Optimal Supply Networks II: Blood, Water, and Truthicide

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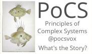
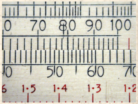
Principles of Complex Systems, Vols. 1, 2, & 3D CSYS/MATH 300, 303, & 394, 2022–2023| @pocsvox

Prof. Peter Sheridan Dodds | @peterdodds

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





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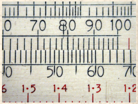
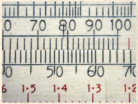
Outline



Stories—The Fraction Assassin:

Law and Order, Special Science Edition: Truthicide Department



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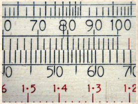

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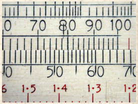

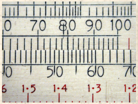

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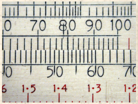

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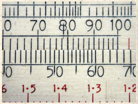
“In the scientific integrity system known as peer review, the people are represented by two highly overlapping yet equally important groups: the independent scientists who review papers and the scientists who punish those who publish garbage. This is one of their stories.”



Animal power

Fundamental biological and ecological constraint:

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

$P =$ basal metabolic rate

$M =$ organismal body mass

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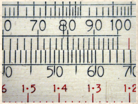
Prefactor c depends on body plan and body temperature:



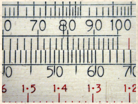
$P = c\,M^{\alpha}$

Prefactor c depends on body plan and body temperature:

Birds	39–$41^{\circ}C$
Eutherian Mammals	36–$38^{\circ}C$
Marsupials	34–$36^{\circ}C$
Monotremes	30–$31^{\circ}C$

What one might expect:

$\alpha = 2/3$



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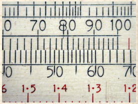
$\alpha = 2/3$ because …

- Dimensional analysis suggests an energy balance surface law:

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



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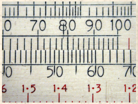

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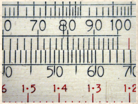
  Gaussian fluctuations in $\log_{10} P$ around $\log_{10} c M^{\alpha}$.



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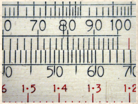
- Stefan-Boltzmann law for radiated energy:

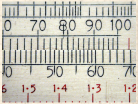
$$\frac{\mathrm{d}E}{\mathrm{d}t} = \sigma \varepsilon S T^4 \propto S$$



The prevailing belief of the Church of Quarterology:

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

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



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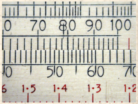

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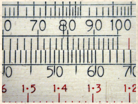
Most obvious concern:

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

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



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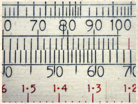
- Organisms must somehow be running ‘hotter’ than they need to balance heat loss.



Related putative scalings:

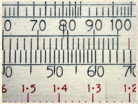
Wait! There's more!:

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

The great ‘law’ of heartbeats:

Assuming:

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



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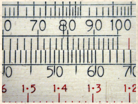

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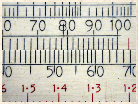

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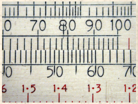

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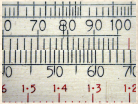

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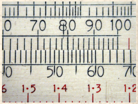

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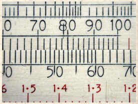

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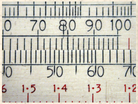
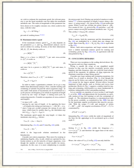
- $\approx$ 1.5 billion ....



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]

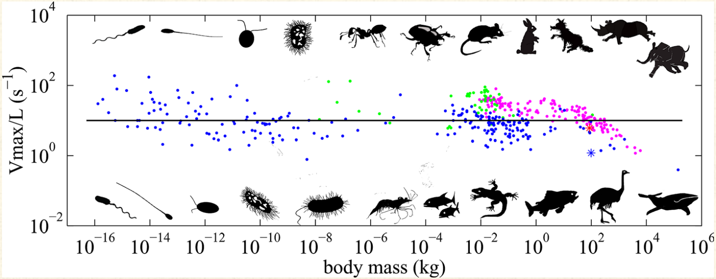
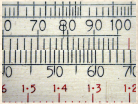


Fig. 1. Maximum relative speed versus body mass for 202 running species (157 mammals plotted in magenta and 45 non-mammals plotted in green), 127 swimming species and 91 micro-organisms (plotted in blue). The sources of the data are given in Ref. 16. The solid line is the maximum relative speed [Eq.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

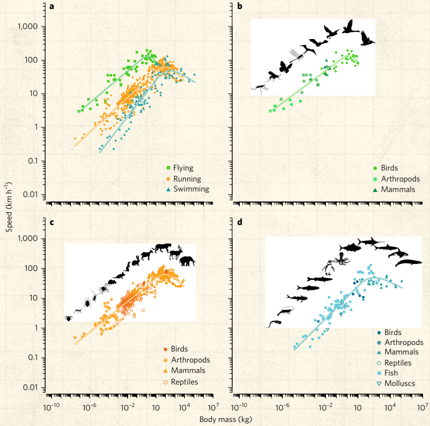
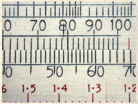


Figure 2 | Empirical data and time-dependent model fit for the allometric scaling of maximum speed. a, Comparison of scaling for the different locomotion modes (flying, running, swimming). **b**–**d**, Taxonomic differences are illustrated separately for flying (**b**; $n = 55$), running (**c**; $n =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



nature ecology & evolution ARTICLES

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

Myriam R. Hirt, Walter Jetz, Björn C. Rall and Ulrich Brose

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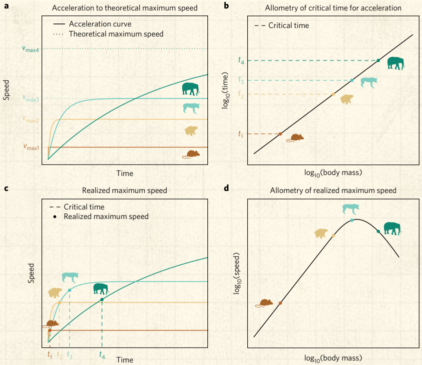


Figure 1 | Concept of time-dependent and mass-dependent realized maximum speed of animals. a, Acceleration of animals follows a saturation curve (solid lines) approaching the theoretical maximum speed (dotted lines) depending on body mass (colour code). **b**, The time available for acceleration increases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

Theoretical story:

- Maximum speed increases with size: $v_{\text{max}} = aM^b$

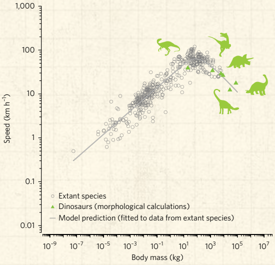
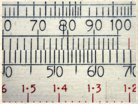


