References

14 of 124

A theory grows:

1883: Rubner^[42] found $\alpha \approx 2/3$.



PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truticide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References

15 of 124

Theory meets a different 'truth':

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



15 of 124

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truticide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References

17 of 124

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truticide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References

18 of 124

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truticide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

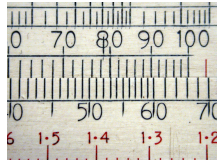
Geometric
argument

Conclusion

References

19 of 124

Our hero faces a shadowy cabal:



- 1932: Kleiber analyzed 13 mammals. [25]
- Found $\alpha = 0.76$ and suggested $\alpha = 3/4$.
- Scaling law of Metabolism became known as [Kleiber's Law](#) (2011 Wikipedia entry is embarrassing).
- 1961 book: "The Fire of Life. An Introduction to Animal Energetics". [26]

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Trutichide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



When a cult becomes a religion:

1950/1960: Hemmingsen [20, 21]
Extension to unicellular organisms.
 $\alpha = 3/4$ assumed true.



PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Trutichide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



Quarterology spreads throughout the land:

The Cabal assassinates 2/3-scaling:

- 1964: Troon, Scotland.
- 3rd Symposium on Energy Metabolism.
- $\alpha = 3/4$ made official ...



...29 to zip.

- But the Cabal slipped up by publishing the conference proceedings ...

- "Energy Metabolism; Proceedings of the 3rd symposium held at Troon, Scotland, May 1964," Ed. Sir Kenneth Blaxter [4]

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Trutichide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



An unsolved truthicide:

So many questions ...

- Did the truth kill a theory? Or did a theory kill the truth?
- Or was the truth killed by just a lone, lowly hypothesis?
- Does this go all the way to the top? To the National Academies of Science?
- Is 2/3-scaling really dead?
- Could 2/3-scaling have faked its own death?
- What kind of people would vote on scientific facts?



Modern Quarterology, Post Trutichide

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

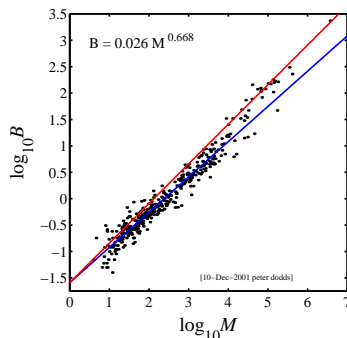


In the Beat of a Heart: Life, Energy, and the Unity of Nature—by John Whitfield

- But: much controversy ...
- See 'Re-examination of the "3/4-law" of metabolism' by the Heretical Unbelievers Dodds, Rothman, and Weitz [14], and ensuing madness ...



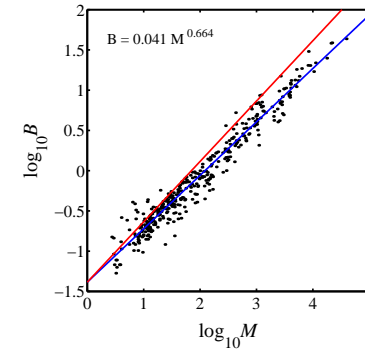
Some data on metabolic rates



- Heusner's data (1991) [22]
- 391 Mammals
- blue line: 2/3
- red line: 3/4.
- ($B = P$)



Some data on metabolic rates



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

- Passerine vs. non-passerine issue ...



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.



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. [43, 41] (aka Reduced Major Axis = RMA.)



PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Trutichide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Trutichide

Death by
fractions

Measuring
exponents

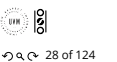
River networks

Earlier theories

Geometric
argument

Conclusion

References



PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Trutichide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



Measuring exponents

For Standardized Major Axis Linear Regression:

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

- Very simple!
- Minimization of sum of areas of triangles induced by vertical and horizontal residuals with best fit line.
- The only linear regression that is Scale invariant.
- Attributed to Nobel Laureate economist Paul Samuelson, but discovered independently by others.
- #somuchwin

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

Hypothesis testing

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

$$H_0 : \alpha = \alpha' \text{ and } H_1 : \alpha \neq \alpha'$$

- Assume each B_i (now a random variable) is normally distributed about $\alpha' \log_{10} M_i + \log_{10} c$.
- Follows that the measured α for one realization 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."

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:

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

- Groovy upshot: If (1) a paper uses OLS regression when RMA would be appropriate, and (2) r is reported, we can figure out the RMA slope.

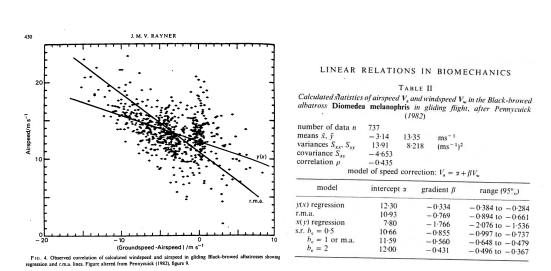
Bennett and Harvey, 1987 (398 birds)

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

Revisiting the past—mammals

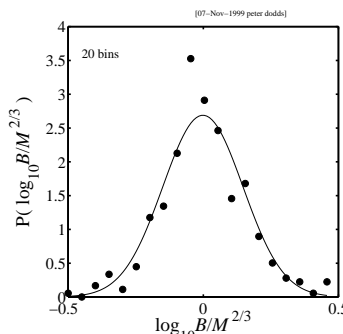
Full mass range:

	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	$< 10^{-15}$



- Disparity between slopes for y on x and x on y regressions is a factor of r^2 (r^{-2})
- (Rayner uses ρ for r .)
- Here: $r^2 = .435^2 = 0.189$, and $r^{-2} = .435^{-2} = 2.29^2 = 5.285$.
- See also: LaBarbera (who resigned...)

Fluctuations—Things look normal ...



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

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

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.

