

Optimal Supply Networks II: Blood, Water, and Truthicide

Last updated: 2019/02/07, 17:04:52

Complex Networks | @networksvox
CSYS/MATH 303, Spring, 2019

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Optimal Supply
Networks II

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Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



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Networks II

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Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References

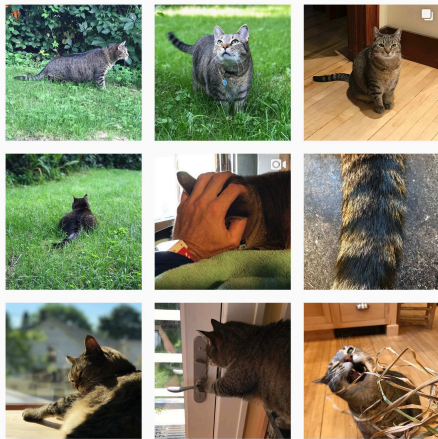


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Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks



Earlier theories

Geometric
argument

Conclusion

References



 On Instagram at [pratchett_the_cat](https://www.instagram.com/pratchett_the_cat) 



Outline

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Optimal Supply
Networks II

Metabolism and Truthicide

Metabolism and
Truthicide

Death by fractions

Death by
fractions

Measuring exponents

Measuring
exponents

River networks

River networks

Earlier theories

Earlier theories

Geometric argument

Geometric
argument

Conclusion

Conclusion

References

References



Stories—The Fraction Assassin:

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Optimal Supply
Networks II



Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



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."

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



Fundamental biological and ecological constraint:

$$P = c M^\alpha$$

P = basal metabolic rate

M = organismal body mass



Metabolism and
Truhticide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



$$P = c M^\alpha$$

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

Birds	39–41 °C
Eutherian Mammals	36–38 °C
Marsupials	34–36 °C
Monotremes	30–31 °C



Metabolism and
Trithicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



What one might expect:

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

- Dimensional analysis suggests an energy balance surface law:

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

- 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:

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



The prevailing belief of the Church of Quarterology:

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Networks II

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References

$$\alpha = 3/4$$

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

Huh?





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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.

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Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References








Related putative scalings:

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

Metabolism and
Truithicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



The great 'law' of heartbeats:

Assuming:

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

Then:

- Average number of heart beats in a lifespan
 \approx (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

Metabolism and
Truithicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories


Geometric
argument

Conclusion

References



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]

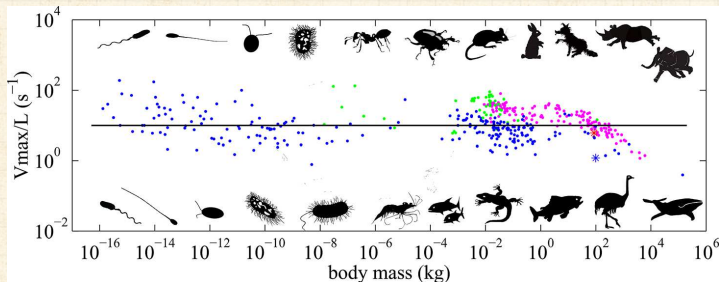


Fig. 1. Maximum relative speed versus body mass for 202 running species (157 mammals plotted in magenta and 45 non-mammals plotted in green), 127 swimming species and 91 micro-organisms (plotted in blue). The sources of the data are given in Ref. 16. The solid line is the maximum relative speed [Eq. (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).





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

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

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Networks II

Metabolism and
Truicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References

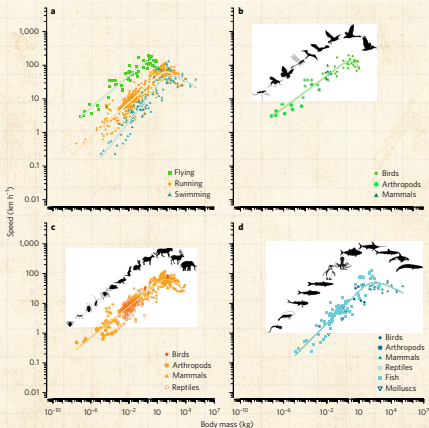


Figure 2 | Empirical data and time-dependent model fit for the allometric scaling of maximum speed. a. Comparison of scaling for the different locomotion modes (flying, running, swimming). **b-d.** Taxonomic differences are illustrated separately for flying (**b**; $n=55$), running (**c**; $n=458$) and swimming (**d**; $n=109$) 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).





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

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

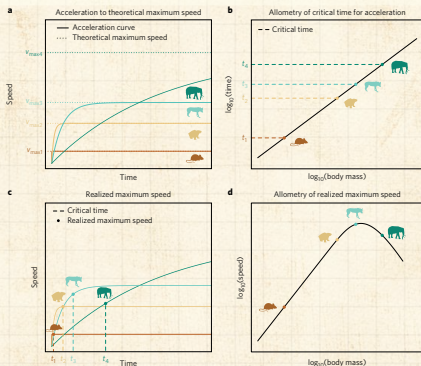


Figure 1 | Concept of time-dependent and mass-dependent realized maximum speed of animals. **a.** Acceleration of animals follows a saturation curve (solid lines) approaching the theoretical maximum speed (dotted lines) depending on body mass (colour code). **b.** The time available for acceleration increases with body mass following a power law. **c.** This critical time determines the realized maximum speed (**c**), yielding a hump-shaped increase of maximum speed with body mass (**d**).