Figure 4 | Predicting the maximum speed of extinct species with the time-dependent model. The model prediction (grey line) is fitted to data of extant species (grey circles) and extended to higher body masses. Speed data for dinosaurs (green triangles) come from detailed morphological model calculations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



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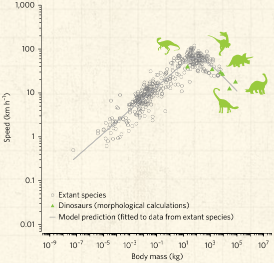

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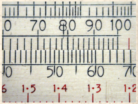

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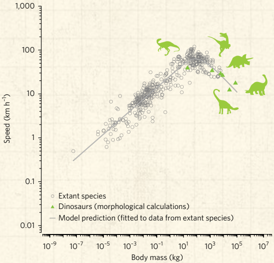

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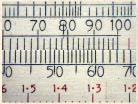
  Literature: $0.75 \lesssim d \lesssim 0.94$



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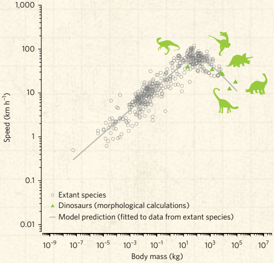

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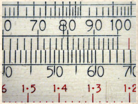
- Acceleration time = depletion time for anaerobic energy: $\tau \sim fM^g$ Literature: $0.76 \lesssim g \lesssim 1.27$



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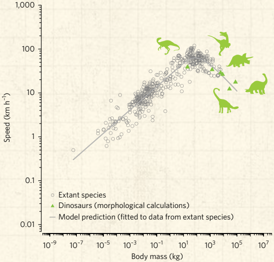

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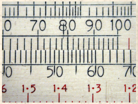

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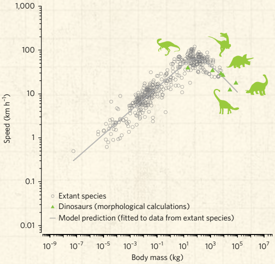
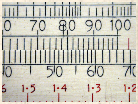


Figure 4 | Predicting the maximum speed of extinct species with the time-dependent model. The model prediction (grey line) is fitted to data of extant species (grey circles) and extended to higher body masses. Speed data for dinosaurs (green triangles) come from detailed morphological model calculations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

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



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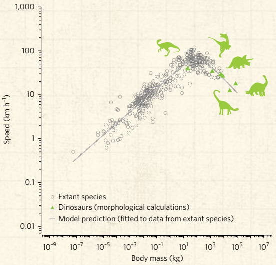

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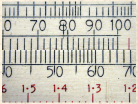

- Literature search for for maximum speeds of running, flying and swimming animals.
- Search terms: “maximum speed”, “escape speed” and “sprint speed”.


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THE END


THE CHURCH OF QUARTEROLOGY

A theory is born:

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

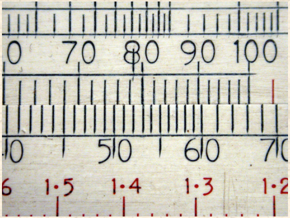
A theory grows:

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

Theory meets a different 'truth':

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

Our hero faces a shadowy cabal:



- 1932: Kleiber analyzed 13 mammals.[25]
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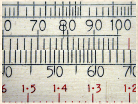

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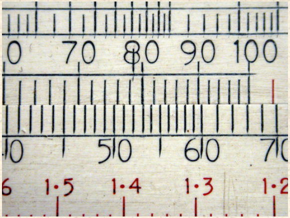

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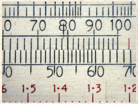
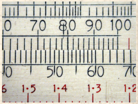
- 1961 book: "The Fire of Life. An Introduction to Animal Energetics". [26]



When a cult becomes a religion:

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



Quarterology spreads throughout the land:

The Cabal assassinates 2/3-scaling:

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

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


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Au
$P_s \sim s^{-\gamma}$
$y = x^{-\alpha}$
1 2 5 4 3 6 7 8 9
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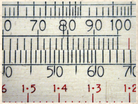
PATHS OF THINKING THAT LEAD TO CERTAIN DESPAIR
CLASSIFIED PHOENIX
"I am the Monarch of the Sea."


$\frac{D-1}{D}$
THE TRUTHICIDE

An unsolved truthicide:

So many questions ...



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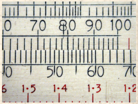

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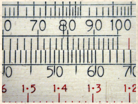

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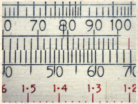

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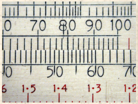

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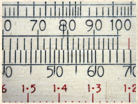

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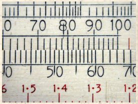

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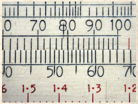

Modern Quarterology, Post Truthicide

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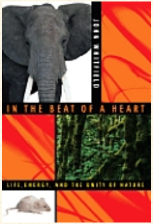
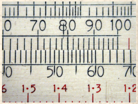


In the Beat of a Heart: Life, Energy, and the Unity of Nature—by John Whitfield



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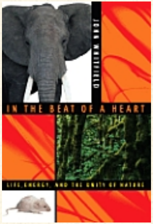

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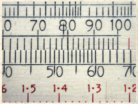

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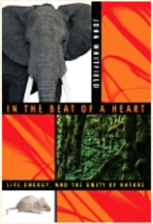

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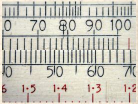
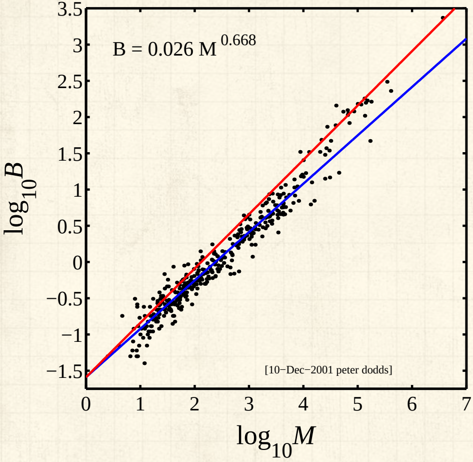
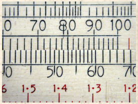


Some data on metabolic rates



[source=/home/dodds/work/biology/allometry/heusner/figures/figheusner391.ps]

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



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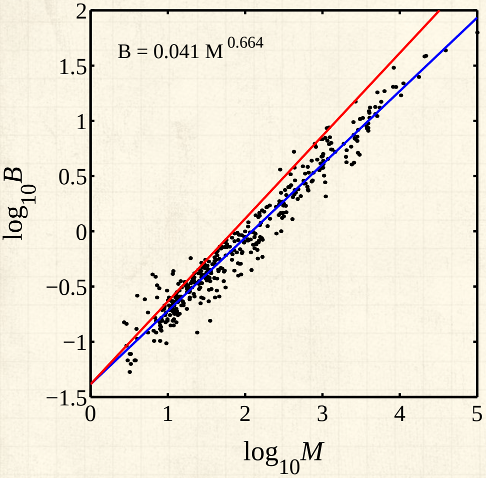


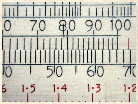
- Bennett and Harvey's data (1987)[3]
- 398 birds
- blue line: 2/3
- red line: 3/4.
- $(B = P)$

- 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.