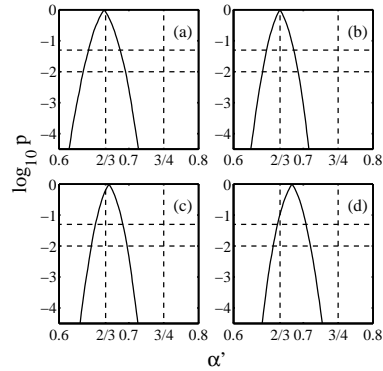
PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthticide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



39 of 124

Analysis of residuals—mammals



- $M < 3.2$ kg,
- $M < 10$ kg,
- $M < 32$ kg,
- all mammals.

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthticide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



42 of 124

Impure scaling?:

- So: The exponent $\alpha = 2/3$ works for all birds and mammals up to 10–30 kg
- For mammals > 10–30 kg, maybe we have a new scaling regime
- Possible connection?: Economos (1983)—limb length break in scaling around 20 kg [15]
- But see later: non-isometric growth leads to lower metabolic scaling. Oops.

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthticide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



45 of 124

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.

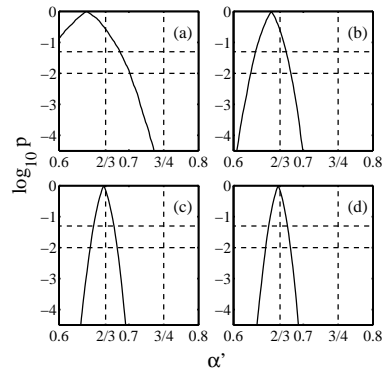
PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthticide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



40 of 124

Analysis of residuals—birds



- $M < 0.1$ kg,
- $M < 1$ kg,
- $M < 10$ kg,
- all birds.

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthticide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



43 of 124

The widening gyre:

Now we're really confused (empirically):

- White and Seymour, 2005: unhappy with large herbivore measurements [56]. Pro 2/3: Find $\alpha \approx 0.686 \pm 0.014$.
- Glazier, BioScience (2006) [18]: "The 3/4-Power Law Is Not Universal: Evolution of Isometric, Ontogenetic Metabolic Scaling in Pelagic Animals."
- Glazier, Biol. Rev. (2005) [17]: "Beyond the 3/4-power law': variation in the intra- and interspecific scaling of metabolic rate in animals."
- Savage et al., PLoS Biology (2008) [45] "Sizing up allometric scaling theory" Pro 3/4: problems claimed to be finite-size scaling.

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthticide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



46 of 124

Analysis of residuals

We assume all rank orderings are equally likely:

- r_s is distributed according to a Student's t -distribution with $N - 2$ degrees of freedom.
- Excellent feature: Non-parametric—real distribution of x 's and y 's doesn't matter.
- Bonus: works for non-linear monotonic relationships as well.
- See Numerical Recipes in C/Fortran which contains many good things. [39]

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthticide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



41 of 124

Other approaches to measuring exponents:

- Clauset, Shalizi, Newman: "Power-law distributions in empirical data" [10] SIAM Review, 2009.
- See Clauset's page on measuring power law exponents (code, other goodies).
- See this collection of tweets for related amusement.

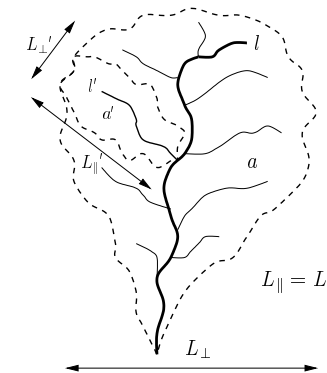
PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthticide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



44 of 124

Somehow, optimal river networks are connected:



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

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthticide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



47 of 124

Mysterious allometric scaling in river networks

1957: J. T. Hack [19]
 "Studies of Longitudinal Stream Profiles in Virginia and Maryland"

$$\ell \sim a^h$$

$$h \sim 0.6$$

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

PoCS
@pocsvox
Optimal Supply Networks II

Metabolism and Truthicide

Death by fractions

Measuring exponents

River networks

Earlier theories

Geometric argument

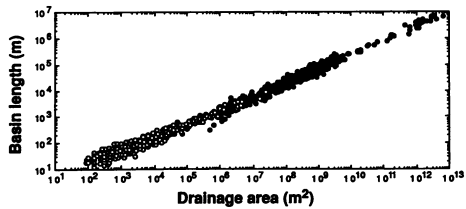
Conclusion

References

48 of 124

Large-scale networks:

(1992) Montgomery and Dietrich [36]:



- 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.

PoCS
@pocsvox
Optimal Supply Networks II

Metabolism and Truthicide

Death by fractions

Measuring exponents

River networks

Earlier theories

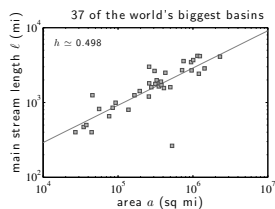
Geometric argument

Conclusion

References

49 of 124

World's largest rivers only:



- Data from Leopold (1994) [31, 13]
- Estimate of Hack exponent: $h = 0.50 \pm 0.06$

PoCS
@pocsvox
Optimal Supply Networks II

Metabolism and Truthicide

Death by fractions

Measuring exponents

River networks

Earlier theories

Geometric argument

Conclusion

References

50 of 124

Earlier theories (1973-):

Building on the surface area idea:

- McMahon (70's, 80's): Elastic Similarity [32, 34]
- Idea is that organismal shapes scale allometrically with 1/4 powers (like trees ...)
- Disastrously, cites Hemmingsen [21] for surface area data.
- Appears to be true for ungulate legs ... [33]
- Metabolism and shape never properly connected.