Theoretical story:

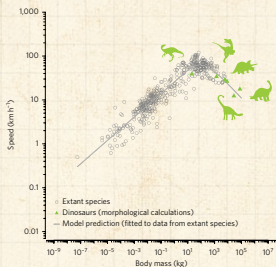


Figure 4 | Predicting the maximum speed of extinct species with the time-dependent model. The model prediction (grey line) is fitted to data of extant species (grey circles) and extended to higher body masses. Speed data for dinosaurs (green triangles) come from detailed morphological model calculations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

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: $0.76 \lesssim g \lesssim 1.27$

$$v_{\max} = aM^b (1 - e^{-hM^i})$$

$$i = d - 1 + g \text{ and } h = cf$$

Literature search for for maximum speeds of running, flying and swimming animals.

Search terms: "maximum speed", "escape speed" and "sprint speed".



A theory is born:

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



Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



A theory grows:

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



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Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



Theory meets a different 'truth':

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



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Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

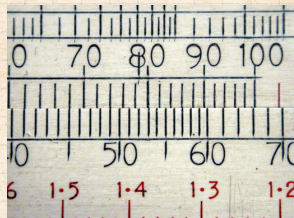
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Our hero faces a shadowy cabal:

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Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References

- 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]



When a cult becomes a religion:

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



Metabolism and
Truthicide

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]



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?

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion


References

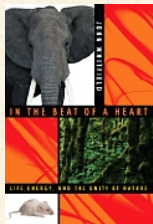


Modern Quarterology, Post Truthicide


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 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 ...

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

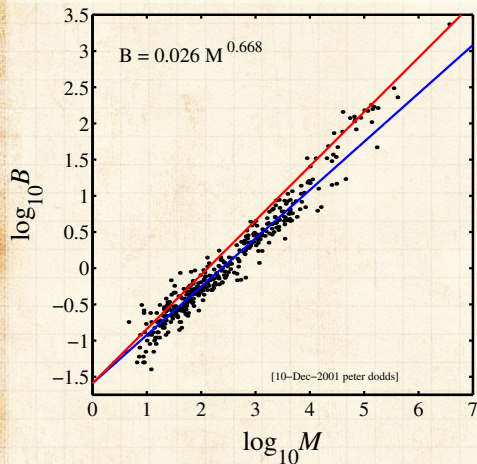
Geometric
argument

Conclusion

References



Some data on metabolic rates



source: huxley.oxfordjournals.org/doi/pdf/figure/2011.pdf



Heusner's
data
(1991) [22]



391
Mammals



blue line: 2/3



red line: 3/4.



($B = P$)

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Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

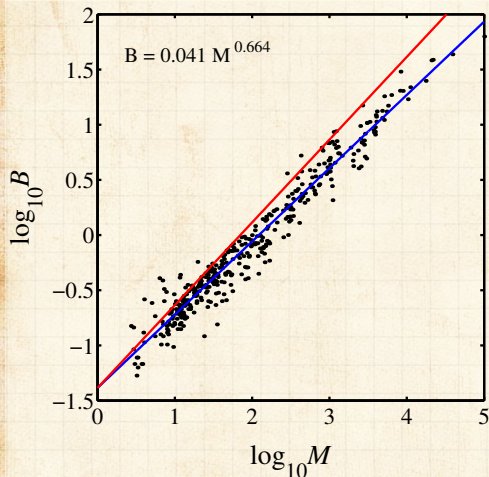
Geometric
argument


Conclusion


References





Some data on metabolic rates




 Bennett and Harvey's data (1987) [3]

 398 birds

 blue line: 2/3

 red line: 3/4.

 ($B = P$)

Metabolism and Truthicide

Death by fractions

Measuring exponents

River networks


Earlier theories

Geometric argument

Conclusion

References



 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.

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



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More on regression:

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

or (b) no variable can be considered independent,

then we need to use

Standardized Major Axis Linear Regression. [43, 41]

(aka Reduced Major Axis = RMA.)

Metabolism and
Truhticide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



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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 ↗, ^[43] but discovered independently by others.
- #somuchwin

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



Measuring exponents

Relationship to ordinary least squares regression is simple:

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

where r = standard correlation coefficient:

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



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. [41, 29]

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



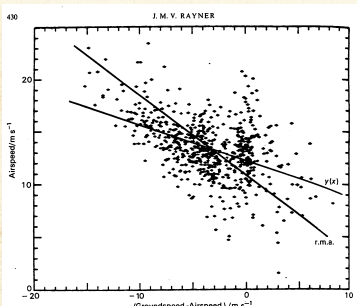


FIG. 4. Observed correlation of calculated windspeed and airspeed in gliding Black-browed albatrosses showing regression and r.m.a. lines. Figure altered from Pennycuik (1982), figure 9.

LINEAR RELATIONS IN BIOMECHANICS

TABLE II

Calculated statistics of airspeed V_a and windspeed V_w in the Black-browed albatross *Diomedea melanophris* in gliding flight, after Pennycuik (1982)

number of data n	737		
means \bar{x}, \bar{y}	-3.14	13.35	ms^{-1}
variances S_{xx}, S_{yy}	13.91	8.218	$(\text{ms}^{-1})^2$
covariance S_{xy}	-4.653		
correlation ρ	-0.435		

model of speed correction: $V_a = \alpha + \beta V_w$

model	intercept α	gradient β	range (95%)
$y(x)$ regression	12.30	-0.334	-0.384 to -0.284
r.m.a.	10.93	-0.769	-0.894 to -0.661
$x(y)$ regression	7.80	-1.766	-2.076 to -1.536
s.r. $b_x = 0.5$	10.66	-0.855	-0.997 to -0.737
$b_x = 1$ or m.a.	11.59	-0.560	-0.648 to -0.479
$b_x = 2$	12.00	-0.431	-0.496 to -0.367

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^[29] (who resigned ...)