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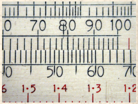

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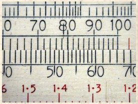

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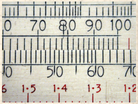
- Linear regression assumes Gaussian errors.

Measuring exponents



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

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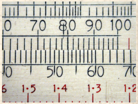

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Measuring exponents

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

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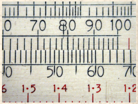
Standardized Major Axis Linear Regression. [43, 41]



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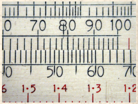
(aka Reduced Major Axis = RMA.)

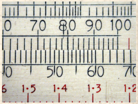


Measuring exponents

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!



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

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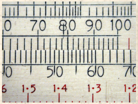
- Minimization of sum of areas of triangles induced by vertical and horizontal residuals with best fit line.

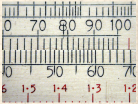


Measuring exponents

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.



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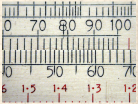

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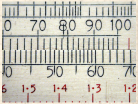
- #somuchwin



Measuring exponents

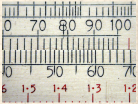
Relationship to ordinary least squares regression is simple:

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

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]



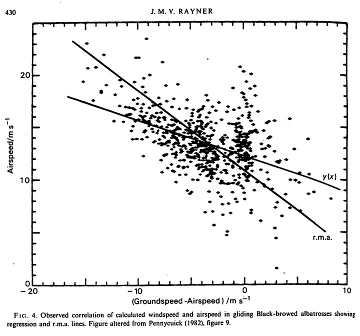


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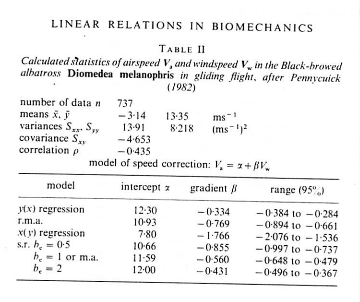
Fig. 4. Observed correlation of calculated windspeed and airspeed in gliding Black-browed albatrosses showing regression and r.m.a. lines. Figure altered from Pennycuick (1982), figure 9.



LINEAR RELATIONS IN BIOMECHANICS

TABLE II

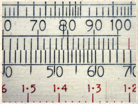
Calculated statistics of airspeed $\mathbf{V}_a$ *and windspeed* $\mathbf{V}_w$ *in the Black-browed albatross* **Diomedea melanophris** *in gliding flight, after Pennycuick (1982)*

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	(ms^{-1})^2
covariance S_{xy}	−4·653		
correlation ρ	−0·435		

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

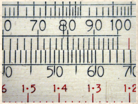
model	intercept α	gradient β	range (95%)
$y(x)$ regression	12·30	−0·334	−0·384 to −0·284
r.m.a.	10·93	−0·769	−0·894 to −0·661
$x(y)$ regression	7·80	−1·766	−2·076 to −1·536
s.r. $b_e = 0{\cdot}5$	10·66	−0·855	−0·997 to −0·737
$b_e = 1$ or m.a.	11·59	−0·560	−0·648 to −0·479
$b_e = 2$	12·00	−0·431	−0·496 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 ...)



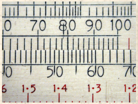
Heusner's data, 1991 (391 Mammals)

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

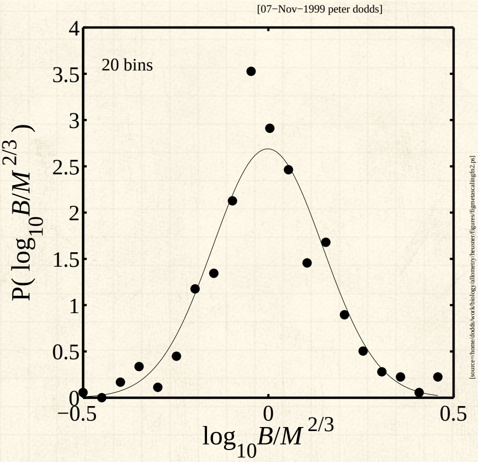


Bennett and Harvey, 1987 (398 birds)

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



Fluctuations—Things look normal ...

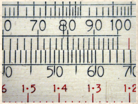


- $P(B\,|\,M) = 1/M^{2/3} f(B/M^{2/3})$
- Use a Kolmogorov-Smirnov test.

Hypothesis testing

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

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



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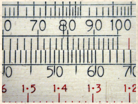

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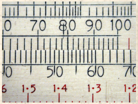

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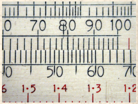

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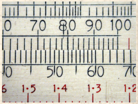
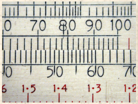
- See, for example, DeGroot and Scherish, “Probability and Statistics.” [11]



Revisiting the past—mammals

Full mass range:

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



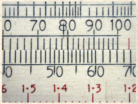
Revisiting the past—mammals

$M \leq 10$ kg:

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

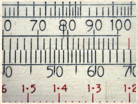
$M \geq 10$ kg:

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



Analysis of residuals

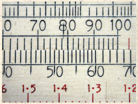
1. Presume an exponent of your choice: 2/3 or 3/4.



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:

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



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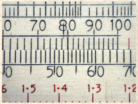
3. H_0: residuals are uncorrelated
   H_1: residuals are correlated.



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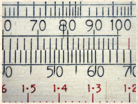
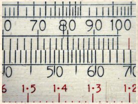
4. Measure the correlations in the residuals and compute a p-value.



Analysis of residuals

We use the spiffing Spearman Rank-Order Correlation Coefficient

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



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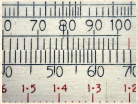

We use the spiffing Spearman Rank-Order Correlation Coefficient

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.

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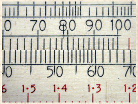
- Now calculate correlation coefficient for ranks, r_s:



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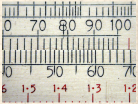

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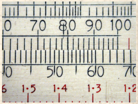
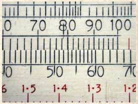
- Perfect correlation: x_i's and y_i's both increase monotonically.