"Size and shape in biology"
 T. McMahon,
 Science, **179**, 1201-1204, 1973. [32]

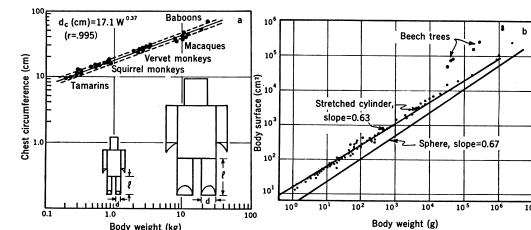
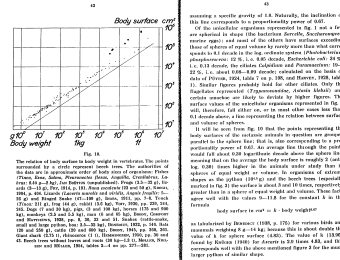


Fig. 3. (a) Chest circumference, d_c , plotted against body weight, W , for five species of primates. The broken lines represent the standard error in this least-squares fit (adapted from [27]). The model proposed here, whereby each length, l , increases as the 3/4 power of diameter, d , is illustrated for two weights differing by a factor of 16. (b) Body surface area plotted against weight for vertebrates. The animal data are reasonably well fitted by the stretched cylinder model (adapted from [34]).



- Hemmingsen's "fit" is for a 2/3 power, notes possible 10 kg transition. [7]
- p 46: "The energy metabolism thus definitely varies interspecifically over similar wide weight ranges with a higher power of the body weight than the body surface."

50 of 124

Earlier theories (1977):

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... [46]

PoCS
@pocsvox
Optimal Supply Networks II

Metabolism and Truthicide

Death by fractions

Measuring exponents

River networks

Earlier theories

Geometric argument

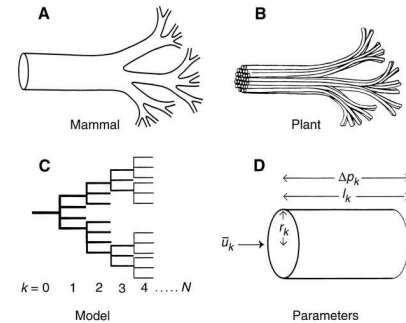
Conclusion

References

51 of 124

Nutrient delivering networks:

- 1960's: Rashevsky considers blood networks and finds a 2/3 scaling.
- 1997: West *et al.* [53] use a network story to find 3/4 scaling.



52 of 124

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

53 of 124

PoCS
@pocsvox
Optimal Supply Networks II

Metabolism and Truthicide

Death by fractions

Measuring exponents

River networks

Earlier theories

Geometric argument

Conclusion

References

54 of 124

PoCS
@pocsvox
Optimal Supply Networks II

Metabolism and Truthicide

Death by fractions

Measuring exponents

River networks

Earlier theories

Geometric argument

Conclusion

References

55 of 124

PoCS
@pocsvox
Optimal Supply Networks II

Metabolism and Truthicide

Death by fractions

Measuring exponents

River networks

Earlier theories

Geometric argument

Conclusion

References

56 of 124

Impedance measures:

☞ Poiseuille flow (outer branches):

$$Z = \frac{8\mu}{\pi} \sum_{k=0}^N \frac{\ell_k}{r_k^4 N_k}$$

☞ Pulsatile flow (main branches):

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

☞ Wheel out Lagrange multipliers ...

☞ Poiseuille gives $P \propto M^1$ with a logarithmic correction.

☞ Pulsatile calculation explodes into flames.



57 of 124

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Trutichide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



58 of 124

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Trutichide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



59 of 124

Data from real networks:

Network	R_n	R_r	R_ℓ	$-\frac{\ln R_n}{\ln R_n}$	$-\frac{\ln R_\ell}{\ln R_n}$	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> [50])	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



60 of 124

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Trutichide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



61 of 124

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Trutichide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



62 of 124

Let's never talk about this again:



"The fourth dimension of life: Fractal geometry and allometric scaling of organisms" [West, Brown, and Enquist, Science, 284, 1677-1679, 1999. \[54\]](#)

☞ No networks: Scaling argument for energy exchange area a .

☞ Distinguish between biological and physical length scales (distance between mitochondria versus cell radius).

☞ Buckingham π action. [9]

☞ Arrive at $a \propto M^{D/D+1}$ and $\ell \propto M^{1/D}$.

☞ New disaster: after going on about fractality of a , then state $v \propto a^\ell$ in general.



63 of 124

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Trutichide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



64 of 124

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Trutichide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



65 of 124

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: [37]

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

☞ Impedance is distributed evenly.

☞ Can still assume networks are fractal.



58 of 124

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Trutichide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



59 of 124

Attempts to look at actual networks:



"Testing foundations of biological scaling theory using automated measurements of vascular networks" [Newberry, Newberry, and Newberry, PLoS Comput Biol, 11, e1004455, 2015. \[38\]](#)



"Power, Sex, Suicide: Mitochondria and the Meaning of Life" [Newberry et al., PLoS Comput Biol, 11, e1004455, . \[7\]](#)



61 of 124

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Trutichide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



62 of 124

Connecting network structure to α

1. Ratios of network parameters:

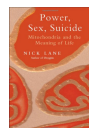
$$R_n = \frac{n_{k+1}}{n_k}, R_\ell = \frac{\ell_{k+1}}{\ell_k}, R_r = \frac{r_{k+1}}{r_k}$$

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)

Some people understand it's truly a disaster:



"Power, Sex, Suicide: Mitochondria and the Meaning of Life" [by Nick Lane \(2005\). \[30\]](#)

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

Really, quite confused:

Whole 2004 issue of Functional Ecology addresses the problem:

☞ J. Kozłowski, M. Konrzewski. "Is West, Brown and Enquist's model of allometric scaling mathematically correct and biologically relevant?" Functional Ecology 18: 283-9, 2004. [28]

☞ J. H. Brown, G. B. West, and B. J. Enquist. "Yes, West, Brown and Enquist's model of allometric scaling is both mathematically correct and biologically relevant." Functional Ecology 19: 735-738, 2005. [7]

☞ J. Kozłowski, M. Konrzewski. "West, Brown and Enquist's model of allometric scaling again: the same questions remain." Functional Ecology 19: 739-743, 2005.