Heusner's data, 1991 (391 Mammals)

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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

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



Bennett and Harvey, 1987 (398 birds)

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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

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

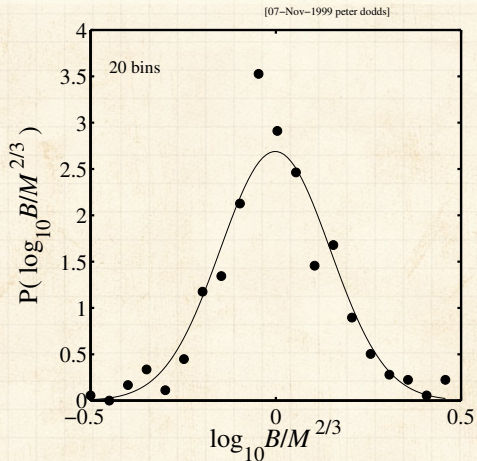
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Fluctuations—Things look normal ...

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

 Use a Kolmogorov-Smirnov test.

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Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



Hypothesis testing

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

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

- Assume each \mathbf{B}_i (now a random variable) is normally distributed about $\alpha' \log_{10} M_i + \log_{10} c$.
- Follows that the measured α for one realization obeys a t distribution with $N - 2$ degrees of freedom.
- Calculate a p -value: probability that the measured α is as least as different to our hypothesized α' as we observe.
- See, for example, DeGroot and Scherish, "Probability and Statistics."^[11]

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



Revisiting the past—mammals

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Networks II

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	$< 10^{-15}$

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



Revisiting the past—mammals

$M \leq 10$ kg:

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

$M \geq 10$ kg:

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

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



Analysis of residuals

1. Presume an exponent of your choice: 2/3 or 3/4.
2. Fit the prefactor ($\log_{10} c$) and then examine the residuals:

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

3. H_0 : residuals are uncorrelated
 H_1 : residuals are correlated.
4. Measure the correlations in the residuals and compute a p -value.

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



Analysis of residuals

We use the spiffing Spearman Rank-Order Correlation Coefficient ↗

Basic idea:

Given $\{(x_i, y_i)\}$, rank the $\{x_i\}$ and $\{y_i\}$ separately from smallest to largest. Call these ranks R_i and S_i .

Now calculate correlation coefficient for ranks, r_s :

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

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

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument







Conclusion

References



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]

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

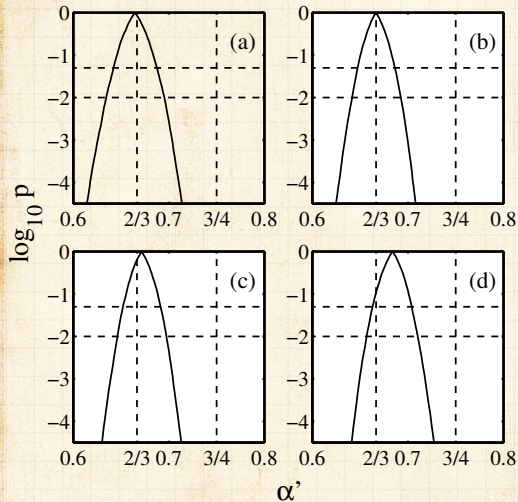
Geometric
argument

Conclusion

References



Analysis of residuals—mammals



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

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

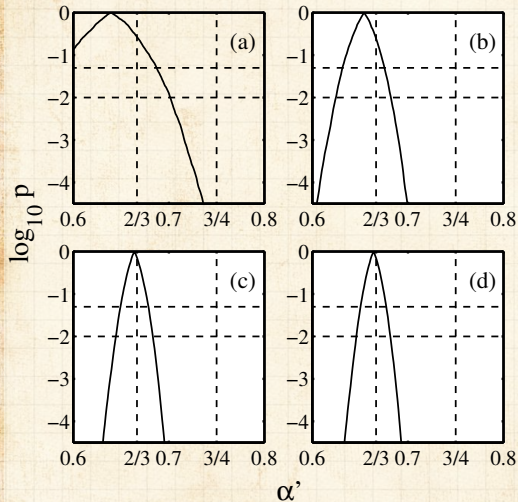
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Analysis of residuals—birds

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Networks II



(a) $M < 0.1$ kg,

(b) $M < 1$ kg,

(c) $M < 10$ kg,

(d) all birds.

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories






Geometric
argument

Conclusion

References



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.

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References







Impure scaling?:

- So: The exponent $\alpha = 2/3$ works for all birds and mammals up to 10–30 kg
- For mammals $> 10\text{--}30$ kg, maybe we have a new scaling regime
- 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.



The widening gyre:

Now we're really confused (empirically):

-  White and Seymour, 2005: unhappy with large herbivore measurements ^[56]. Pro 2/3: Find $\alpha \simeq 0.686 \pm 0.014$.
-  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.