Analysis of residuals

We assume all rank orderings are equally likely:



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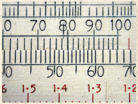

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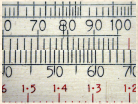
- Excellent feature: Non-parametric—real distribution of x's and y's doesn't matter.



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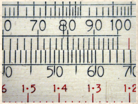
- Bonus: works for non-linear monotonic relationships as well.



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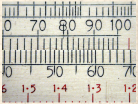
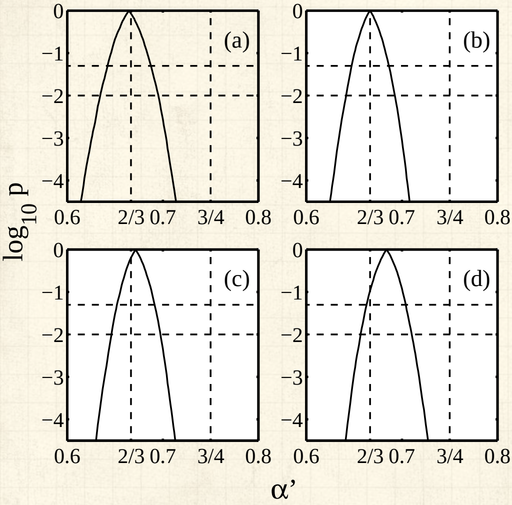
- Bonus: works for non-linear monotonic relationships as well.
- See Numerical Recipes in C/Fortran which contains many good things. [39]

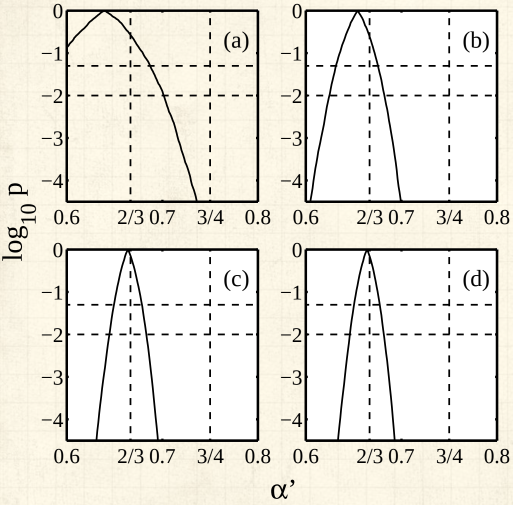


Analysis of residuals—mammals



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

Analysis of residuals—birds

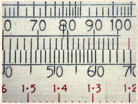


(a) $M < 0.1$ kg,

(b) $M < 1$ kg,

(c) $M < 10$ kg,

(d) all birds.

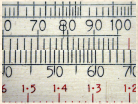


Other approaches to measuring exponents:

- 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.

Impure scaling?:

- So: The exponent $\alpha = 2/3$ works for all birds and mammals up to 10–30 kg



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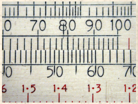
- So: The exponent $\alpha = 2/3$ works for all birds and mammals up to 10–30 kg
- For mammals $>$ 10–30 kg, maybe we have a new scaling regime



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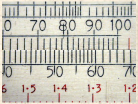
- Possible connection?: Economos (1983)—limb length break in scaling around 20 kg [15]



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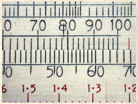
- Possible connection?: Economos (1983)—limb length break in scaling around 20 kg [15]
- But see later: non-isometric growth leads to lower metabolic scaling. Oops.



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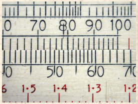
Now we're really confused (empirically):

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



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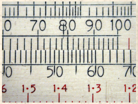

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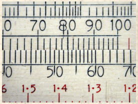

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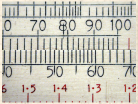
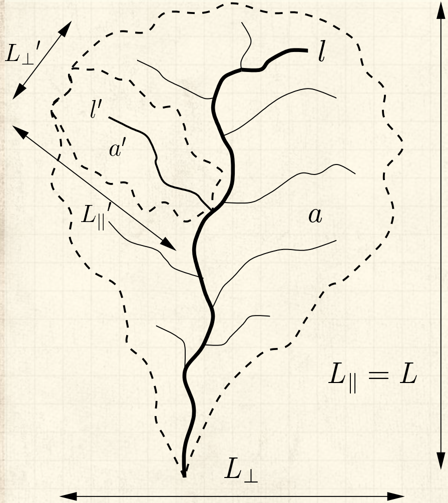
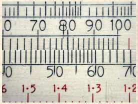
- Savage et al., PLoS Biology (2008) [45] "Sizing up allometric scaling theory" Pro $3/4$: problems claimed to be finite-size scaling.



Somehow, optimal river networks are connected:



- a = drainage basin area
- ℓ = length of longest (main) stream
- $L = L_\parallel$ = longitudinal length of basin

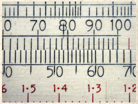


Mysterious allometric scaling in river networks

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

$$\ell \sim a^h$$

$$h \sim 0.6$$



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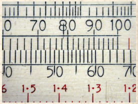

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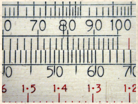

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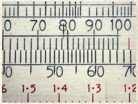

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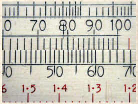

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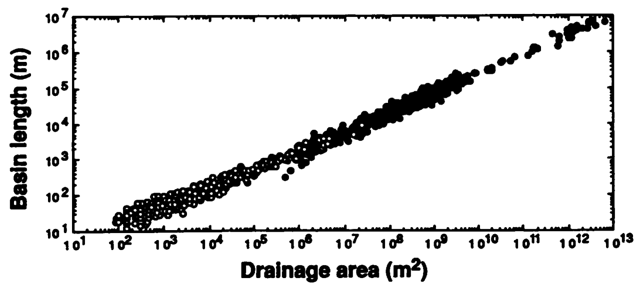
- Another quest to find universality/god ...
- A catch: studies done on small scales.

Large-scale networks:

(1992) Montgomery and Dietrich [36]:

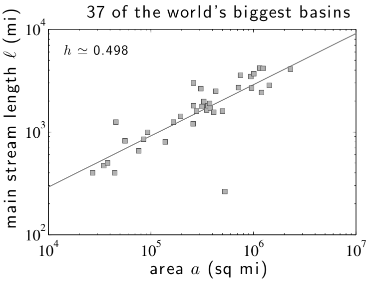


- Composite data set: includes everything from unchanneled valleys up to world's largest rivers.
- Estimated fit:

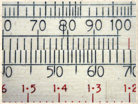
$$L \simeq 1.78a^{0.49}$$

- Mixture of basin and main stream lengths.

World's largest rivers only:



- 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:

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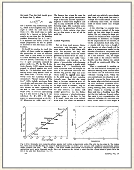
- Metabolism and shape never properly connected.