64 of 124

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Trutichide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



65 of 124



“Curvature in metabolic scaling”
Kolokotronis, Savage, Deeds, and Fontana.
Nature, **464**, 753, 2010. [27]

Let's try a quadratic:

$$\log_{10} P \sim \log_{10} c + \alpha_1 \log_{10} M + \alpha_2 \log_{10} M^2$$

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthticide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



66 of 124

Yah:

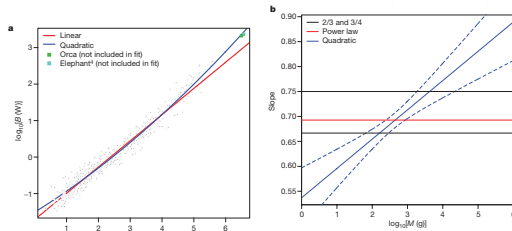


Figure 1 | Curvature in metabolic scaling. a. Linear (red) and quadratic (blue) fits (not including temperature) of $\log_{10}P$ versus $\log_{10}M$. The orca (green square) and Asian elephant (red square at larger mass) are not included in the fit, but are predicted well. Differences in the quality of fit are best seen in terms of the conditional mean of the error, estimated by the loess (locally-weighted scatterplot smoothing) fit of the residuals (Supplementary Information). See Table 1 for the values of the coefficients obtained from the fit. b. Slope of the quadratic fit (including temperature) with pointwise 90% confidence intervals (black). The slope of the power law fit (red) and models with fixed 2/3 and 3/4 exponents (black) are included for comparison. This panel suggests that exponents estimated by assuming a power law will be highly sensitive to the mass range of the data set used, as shown in Fig. 2.



67 of 124

“This raises the question of whether the theory can be adapted to agree with the data”¹

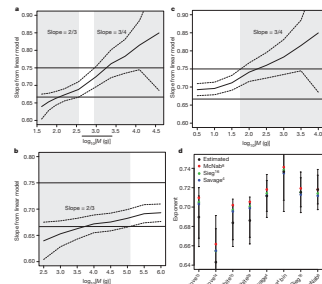
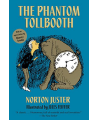


Figure 2 | Scaling exponent depends on mass range. a. Slope estimated by linear regression within a three log and mass range (smaller size than the boundaries). Values on the absolute discrete axes $\log_{10}M$ within the range. When the 90% confidence regions (dashed lines) include the 2/3 and 3/4 slopes, the local slope is consistent with a 2/3 or 3/4 exponent, respectively. These cases are indicated by the shaded regions (left and right) on the right. b. Slope estimated by using all data points with $M < c$. The shaded region is consistent with 2/3 slope estimate. c. Slope estimated by using all data points with $M > c$. The shaded region is consistent with 3/4 slope estimate. d. Exponents estimated for eight historical data sets using linear regression (think Bill Gates's Longevity, Leonardo's Whales, Wang's Ship, McNAM and Savage's using ocean average data (Cherage) and historical data (Cherage's fish)). Exponents predicted using coefficients from quadratic fits to McNAM's (red), Ship's (green), or Savage's (black) data and the first three elements of log-M (Supplementary Information). Thick lines represent uncorrected 90% confidence intervals. Thin lines are multiplicity corrected intervals.



68 of 124

Evolution has generally made things bigger¹



“The Phantom Tollbooth”
by Norton Juster (1961). [24]

- Regression starting at low M makes sense
- Regression starting at high M makes ...no sense

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthticide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



67 of 124

Still going:



“A general model for metabolic scaling in self-similar asymmetric networks”
Brummer, Brummer, and Enquist,
PLoS Comput Biol, **13**, e1005394, 2017. [8]

Wut?:

“Most importantly, we show that the 3/4 metabolic scaling exponent from Kleiber’s Law can still be attained within many asymmetric networks.”

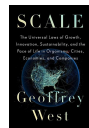
PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthticide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



68 of 124

Oh no:



“Scale: The Universal Laws of Growth, Innovation, Sustainability, and the Pace of Life in Organisms, Cities, Economies, and Companies”
by Geoffrey B. West (2017). [52]

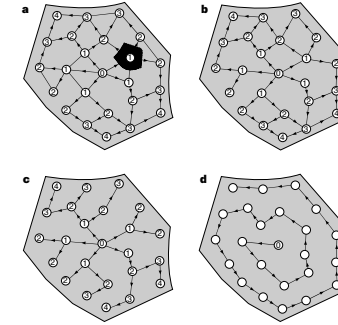
Amazon reviews excerpts (so, so not fair but ...):

- “Full of intriguing, big ideas but amazingly sloppy both in details and exposition, especially considering the author is a theoretical physicist.”
- “The beginning is terrible. He shows four graphs to illustrate scaling relationships, none of which have intelligible scales”
- “(he actually repeats several times that businesses can die but are not really an animal - O RLY?)”