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

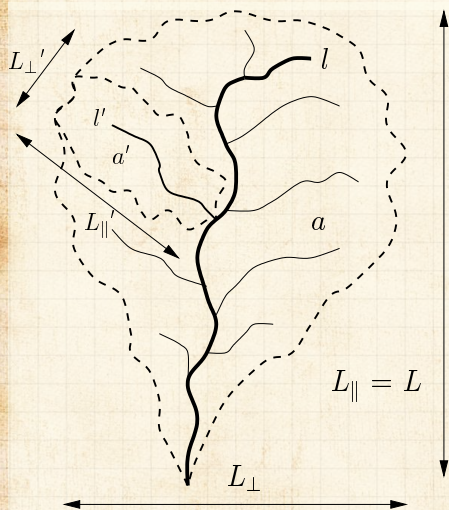
Geometric
argument


Conclusion


References




Somehow, optimal river networks are connected:



 a = drainage basin area

 l = length of longest (main) stream

 $L = L_{\parallel} =$
longitudinal length of basin

Metabolism and Truthicide

Death by fractions

Measuring exponents

River networks

Earlier theories

Geometric argument

Conclusion

References



Mysterious allometric scaling in river networks

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

$$l \sim a^h$$

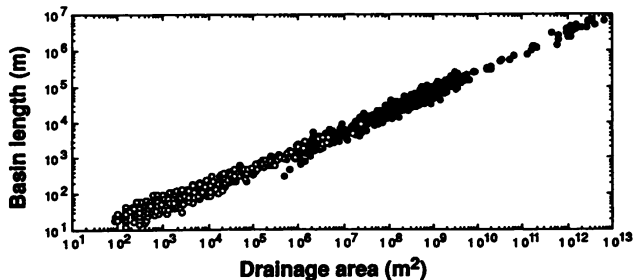
$$h \sim 0.6$$


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




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.**

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Optimal Supply
Networks II

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

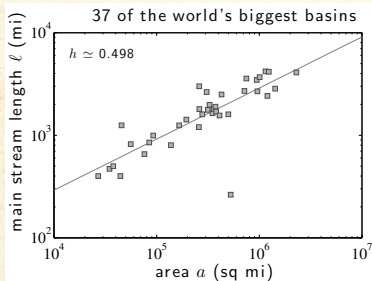
References



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Networks II



Metabolism and
Truthicide

Death by
fractions

Measuring
exponents


River networks


Earlier theories

Geometric
argument

Conclusion

References

 Data from Leopold (1994) [31, 13]

 Estimate of Hack exponent: $h = 0.50 \pm 0.06$



Earlier theories (1973-):

Building on the surface area idea:

- 🧱 McMahan (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.

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References





"Size and shape in biology" ↗

T. McMahon,

Science, **179**, 1201-1204, 1973. [32]

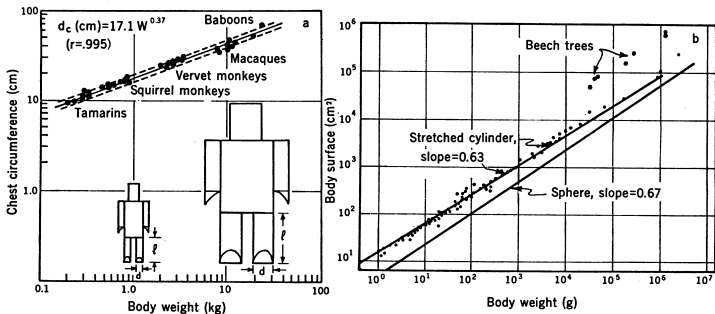


Fig. 3. (a) Chest circumference, d_c , plotted against body weight, W , for five species of primates. The broken lines represent the standard error in this least-squares fit [adapted from (21)]. The model proposed here, whereby each length, l , increases as the $2/3$ power of diameter, d , is illustrated 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 (8)].

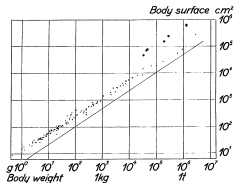


Fig. 10.

The relation of body surface to body weight in vertebrates. The points surrounded by a circle represent beech trees. The authorities of the data are in approximate order of body sizes of organisms: Fishes (7) *Uca*, *Esox*, *Salmo*, *Pleuronectes flexus*, *Aspinella*, *Crenilabrus*, *Lepomis* (5.4 g—2 kg), *Sea haddock* (unpublished), Frogs (3.5—32 g), Birds (3—18 g), *Fer*, 1914, p. 191. *Mus musculus* (23 and 50 g), *Kramer*, 1904, p. 404. Lizards (*Lacerta nurella* and *otelloi*, *Aspasia fragilis*: 5—24 g) and Ringed Snake (33—100 g), *Beale*, 1911, pp. 7-8. Turtles (7) *Testudo*: 211 g), frog (44 g), rabbit (3.5 kg), *Votr*, 1930, pp. 239, 244, 245. Dogs (7 and 30 kg), pigs (3 and 100 kg), horses (175 and 900 kg), monkeys (2.5 and 5.5 kg), mice (5 and 60 kg), *Shover*, *Cooper* and *Martynovs*, 1926, pp. 8, 30, 33 and 51. Snake (turtle-snake, small and large pythons, boa: 3.5—30 kg), *Reussner*, 1932, p. 145. Bats (20 and 250 g), cattle (20 and 600 kg), *Shover*, 1945, pp. 360, 361. Giant shark (2.75 t), rhinoceros (1 t), *Hassamowski*, 1910, pp. 30 and 63. Beech trees without leaves and roots (30 kg—12 t), *Melán*, *Stomsov* and *Melán*, 1954, tables 2—4 on pp. 227—231.

assuming a specific gravity of 1.0. Naturally, the inclination of this line corresponds to a proportionality power of 0.67.