“Size and shape in biology”
T. McMahon,
Science, **179**, 1201–1204, 1973. [32]

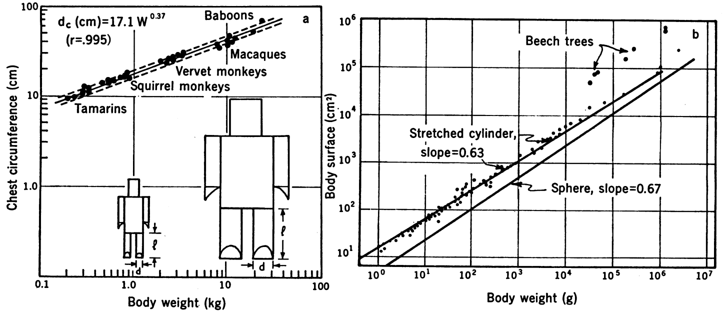


Fig. 3. (a) Chest circumference, d_c, plotted against body weight, W, for five species of primates. The broken lines represent the standard error in this least-squares fit [adapted from (*21*)]. The model proposed here, whereby each length, l, increases as the ⅔ power of diameter, d, is illustrated for 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*)].

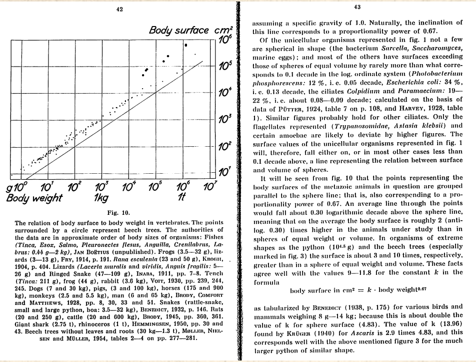


Fig. 10.

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 *(Tinca, Esox, Salmo, Pleuronectes flesus, Anguilla, Crenilabrus, Labrus: 0.44 g—2 kg)*, JAN BOËTIUS (unpublished). Frogs (3.5—32 g), lizards (3—13 g), FRY, 1914, p. 191. *Rana esculenta* (23 and 50 g), KROGH, 1904, p. 404. Lizards *(Lacerta muralis* and *viridis, Anguis fragilis:* 5—26 g) and Ringed Snake (47—109 g), INABA, 1911, pp. 7–8. Tench (*Tinca:* 211 g), frog (44 g), rabbit (3.6 kg), VOIT, 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), man (6 and 65 kg), BRODY, COMFORT and MATTHEWS, 1928, pp. 8, 30, 33 and 51. Snakes (rattle-snake, small and large python, boa: 3.5—32 kg), BENEDICT, 1932, p. 146. Rats (20 and 250 g), cattle (20 and 600 kg), BRODY, 1945, pp. 360, 361. Giant shark (2.75 t), rhinoceros (1 t), HEMMINGSEN, 1950, pp. 30 and 43. Beech trees without leaves and roots (30 kg—1.3 t), MØLLER, NIELSEN and MÜLLER, 1954, tables 2—4 on pp. 277—281.

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 *Sarcella, Saccharomyces,* 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 (*Photobacterium phosphorescens:* 12 %, i. e. 0.05 decade, *Escherichia coli:* 34 %, i. e. 0.13 decade, the ciliates *Colpidium* and *Paramaecium:* 19—22 %, i. e. about 0.08—0.09 decade; calculated on the basis of data of PÜTTER, 1924, table 7 on p. 108, and HARVEY, 1928, table 1). Similar figures probably hold for other ciliates. Only the flagellates represented (*Trypanosomidae, Astasia klebsii*) 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 (antilog. 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. 3) 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 9—11.8 for the constant k in the formula

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

as tabularized by BENEDICT (1938, p. 175) for various birds and mammals weighing 8 g—14 kg; because this is about double the value of k for sphere surface (4.83). The value of k (13.96) found by KRÜGER (1940) 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."

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- Obviously, a bit silly...[46]

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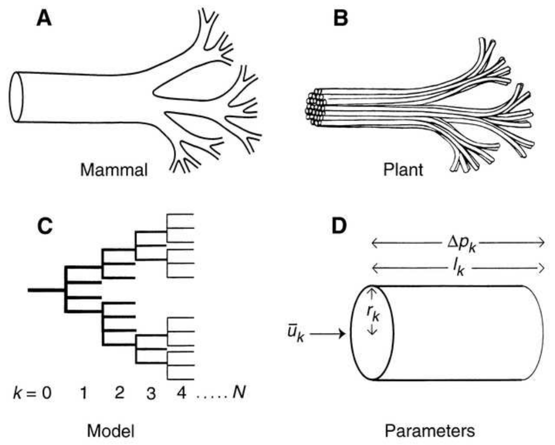

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Claims:

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

Not so fast …

Actually, model shows:

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Do find:

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

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

Connecting network structure to α

1. Ratios of network parameters:

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Obliviously soldiering on, we could assert:

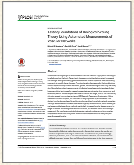
- area-preservingness: $R_r = R_n^{-1/2}$
- space-fillingness: $R_\ell = R_n^{-1/3}$

$\Rightarrow \alpha = 3/4$

Data from real networks:

Network	R_n	R_r	R_ℓ	$-\frac{\ln R_r}{\ln R_n}$	$-\frac{\ln R_\ell}{\ln R_n}$	α
West *et al.*	–	–	–	1/2	1/3	3/4
rat (PAT)	2.76	1.58	1.60	0.45	0.46	0.73
cat (PAT)	3.67	1.71	1.78	0.41	0.44	0.79
(Turcotte *et al.* [50])						
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

Attempts to look at actual networks:



PLOS COMPUTATIONAL BIOLOGY

Testing Foundations of Biological Scaling Theory Using Automated Measurements of Vascular Networks

Abstract

PLOS COMPUTATIONAL BIOLOGY

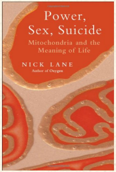
Do Vascular Networks Branch Optimally or Randomly across Spatial Scales?

Abstract

"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, . [?]

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.”

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]

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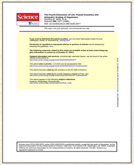
- Arrive at $a \propto M^{D/D+1}$ and $\ell \propto M^{1/D}$.
- New disaster: after going on about fractality of a, then state $v \propto a\ell$ in general.

“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]



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West, Brown, and Enquist,
Science, **284**, 1677–1679, 1999. [54]

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- J. Kozlowski, M. Konarzewski. “West, Brown and Enquist’s model of allometric scaling again: the same questions remain.” Functional Ecology 19: 739–743, 2005.