68 of 124

Simple supply networks:



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



69 of 124

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthticide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



70 of 124

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

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthticide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



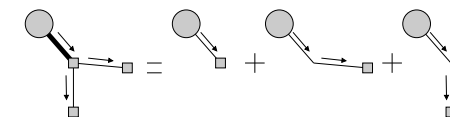
71 of 124

Geometric argument



“Optimal Form of Branching Supply and Collection Networks”
Peter Sheridan Dodds,
Phys. Rev. Lett., **104**, 048702, 2010. [12]

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



PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthticide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



72 of 124

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthticide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



73 of 124

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthticide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



75 of 124

¹Already raised and fully established 9 years earlier. [14]

Geometric argument

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Trutichide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References

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

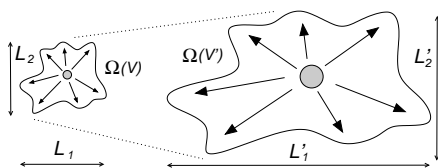
76 of 124

Geometric argument

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Trutichide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References

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

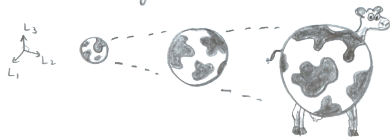
77 of 124

Spherical cows and pancake cows:

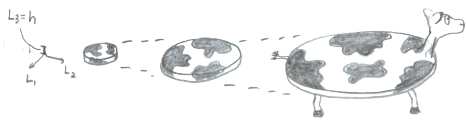
PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Trutichide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References

Assume an isometrically scaling family of cows:



Extremes of allometry:
The pancake cows—



78 of 124

Spherical cows and pancake cows:

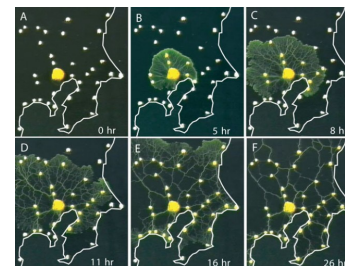
- Question:** How does the surface area S_{cow} of our two types of cows scale with cow volume V_{cow} ? [Insert question from assignment 4](#)
- Question:** For general families of regions, how does surface area S scale with volume V ? [Insert question from assignment 4](#)

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Trutichide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



“Rules for Biologically Inspired Adaptive Network Design”
Tero et al.,
Science, **327**, 439-442, 2010. [49]



PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Trutichide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References

Urban deslime in action:

<https://www.youtube.com/watch?v=GwKuFREOgmo>

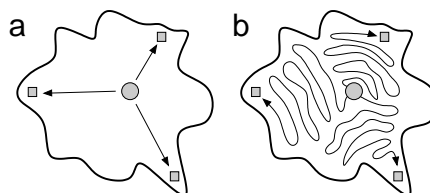
81 of 124

Geometric argument

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Trutichide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References

Best and worst configurations (Banavar et al.)

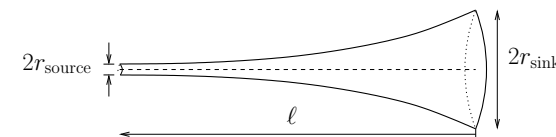


Rather obviously:
 $\min V_{\text{net}} \propto \sum \text{distances from source to sinks.}$

82 of 124

Minimal network volume:

We add one more element:



- Vessel cross-sectional area may vary with distance from the source.
- Flow rate increases as cross-sectional area decreases.
- e.g., a collection network may have vessels tapering as they approach the central sink.
- Find that vessel volume v must scale with vessel length l to affect overall system scalings.

84 of 124

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Trutichide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References

Minimal network volume:

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Trutichide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References

Real supply networks are close to optimal:

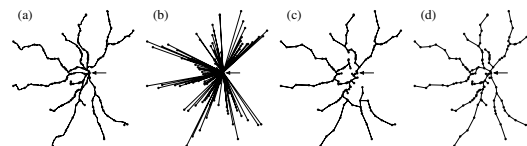


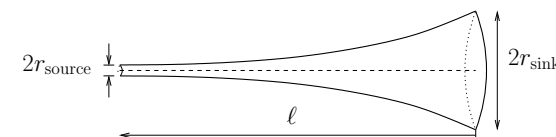
Figure 1. (a) Commuter rail network in the Boston area. The arrow marks the assumed root of the network. (b) Star graph. (c) Minimum spanning tree. (d) The model of equation (3) applied to the same set of stations.

Gastner and Newman (2006): “Shape and efficiency in spatial distribution networks” [16]

83 of 124

Minimal network volume:

Effecting scaling:



- Consider vessel radius $r \propto (l + 1)^{-\epsilon}$, tapering from $r = r_{\text{max}}$ where $\epsilon \geq 0$.
- Gives $v \propto l^{1-2\epsilon}$ if $\epsilon < 1/2$
- Gives $v \propto 1 - l^{-(2\epsilon-1)} \rightarrow 1$ for large l if $\epsilon > 1/2$
- Previously, we looked at $\epsilon = 0$ only.

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Trutichide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References

86 of 124

Minimal network volume:

For $0 \leq \epsilon < 1/2$, approximate network volume by integral over region:

$$\min V_{\text{net}} \propto \int_{\Omega_{d,D}(V)} \rho \|\vec{x}\|^{1-2\epsilon} d\vec{x}$$

Insert question from assignment 4 [↗](#)

$$\propto \rho V^{1+\gamma_{\max}(1-2\epsilon)} \text{ where } \gamma_{\max} = \max_i \gamma_i.$$

For $\epsilon > 1/2$, find simply that

$$\min V_{\text{net}} \propto \rho V$$

- So if supply lines can taper fast enough and without limit, minimum network volume can be made negligible.

For $0 \leq \epsilon < 1/2$:

$$\min V_{\text{net}} \propto \rho V^{1+\gamma_{\max}(1-2\epsilon)}$$

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

$$\min V_{\text{net/iso}} \propto \rho V^{1+(1-2\epsilon)/d}$$

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

$$\min V_{\text{net/allo}} \propto \rho V^{1+(1-2\epsilon)\gamma_{\text{allo}}}$$

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

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

For $\epsilon > 1/2$:

$$\min V_{\text{net}} \propto \rho V$$

- Network volume scaling is now independent of overall shape scaling.

Limits to scaling

- Can argue that ϵ must effectively be 0 for real networks over large enough scales.
- Limit to how fast material can move, and how small material packages can be.
- e.g., blood velocity and blood cell size.