Of the unicellular organisms represented in fig. 1 not a few are spherical in shape (the bacterium *Sarcocolla*, *Sarcocolla*, marine eggs); and most of the others have surfaces exceeding those of spheres of equal volume by rarely more than what corresponds to 0.1 decade in the log. ordinate system (*Phalobacterium phalobacterium*: 12 %, i. e. 0.05 decade, *Escherichia coli*: 24 %, i. e. 0.13 decade, the ciliates *Colpistoma* and *Paramecium*): 18—22 %, i. e. about 0.08—0.09 decade; calculated on the basis of data of *PÖRTER*, 1924, table 7 on p. 108, and *HANSEN*, 1928, table 1). Similar figures probably hold for other ciliates. Only the flagellates represented (*Typhlozoosima*, *Asterion kühlii*) and certain amoebae are likely to deviate by higher figures. The surface values of the unicellular organisms represented in fig. 1 will, therefore, fall either on, or in most other cases less than 0.1 decade above, a line representing the relation between surface and volume of spheres.

It will be seen from fig. 10 that the points representing the body surfaces of the metazoic animals in question are grouped parallel to the sphere line; that is, also corresponding to a proportionality power of 0.67. An average line through the points would fall about 0.30 logarithmic decade above the sphere line, meaning that on the average the body surface is roughly 2 (anti-log. 0.30) times higher in the animals under study than in spheres of equal weight or volume. In organisms of extreme shapes as the python (10^{4.5} g) and the beech trees (especially marked in fig. 2) the surface is about 3 and 10 times, respectively, greater than in a sphere of equal weight and volume. These facts agree well with the values 3—11.5 for the constant *k* in the formula

$$\text{body surface in cm}^2 = k \cdot \text{body weight}^{0.67}$$

as tabulated by *REUSSNER* (1928, p. 175) for various birds and mammals weighing 5 g—14 kg; because this is about double the value of *k* for sphere surface (4.83). The value of *k* (13.05) found by *KALDAS* (1910) for *Ascaris* is 2.9 times 4.83, and this corresponds well with the above mentioned figure 3 for the much larger python of similar shape.



Hemmingsen's "fit" is for a 2/3 power, notes possible 10 kg transition. [?]




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."





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]

Metabolism and
Truicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

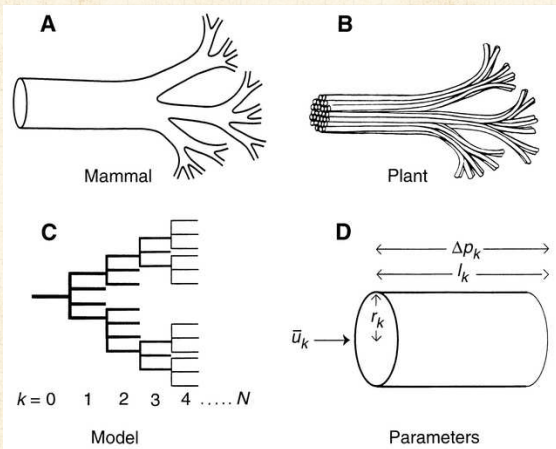
References



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.



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Optimal Supply
Networks II

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



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Optimal Supply
Networks II

West et al.'s assumptions:

1. hierarchical network
2. capillaries (delivery units) invariant
3. network impedance is minimized via evolution

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks


Earlier theories


Geometric
argument


Conclusion

References

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):

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

 Wheel out Lagrange multipliers ...

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

 Pulsatile calculation explodes into flames.

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



Not so fast ...

Actually, model shows:

- ✉ $P \propto M^{3/4}$ does not follow for pulsatile flow
- ✉ networks are not necessarily fractal.

Do find:

- ✉ Murray's cube law (1927) for outer branches: [37]

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

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

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



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)

Obliviously soldiering on, we could assert:

 area-preservingness:

$$R_r = R_n^{-1/2}$$

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

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

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



Data from real networks:

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

Metabolism and
TruthicideDeath by
fractionsMeasuring
exponents

River networks

Earlier theoriesGeometric
argument


Conclusion

References



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]



"—" 

Newberry et al.,
PLoS Comput Biol, **11**, e1004455, . [?]

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

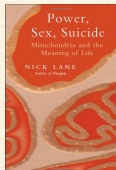
Geometric
argument

Conclusion

References



Some people understand it's truly a disaster:



“Power, Sex, Suicide: Mitochondria and the
Meaning of Life” [a](#) [↗](#)
by Nick Lane (2005). [30]

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

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument


Conclusion

References








Let's never talk about this again:



"The fourth dimension of life: Fractal geometry and allometric scaling of organisms" 

West, Brown, and Enquist,
Science Magazine, **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.

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



“It was the epoch of belief, it was the epoch of incredulity”



“A General Model for the Origin of Allometric Scaling Laws in Biology”
West, Brown, and Enquist,
Science, **276**, 122–126, 1997. [53]



“Nature”
West, Brown, and Enquist,
Nature, **400**, 664–667, 1999. [55]



“The fourth dimension of life: Fractal geometry and allometric scaling of organisms”
West, Brown, and Enquist,
Science Magazine, **284**, 1677–1679,
1999. [54]

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument


Conclusion


References




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.