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

Let's try a quadratic:

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

Yah:

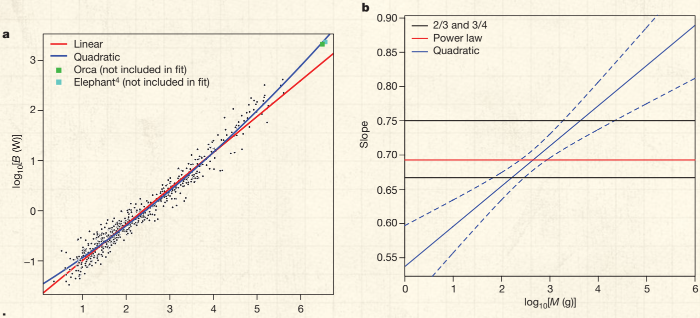

Figure 1 | Curvature in metabolic scaling. **a**, Linear (red) and quadratic (blue) fits (not including temperature) of $\log_{10}B$ versus $\log_{10}M$. The orca (green square) and Asian elephant (ref. 4; turquoise square at larger mass) are not included in the fit, but are predicted well. Differences in the quality of fit are best seen in terms of the conditional mean of the error, estimated by the lowess (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.

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

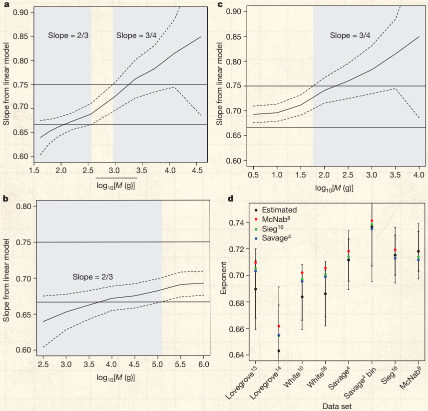

Figure 2 | Scaling exponent depends on mass range. a, Slope estimated by linear regression within a three log-unit mass range (smaller near the boundaries). Values on the abscissa denote mean $\log_{10}M$ within the range. When the 95% confidence regions (dashed lines) include the 2/3 or 3/4 lines, the 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): Lovegrove[13], Lovegrove[14], White[10], White[28], Sieg[16], McNab[8], and Savage[4] using species average data ('Savage[4]') and binned data ('Savage[4] 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.

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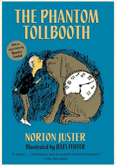
[1] Already raised and fully established 9 years earlier. [14]

Evolution has generally made things bigger[1]



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

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[1] Yes, yes, yes: insular dwarfism with the shrinkage

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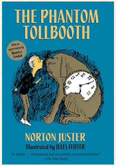

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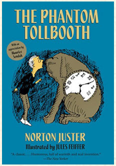

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- Regression starting at high M makes ...no sense

---

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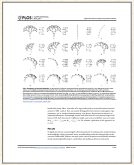
Still going:

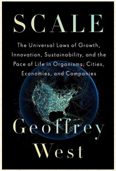


"A general model for metabolic scaling in self-similar asymmetric networks"
Brummer, Brummer, and Enquist,
PLoS Comput Biol, **13**, e1005394, 2017.[8]

Wut?:

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

Oh no:



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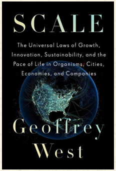

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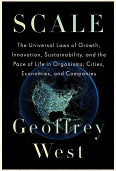

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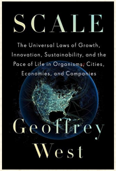

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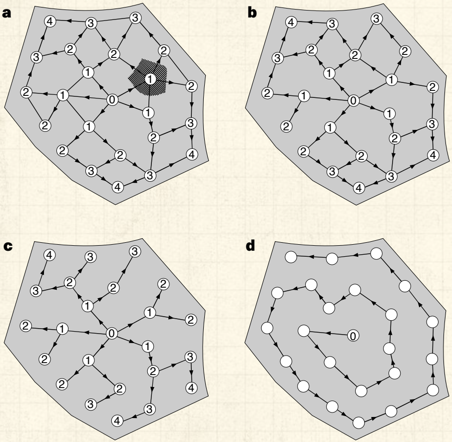
- "(he actually repeats several times that businesses can die but are not really an animal - O RLY?)"

Simple supply networks:



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

Simple supply networks

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

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

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


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THE IMPROBABLE PACHYDERM

Geometric argument

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

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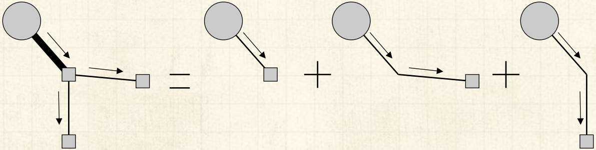


Geometric argument

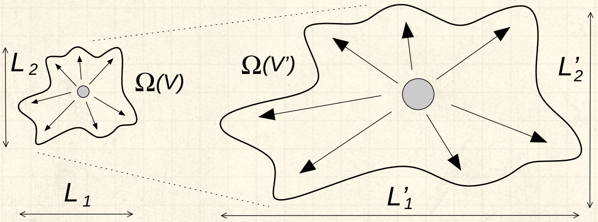
- Q: how does the number of sustainable sinks N_{sinks} scale with volume V for the most efficient network design?

Geometric argument

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

Geometric argument

- Allometrically growing regions:



- Have d length scales which scale as

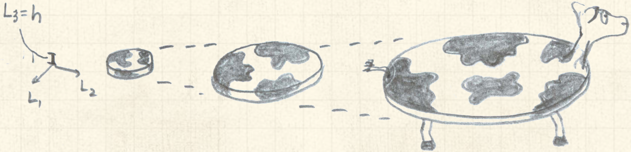
$$L_i \propto V^{\gamma_i} \text{ where } \gamma_1 + \gamma_2 + \ldots + \gamma_d = 1.$$

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

Spherical cows and pancake cows:

Assume an isometrically scaling family of cows:

Extremes of allometry:
The pancake cows—

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THE FAMILY OF SPHERICAL COWS

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

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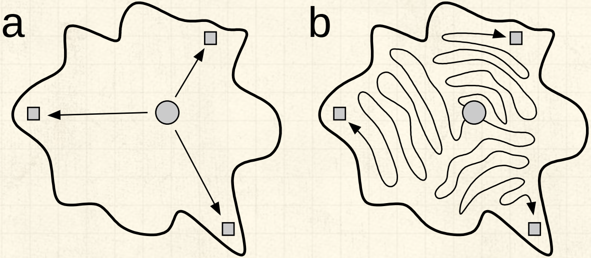
- **Question:** For general families of regions, how does surface area S scale with volume V? Insert question from assignment 4

Geometric argument

- Best and worst configurations (Banavar et al.)