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Trutichide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



87 of 124

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Trutichide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



88 of 124

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Trutichide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



89 of 124

This
is a
really
clean
slide

Blood networks

- Velocity at capillaries and aorta approximately constant across body size [51]: $\epsilon = 0$.
- Material costly** \Rightarrow expect lower optimal bound of $V_{\text{net}} \propto \rho V^{(d+1)/d}$ to be followed closely.
- For cardiovascular networks, $d = D = 3$.
- Blood volume scales linearly with body volume [47], $V_{\text{net}} \propto V$.
- Sink density must \therefore decrease as volume increases:

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

- Density of suppliable sinks **decreases** with organism size.

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

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

- Including other constraints may raise scaling exponent to a higher, less efficient value.

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Trutichide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



90 of 124

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Trutichide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



91 of 124

PoCS
@pocsvox
Optimal Supply
Networks II

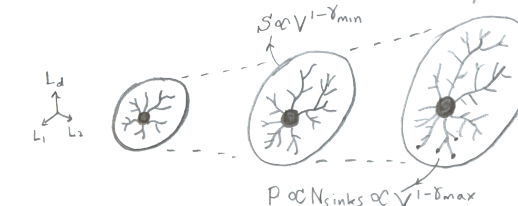
Metabolism and
Trutichide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



92 of 124

- Exciting bonus:** Scaling obtained by the supply network story and the surface-area law **only match** for isometrically growing shapes. Insert question from assignment 4 [↗](#)

The surface area-supply network mismatch for allometrically growing shapes:



90 of 124

Recall:

- 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 $\alpha \approx 0.686 \pm 0.014$

Prefactor:

Stefan-Boltzmann law: [↗](#)

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

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 :

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

- Measured for $M \leq 10$ kg:

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

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Trutichide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



93 of 124

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Trutichide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



95 of 124

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Trutichide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
References



96 of 124

River networks

- View river networks as collection networks.
- Many sources and one sink.
- ϵ ?
- Assume ρ is constant over time and $\epsilon = 0$:

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

- Network volume grows faster than basin 'volume' (really area).
- It's all okay:** Landscapes are $d=2$ surfaces living in $D=3$ dimensions.
- Streams can grow not just in width but in depth ...
- If $\epsilon > 0$, V_{net} will grow more slowly but $3/2$ appears to be confirmed from real data.

PoCS
@pocsvox
Optimal Supply Networks II

Metabolism and Truthicide
Death by fractions
Measuring exponents
River networks
Earlier theories
Geometric argument
Conclusion
References



97 of 124

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:

$$\ell \sim a^h$$

- Can argue

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

where h is Hack's exponent.

- ∴ minimal volume calculations gives

$$h = 1/2$$

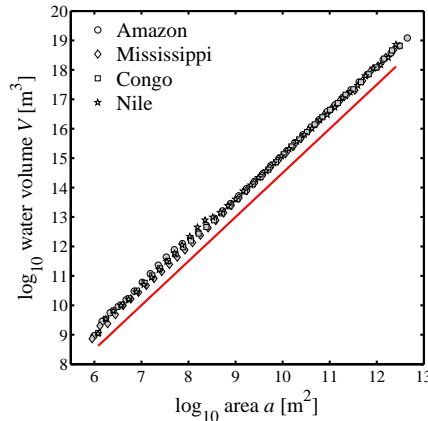
PoCS
@pocsvox
Optimal Supply Networks II

Metabolism and Truthicide
Death by fractions
Measuring exponents
River networks
Earlier theories
Geometric argument
Conclusion
References



98 of 124

Even better—prefactors match up:



PoCS
@pocsvox
Optimal Supply Networks II

Metabolism and Truthicide
Death by fractions
Measuring exponents
River networks
Earlier theories
Geometric argument
Conclusion
References



100 of 124

The Cabal strikes back:

- Banavar et al., 2010, PNAS: "A general basis for quarter-power scaling in animals." [2]
- "It has been known for decades that the metabolic rate of animals scales with body mass with an exponent that is almost always < 1 , $> 2/3$, and often very close to $3/4$."
- Cough, cough, cough, hack, wheeze, cough.

PoCS
@pocsvox
Optimal Supply Networks II

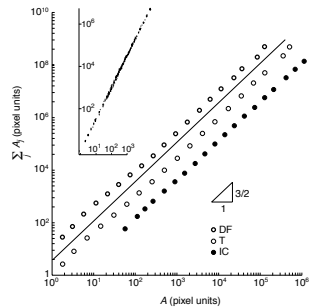
Metabolism and Truthicide
Death by fractions
Measuring exponents
River networks
Earlier theories
Geometric argument
Conclusion
References



101 of 124

Real data:

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



From Banavar et al. (1999) [1]

PoCS
@pocsvox
Optimal Supply Networks II

Metabolism and Truthicide
Death by fractions
Measuring exponents
River networks
Earlier theories
Geometric argument
Conclusion
References



99 of 124

Stories—Darth Quarter:



PoCS
@pocsvox
Optimal Supply Networks II

Metabolism and Truthicide
Death by fractions
Measuring exponents
River networks
Earlier theories
Geometric argument
Conclusion
References



102 of 124

Some people understand it's truly a disaster: [8]

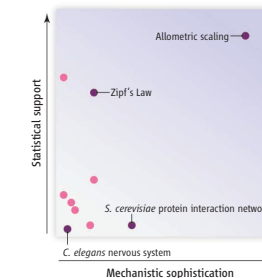
The unnecessary bafflement continues:

"Testing the metabolic theory of ecology" [40]

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

Artisanal, handcrafted silliness:

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



How good is your power law? The chart reflects the level of statistical support—as measured in (16, 21)—and our opinion about the mechanistic sophistication underlying hypothetical generative models for various reported power laws. Some relationships are identified by name; the others reflect the general characteristics of a wide range of reported power laws. Allometric scaling stands out from the other power laws reported for complex systems.