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories


Geometric
argument

Conclusion

References





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

Let's try a quadratic:

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

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



Yah:

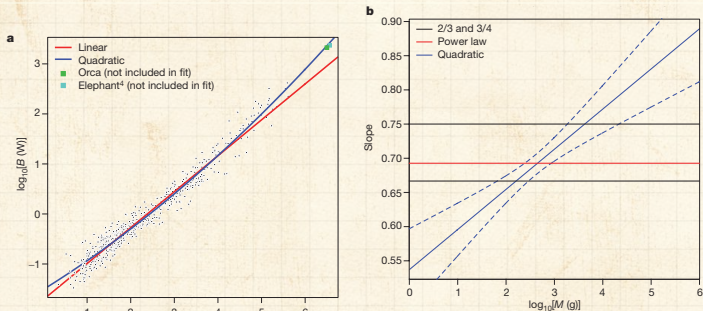


Figure 1 | Curvature in metabolic scaling. **a**, Linear (red) and quadratic (blue) fits (not including temperature) of $\log_{10}B$ versus $\log_{10}M$. The orca (green square) and Asian elephant (ref. 4; turquoise square at larger mass) are not included in the fit, but are predicted well. Differences 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 95% confidence intervals (blue). 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.

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



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

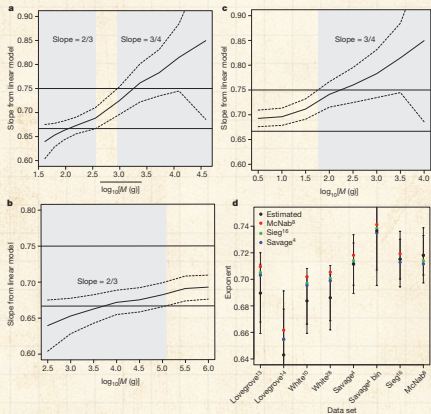


Figure 2 | Scaling exponent depends on mass range. **a**, Slope estimated by linear regression within a three log-unit mass range (smaller near the boundaries). Values on the abscissa denote mean $\log_{10}M$ within the range. When the 95% confidence regions (dashed lines) include the 2/3 or 3/4 lines, the local slope is consistent with a 2/3 or 3/4 exponent, respectively. These cases are indicated by the shaded regions (2/3 on the left and 3/4 on the right). **b**, Slope estimated by using all data points with $M < x$. The shaded region is consistent with 2/3 slope estimates. **c**, Slope estimated by using all data points with $M > x$. The shaded region is consistent with 3/4 slope

estimates. **d**, Exponents estimated for eight historical data sets using linear regression (black filled circles): Lovegrove¹³, Lovegrove¹⁴, White¹⁵, White¹⁶, Sieg¹⁸, McNab⁸, and Savage⁹ using species average data ("Savage") and binned data ("Savage" bin). Exponents predicted using coefficients from quadratic fits to McNab's (red), Sieg's (green), or Savage's (blue) data and the first three moments of $\log_{10}M$ (Supplementary Information). Thick lines represent uncorrected 95% confidence intervals. Thin lines are multiplicity corrected intervals.

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

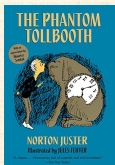
Conclusion

References





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

Evolution has generally made things bigger¹



“The Phantom Tollbooth” [a](#) [↗](#)
by Norton Juster (1961). ^[24]

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

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion


References



¹Yes, yes, yes: insular dwarfism [↗](#) with the shrinkage [↗](#)

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."

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

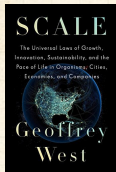
Geometric
argument



Conclusion

References






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?)”

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Optimal Supply
Networks II

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

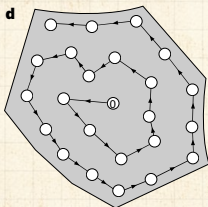
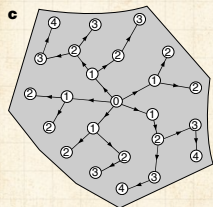
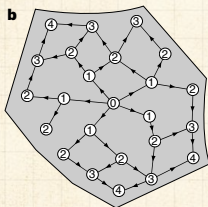
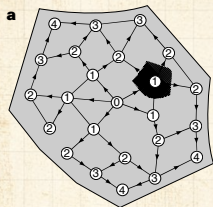
References



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Networks II



Banavar et al.,
Nature,
(1999) ^[1].



Flow rate
argument.



Ignore
impedance.



Very general
attempt to
find most
efficient
transportation
networks.

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories


Geometric
argument

Conclusion


References




Simple supply networks

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


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


 ...but also find

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

 $d = 3$:

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

 Consider a 3 g shrew with $V_{\text{blood}} = 0.1V_{\text{body}}$

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

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



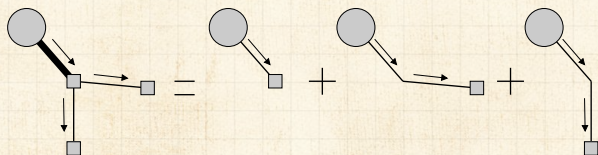
Geometric argument



“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:



Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



Geometric argument

COcoNuTS
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Optimal Supply
Networks II

Metabolism and
Truhticide

Death by
fractions

Measuring
exponents

River networks


Earlier theories


Geometric
argument

Conclusion

References




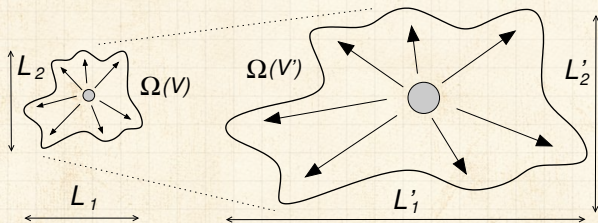
 **Q:** how does the number of sustainable sinks N_{sinks} scale with volume V for the most efficient network design?


 **Or:** what is the highest α for $N_{\text{sinks}} \propto V^\alpha$?




Geometric argument


 Allometrically growing regions:



 Have d length scales which scale as

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

 For **isometric** growth, $\gamma_i = 1/d$.