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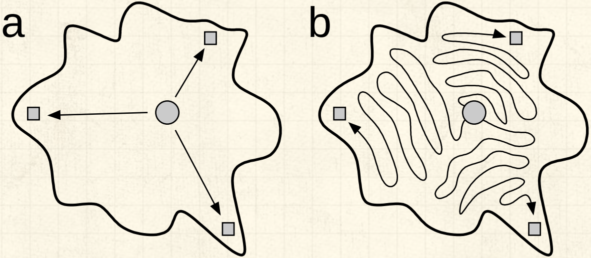


- Rather obviously:
  $\min V_{\text{net}} \propto \sum$ distances from source to sinks.

Minimal network volume:

Real supply networks are close to optimal:

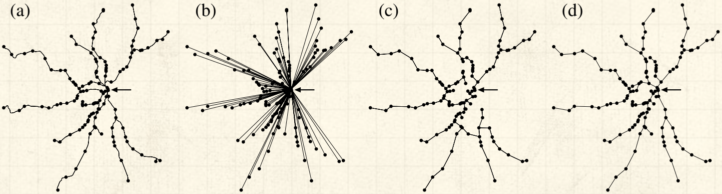
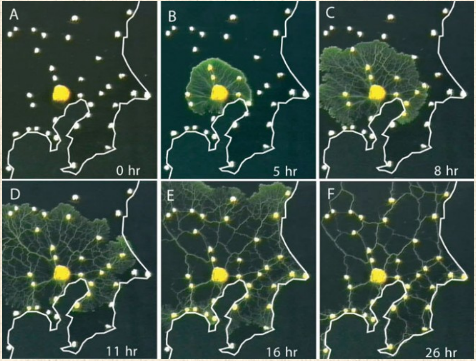


Figure 1. (a) Commuter rail network in the Boston area. The arrow marks the assumed root of the network. (b) Star graph. (c) Minimum spanning tree. (d) The model of equation (3) applied to the same set of stations.

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

“Rules for Biologically Inspired Adaptive Network Design”

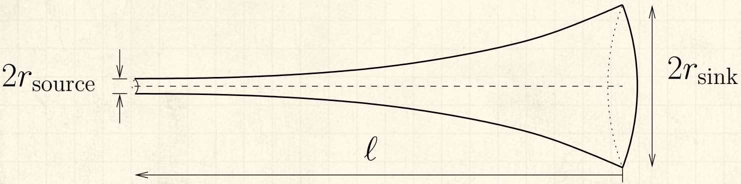
Tero et al.,
Science, **327**, 439-442, 2010. [49]



Urban deslime in action:
https://www.youtube.com/watch?v=GwKuFREOgmo

Minimal network volume:

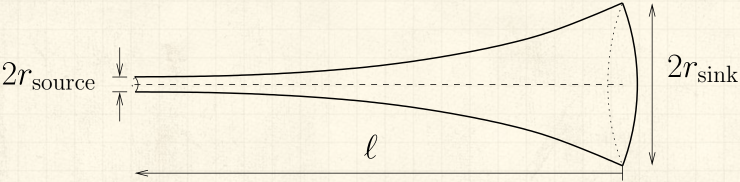
We add one more element:



- 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.

Minimal network volume:

Effecting scaling:



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

Minimal network volume:

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

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

Insert question from assignment 4

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Insert question from assignment 4 ↗

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

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

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

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

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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.

This
is a
really
clean

slide

Blood networks

- Velocity at capillaries and aorta approximately constant across body size [51]: $\epsilon = 0$.

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- Density of suppliable sinks decreases with organism size.

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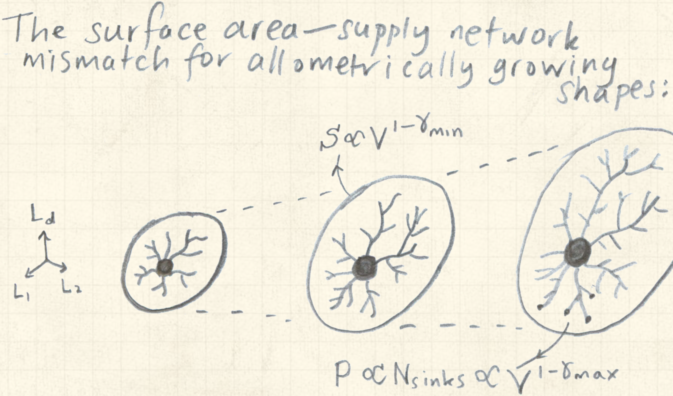
- Including other constraints may raise scaling exponent to a higher, less efficient value.

- 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 SUN
THE GOLDEN AGE OF REDUCTIONISM
THE MANIFESTO
THE WELL OF SCALES
THE LAWS OF DECAYING POWER
THE UNEXPECTED TRANSFIGURATION
MINISTRY OF RANDOM WALKS
THE RICH GET RICHER
THE DREAM OF EFFICIENT LANGUAGE
THE LAW OF DIGITS FIRST
THE SURPRISE OF BEING ROBUST YET FRAGILE
THE MISREADING OF THE BOOK OF SAND
THE MANY TALES OF MANY TAILS
THE MEASURING
THE DATA POOR
THE POURING DATA
THE CHARMS OF THE MANY WRONG PATHS
THE DOORS THAT SHOULD NOT BE OPENED
THE KNOWLEDGE OF DEAD MONKS
THE EMERGENCE OF STRUCTURE
THE EMERGENCE OF DESTRUCTION
THE EMERGENCE OF THINKING
THE EMERGENCE OF STORIES
THE MECHANICS STATISTICAL
THE THRESHOLDS OF PERCOLATION
THE NETWORKS COMPLEX
THE ELEMENTS OF WEBS
THE BIRDS OF A FEATHER
THE BIRDS OF NOT A FEATHER
THE ARK OF THE RANDOM NETWORK
THE STRANGENESS OF FRIENDS
THE SMALLNESS OF WORLDS
THE THEORY OF SIX DEGREES
THE NETWORKS FREE OF SCALE
THE CONTAGION
THE CONFUSION OF CONTAGIONS
THE DISEASE OF RANDOM MIXING
THE UNENDING PANDEMICS
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THE SOCIAL WILD
THE SOCIAL CONTAGION
THE RATIO OF GAIN
THE MECHANICS OF FAME
THE TALK OF FAME
THE STORIES CONTAGIOUS
THE JOHN DORY
THE ADJACENT NARRATIVES
THE STORYTELLERS
THE FATED ASTRAL PATH
THE PATHS OF UNIVERSALITY
THE DEPENDENT PATHS
THE TROUSERS OF BIFURCATING REALITIES
THE UNKNOWN MECHANISM
THE LANDSCAPES OF FORKING PATHS
THE NETWORKS OF BLOOD
THE TREES OF REALITY
THE ORDERS OF STREAMS
THE LAWS OF BRANCHING
THE SCALING OF BROKEN HIERARCHIES
THE BRAID OR THE BRANCH
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THE CHURCH OF QUARTEROLOGY
THE TRUTHICIDE
THE FAMILY OF PANCAKE COWS
THE FAMILY OF SPHERICAL COWS
THE IMPROBABLE PACHYDERM
THE SUPPLY MOST FAIR
THE SUPPLY TO THE MOST
THE DARK ART OF GENERATING FUNCTIONS
THE RANDOM SUM OF RANDOMNESS
THE TWO-SIDED WORLDS
THE STORIES AND THE TROPES
THE TRUTH OF DIFFUSION
THE UNVEILING OF HIDDEN POWERS
THE SCRYING FOR THE SHAPES OF THINGS
THE LIMITS OF ORGANIZATIONS
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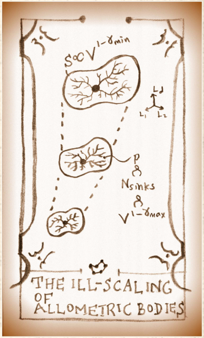
THE TROUBLES ILL-FORMED
THE NETWORKS OF MANY ILKS
THE CHAOS OF FETTERED CONTAGION
THE END