- Call generalization of Central Limit Theorem, stable distributions. Also: PLIPL0 action.
- Summary: Wow.

PoCS
@pocsvox
Optimal Supply Networks II

Metabolism and Truthicide
Death by fractions
Measuring exponents
River networks
Earlier theories
Geometric argument
Conclusion
References



103 of 124

PoCS
@pocsvox
Optimal Supply Networks II

Metabolism and Truthicide
Death by fractions
Measuring exponents
River networks
Earlier theories
Geometric argument
Conclusion
References



104 of 124

PoCS
@pocsvox
Optimal Supply Networks II

Metabolism and Truthicide
Death by fractions
Measuring exponents
River networks
Earlier theories
Geometric argument
Conclusion
References



105 of 124

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.
- 2/3-scaling lives on, largely in hiding.
- 3/4-scaling? Jury ruled a mistrial.
- The truth will out. Maybe.

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthticide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



106 of 124

References I

- J. R. Banavar, A. Maritan, and A. Rinaldo. Size and form in efficient transportation networks. [Nature](#), 399:130–132, 1999. [pdf](#)
- J. R. Banavar, M. E. Moses, J. H. Brown, J. Damuth, A. Rinaldo, R. M. Sibly, and A. Maritan. A general basis for quarter-power scaling in animals. [Proc. Natl. Acad. Sci.](#), 107:15816–15820, 2010. [pdf](#)
- P. Bennett and P. Harvey. Active and resting metabolism in birds—allometry, phylogeny and ecology. [J. Zool.](#), 213:327–363, 1987. [pdf](#)

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthticide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



107 of 124

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. [pdf](#)
- S. Brody. [Bioenergetics and Growth.](#) Reinhold, New York, 1945. reprint, . [pdf](#)

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthticide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



108 of 124

References III

- J. H. Brown, G. B. West, and B. J. Enquist. Yes, West, Brown and Enquist’s model of allometric scaling mathematically correct and biologically relevant? [Functional Ecology](#), 19:735–738, 2005. [pdf](#)
- A. B. Brummer, S. V. M., and B. J. Enquist. A general model for metabolic scaling in self-similar asymmetric networks. [PLoS Comput Biol](#), 13, 2017. [pdf](#)
- E. Buckingham. On physically similar systems: Illustrations of the use of dimensional equations. [Phys. Rev.](#), 4:345–376, 1914. [pdf](#)

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthticide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



109 of 124

References IV

- A. Clauset, C. R. Shalizi, and M. E. J. Newman. Power-law distributions in empirical data. [SIAM Review](#), 51:661–703, 2009. [pdf](#)
- M. H. DeGroot. [Probability and Statistics.](#) Addison-Wesley, Reading, Massachusetts, 1975.
- P. S. Dodds. Optimal form of branching supply and collection networks. [Phys. Rev. Lett.](#), 104(4):048702, 2010. [pdf](#)
- P. S. Dodds and D. H. Rothman. Scaling, universality, and geomorphology. [Annu. Rev. Earth Planet. Sci.](#), 28:571–610, 2000. [pdf](#)

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthticide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



110 of 124

References V

- P. S. Dodds, D. H. Rothman, and J. S. Weitz. Re-examination of the “3/4-law” of metabolism. [Journal of Theoretical Biology](#), 209:9–27, 2001. [pdf](#)
- A. E. Economos. Elastic and/or geometric similarity in mammalian design. [Journal of Theoretical Biology](#), 103:167–172, 1983. [pdf](#)
- M. T. Gastner and M. E. J. Newman. Shape and efficiency in spatial distribution networks. [J. Stat. Mech.: Theor. & Exp.](#), 1:P01015, 2006. [pdf](#)

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthticide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



111 of 124

References VI

- D. S. Glazier. Beyond the ‘3/4-power law’: variation in the intra- and interspecific scaling of metabolic rate in animals. [Biol. Rev.](#), 80:611–662, 2005. [pdf](#)
- D. S. Glazier. The 3/4-power law is not universal: Evolution of isometric, ontogenetic metabolic scaling in pelagic animals. [BioScience](#), 56:325–332, 2006. [pdf](#)
- J. T. Hack. Studies of longitudinal stream profiles in Virginia and Maryland. [United States Geological Survey Professional Paper](#), 294-B:45–97, 1957. [pdf](#)

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthticide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



112 of 124

References VII

- A. Hemmingsen. The relation of standard (basal) energy metabolism to total fresh weight of living organisms. [Rep. Steno Mem. Hosp.](#), 4:1–58, 1950. [pdf](#)
- A. Hemmingsen. Energy metabolism as related to body size and respiratory surfaces, and its evolution. [Rep. Steno Mem. Hosp.](#), 9:1–110, 1960. [pdf](#)
- A. A. Heusner. Size and power in mammals. [Journal of Experimental Biology](#), 160:25–54, 1991. [pdf](#)

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthticide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



113 of 124

References VIII

- M. R. Hirt, W. Jetz, B. C. Rall, and U. Brose. A general scaling law reveals why the largest animals are not the fastest. [Nature Ecology & Evolution](#), 1:1116, 2017. [pdf](#)
- N. Juster. [The Phantom Tollbooth.](#) Random House, 1961.
- M. Kleiber. Body size and metabolism. [Hilgardia](#), 6:315–353, 1932. [pdf](#)
- M. Kleiber. [The Fire of Life. An Introduction to Animal Energetics.](#) Wiley, New York, 1961.