 For **allometric** growth, we must have at least two of the $\{\gamma_i\}$ being different

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References

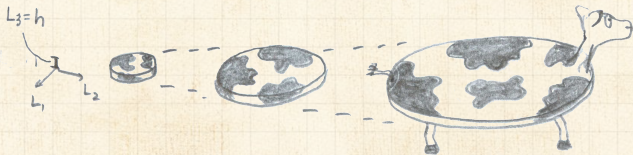


Spherical cows and pancake cows:

Assume an isometrically scaling family of cows:



Extremes of allometry:
The pancake cows—



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Optimal Supply
Networks II

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories



Geometric
argument



Conclusion

References



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 

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References

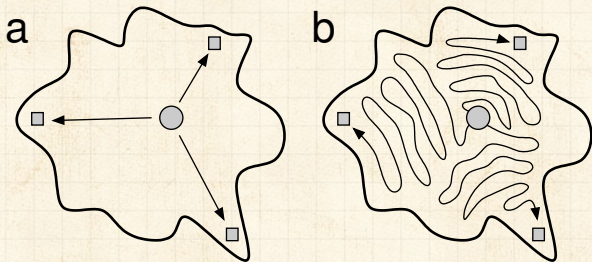



Geometric argument

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Networks II

Best and worst configurations (Banavar et al.)



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

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



Minimal network volume:

Real supply networks are close to optimal:

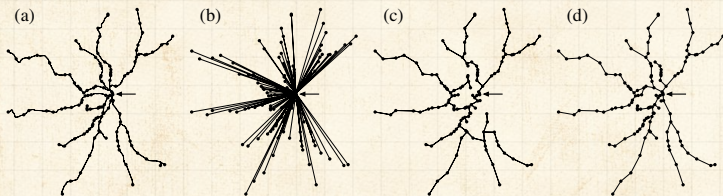


Figure 1. (a) Commuter rail network in the Boston area. The arrow marks the assumed root of the network. (b) Star graph. (c) Minimum spanning tree. (d) The model of equation (3) applied to the same set of stations.

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

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

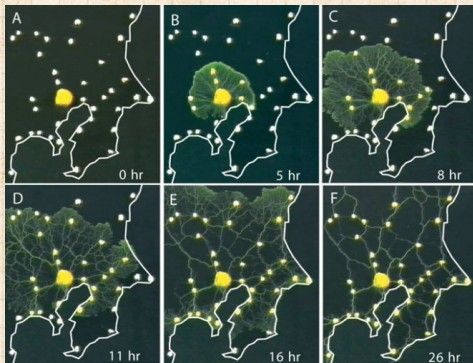
References





"Rules for Biologically Inspired Adaptive Network Design"

Tero et al.,
Science, **327**, 439-442, 2010. ^[49]



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Optimal Supply
Networks II

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories


Geometric
argument

Conclusion

References



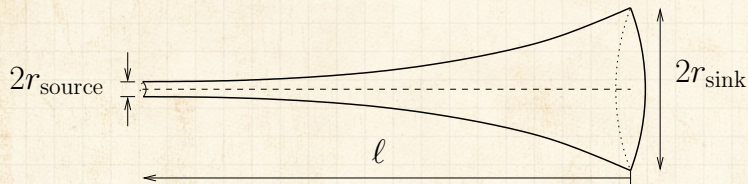
Urban deslime in action:





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



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.

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

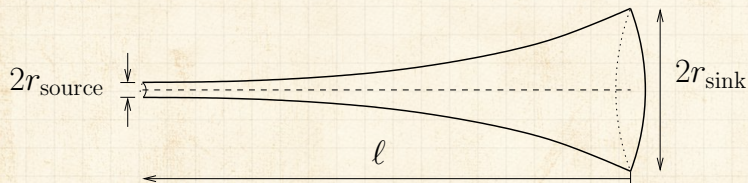
Conclusion

References



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.

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion


References



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:

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

Metabolism and
TruthicideDeath by
fractionsMeasuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



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.

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



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is a
really
clean
slide

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



- 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 supplyable sinks **decreases** with organism size.

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks


Earlier theories

Geometric
argument


Conclusion

References




 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.

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks


Earlier theories


Geometric
argument

Conclusion

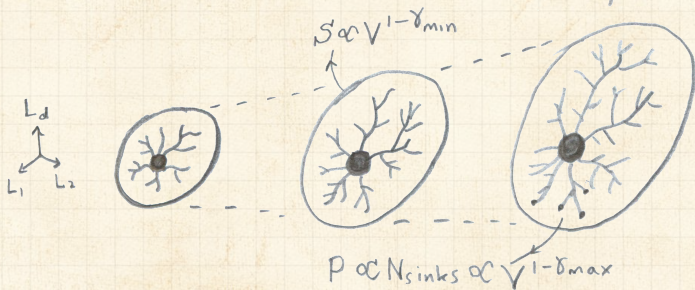
References







 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:



Recall:

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

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories


Geometric
argument

Conclusion

References



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 :

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



Measured for $M \leq 10$ kg:

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

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories


Geometric
argument


Conclusion

References




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.




Hack's law


 Volume of water in river network can be calculated by adding up basin areas

 Flows sum in such a way that

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


 Hack's law again:

$$l \sim a^h$$

 Can argue

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


where h is Hack's exponent.