$S \propto V^{1-\gamma_{min}}$
L_1
L_2
L_3
P
&
N_{sinks}
&
$V^{1-\gamma_{max}}$
THE ILL-SCALING OF ALLOMETRIC BODIES

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- White and Seymour, 2005: unhappy with large herbivore measurements. Find $\alpha \simeq 0.686 \pm 0.014$

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Stefan-Boltzmann law:

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

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- If $\epsilon > 0$, V_{net} will grow more slowly but 3/2 appears to be confirmed from real data.

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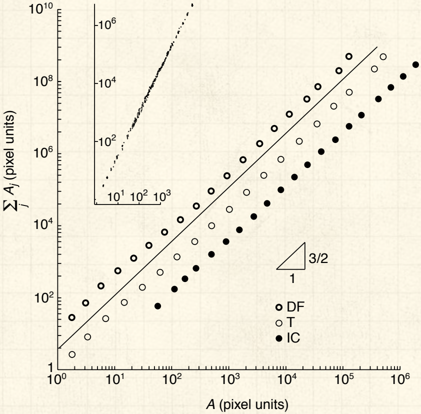

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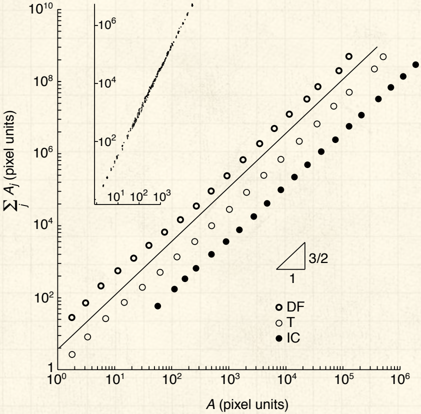

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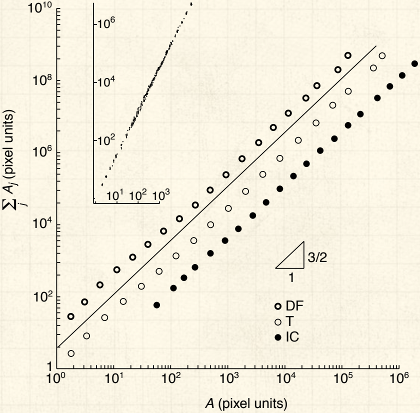

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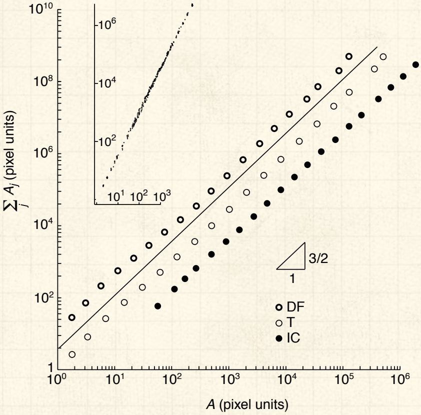

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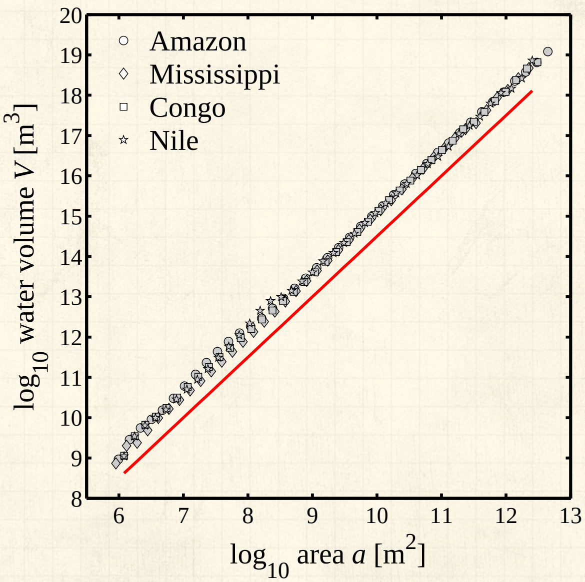
Even better—prefactors match up:



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- Cough, cough, cough, hack, wheeze, cough.

Stories—Darth Quarter:

Some people understand it's truly a disaster:

Peter Sheridan Dodds, Theoretical Biology's Buzzkill

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

Mark Changizi

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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

MORE ARTICLES

- 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...***

View Mark's Profile

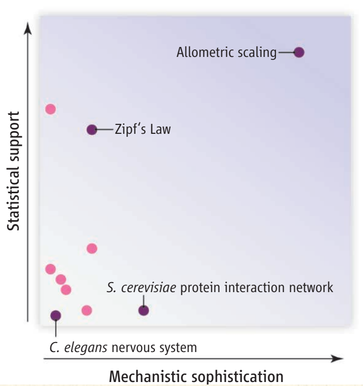
The unnecessary bafflement continues:

“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. Olff, 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: PLIPLO action.

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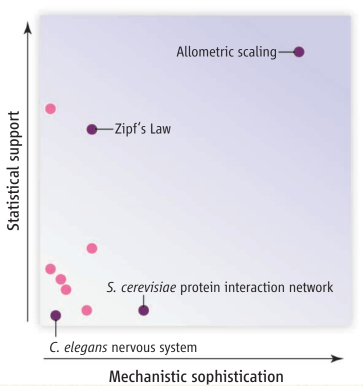

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- Summary: Wow.

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- 2/3-scaling lives on, largely in hiding.

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