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthticide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



114 of 124

References IX

- [27] T. Kolokotronis, V. Savage, E. J. Deeds, and W. Fontana.
Curvature in metabolic scaling.
Nature, 464:753, 2010. [pdf](#)
- [28] J. Kozłowski and M. Konarzewski.
Is West, Brown and Enquist's model of allometric scaling mathematically correct and biologically relevant?
Functional Ecology, 18:283–289, 2004. [pdf](#)
- [29] P. La Barbera and R. Rosso.
On the fractal dimension of stream networks.
Water Resources Research, 25(4):735–741, 1989. [pdf](#)

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Trutichide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
[References](#)



115 of 124

References X

- [30] N. Lane.
Power, Sex, Suicide: Mitochondria and the Meaning of Life.
Oxford University Press, Oxford, UK, 2005.
- [31] L. B. Leopold.
A View of the River.
Harvard University Press, Cambridge, MA, 1994.
- [32] T. McMahon.
Size and shape in biology.
Science, 179:1201–1204, 1973. [pdf](#)
- [33] T. A. McMahon.
Allometry and biomechanics: Limb bones in adult ungulates.
The American Naturalist, 109:547–563, 1975. [pdf](#)

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Trutichide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
[References](#)



116 of 124

References XI

- [34] T. A. McMahon and J. T. Bonner.
On Size and Life.
Scientific American Library, New York, 1983.
- [35] N. Meyer-Vernet and J.-P. Rospars.
How fast do living organisms move: Maximum speeds from bacteria to elephants and whales.
American Journal of Physics, pages 719–722, 2015. [pdf](#)
- [36] D. R. Montgomery and W. E. Dietrich.
Channel initiation and the problem of landscape scale.
Science, 255:826–30, 1992. [pdf](#)

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Trutichide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
[References](#)



117 of 124

References XII

- [37] C. D. Murray.
A relationship between circumference and weight in trees and its bearing on branching angles.
J. Gen. Physiol., 10:725–729, 1927. [pdf](#)
- [38] M. G. Newberry, E. D. B., and S. V. M.
Testing foundations of biological scaling theory using automated measurements of vascular networks.
PLoS Comput Biol, 11:e1004455, 2015. [pdf](#)
- [39] W. H. Press, S. A. Teukolsky, W. T. Vetterling, and B. P. Flannery.
Numerical Recipes in C.
Cambridge University Press, second edition, 1992.

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Trutichide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
[References](#)



118 of 124

References XIII

- [40] C. Price, J. S. Weitz, V. Savage, S. Stegen, A. Clarke, D. Coomes, P. S. Dodds, R. Etienne, A. Kerkhoff, K. McCulloh, K. Niklas, H. Olff, and N. Swenson.
Testing the metabolic theory of ecology.
Ecology Letters, 15:1465–1474, 2012. [pdf](#)
- [41] J. M. V. Rayner.
Linear relations in biomechanics: the statistics of scaling functions.
J. Zool. Lond. (A), 206:415–439, 1985. [pdf](#)
- [42] M. Rubner.
Ueber den einfluss der körpergrösse auf stoffund kraftwechsel.
Z. Biol., 19:535–562, 1883. [pdf](#)

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Trutichide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
[References](#)



119 of 124

References XIV

- [43] P. A. Samuelson.
A note on alternative regressions.
Econometrica, 10:80–83, 1942. [pdf](#)
- [44] Sarrus and Rameaux.
Rapport sur une mémoire adressé à l'Académie de Médecine.
Bull. Acad. R. Méd. (Paris), 3:1094–1100, 1838–39.
- [45] V. M. Savage, E. J. Deeds, and W. Fontana.
Sizing up allometric scaling theory.
PLoS Computational Biology, 4:e1000171, 2008. [pdf](#)

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Trutichide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
[References](#)



120 of 124

References XV

- [46] J. Speakman.
On Blum's four-dimensional geometric explanation for the 0.75 exponent in metabolic allometry.
J. Theor. Biol., 144(1):139–141, 1990. [pdf](#)
- [47] W. R. Stahl.
Scaling of respiratory variables in mammals.
Journal of Applied Physiology, 22:453–460, 1967.
- [48] M. P. H. Stumpf and M. A. Porter.
Critical truths about power laws.
Science, 335:665–666, 2012. [pdf](#)

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Trutichide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
[References](#)



121 of 124

References XVI

- [49] A. Tero, S. Takagi, T. Saigusa, K. Ito, D. P. Bebbler, M. D. Fricker, K. Yumiki, R. Kobayashi, and T. Nakagaki.
Rules for biologically inspired adaptive network design.
Science, 327(5964):439–442, 2010. [pdf](#)
- [50] D. L. Turcotte, J. D. Pelletier, and W. I. Newman.
Networks with side branching in biology.
Journal of Theoretical Biology, 193:577–592, 1998. [pdf](#)
- [51] P. D. Weinberg and C. R. Ethier.
Twenty-fold difference in hemodynamic wall shear stress between murine and human aortas.
Journal of Biomechanics, 40(7):1594–1598, 2007. [pdf](#)

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Trutichide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
[References](#)



122 of 124

References XVII

- [52] G. B. West.
Scale: The Universal Laws of Growth, Innovation, Sustainability, and the Pace of Life in Organisms, Cities, Economies, and Companies.
Penguin Press, New York, 2017.
- [53] 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](#)
- [54] G. B. West, J. H. Brown, and J. Enquist.
The fourth dimension of life: Fractal geometry and allometric scaling of organisms.
Science, 284:1677–1679, 1999. [pdf](#)



PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Trutichide
Death by
fractions
Measuring
exponents
River networks
Earlier theories
Geometric
argument
Conclusion
[References](#)



123 of 124

References XVIII

- [55] G. B. West, J. H. Brown, and J. Enquist.
Nature.
[Nature](#), 400:664–667, 1999. [pdf](#) 
- [56] C. R. White and R. S. Seymour.
Allometric scaling of mammalian metabolism.
[J. Exp. Biol.](#), 208:1611–1619, 2005. [pdf](#) 

PoCS
@pocsvox
Optimal Supply
Networks II

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References