 \therefore minimal volume calculations gives


$$h = 1/2$$




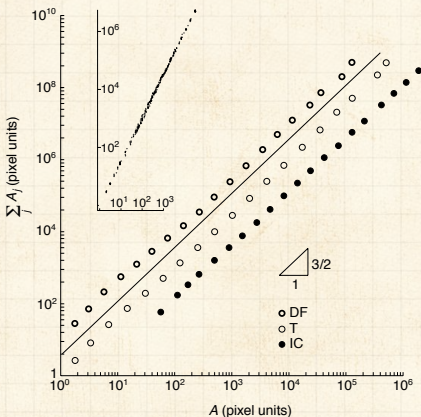
Real data:

 Banavar et al.'s approach^[1] is okay because ρ really is constant.

 **The irony:** shows optimal basins are isometric

 Optimal Hack's law: $l \sim a^h$ with $h = 1/2$

 (Zzzzz)



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

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

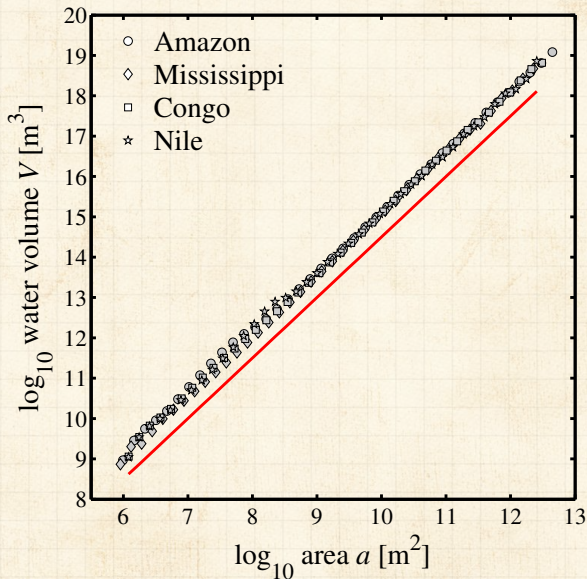
Geometric
argument

Conclusion

References



Even better—prefactors match up:



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Optimal Supply
Networks II

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion




References



The Cabal strikes back:

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Optimal Supply
Networks II

-  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.

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



Stories—Darth Quarter:

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Optimal Supply
Networks II



Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



Some people understand it's truly a disaster: ↗

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Optimal Supply
Networks II



Peter Sheridan Dodds, Theoretical Biology's Buzzkill

By Mark Changizi | February 9th 2010 03:24 PM | 1 comment | [Print](#) | [E-mail](#) | [Track Comments](#)

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Mark Changizi

Search This Blog

There is an apocryphal story about a graduate mathematics student at the University of Virginia studying the properties of certain mathematical objects. In his fifth year some killjoy bastard elsewhere published a paper proving that there are no such mathematical objects. He dropped out of the program, and I never did hear where he is today. He's probably making my cappuccino right now.

This week, a professor named Peter Sheridan Dodds published a new paper in *Physical Review Letters* further fleshing out a theory concerning why a $2/3$ power law may apply for metabolic rate. The $2/3$ law says that metabolic rate in animals rises as the $2/3$ power of body mass. It was in a 2001 *Journal of Theoretical Biology* paper that he first argued that perhaps a $2/3$ law applies, and that paper – along with others such as the one that just appeared -- is what has put him in the Killjoy Hall of Fame. The University of Virginia's killjoy was a mere amateur.

Mark Changizi

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- [The Ravenous Color-Blind: New Developments For Color-Deficients](#)
- [Don't Hold Your Breath Waiting For Artificial Brains](#)
- [Welcome To Humans, Version 3.0](#)

All Articles

ABOUT MARK

Mark Changizi is Director of Human Cognition at 2AI, and the author of *The Vision Revolution* (Benbella 2009) and *Harnessed: How...*

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Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



The unnecessary bafflement continues:

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Optimal Supply
Networks II

“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.

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

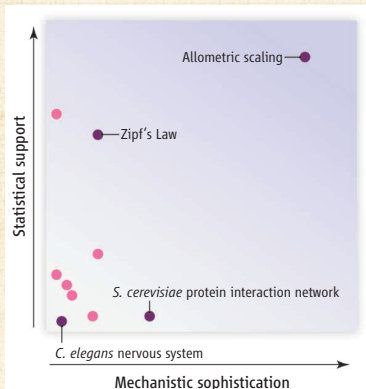
Conclusion

References



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.

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Optimal Supply
Networks II

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



Conclusion

- Supply network story consistent with dimensional analysis.
- Isometrically growing regions can be more efficiently supplied than allometrically growing ones.
- Ambient and region dimensions matter ($D = d$ versus $D > d$).
- Deviations from optimal scaling suggest inefficiency (e.g., gravity for organisms, geological boundaries).
- Actual details of branching networks not that important.
- Exact nature of self-similarity varies.
- 2/3-scaling lives on, largely in hiding.
- 3/4-scaling? Jury ruled a mistrial.
- The truth will out. Maybe.

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Optimal Supply
Networks II

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



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Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories



Geometric
argument

Conclusion

References



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Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



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Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



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Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories




Geometric
argument

Conclusion

References



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Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion


References



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Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References 



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Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories



Geometric
argument

Conclusion

References



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Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



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Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories



Geometric
argument

Conclusion

References





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Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



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Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



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Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



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Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories



Geometric
argument

Conclusion

References



References XV

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Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



References XVI

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Optimal Supply
Networks II

Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



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Metabolism and
Truthicide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References



References XVIII

COcoNuTS
@networksvox

Optimal Supply
Networks II

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Metabolism and
Truhticide

Death by
fractions

Measuring
exponents

River networks

Earlier theories

Geometric
argument

Conclusion

References

