Size matters

***„You can drop a mouse down a thousand-yard mine shaft;
and, on arriving at the bottom,
it gets a slight shock and walks away,
provided the ground is fairly soft.
A rat is killed, a man is broken, a horse splashes.“***

(J.B.S. Haldane, 1928: On being the right size)

Allometric principles and metabolic allometry

Marcus Clauss

Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Switzerland

Wildlife Digestive Physiology Course Vienna 2013

University of Zurich
Vetsuisse Faculty

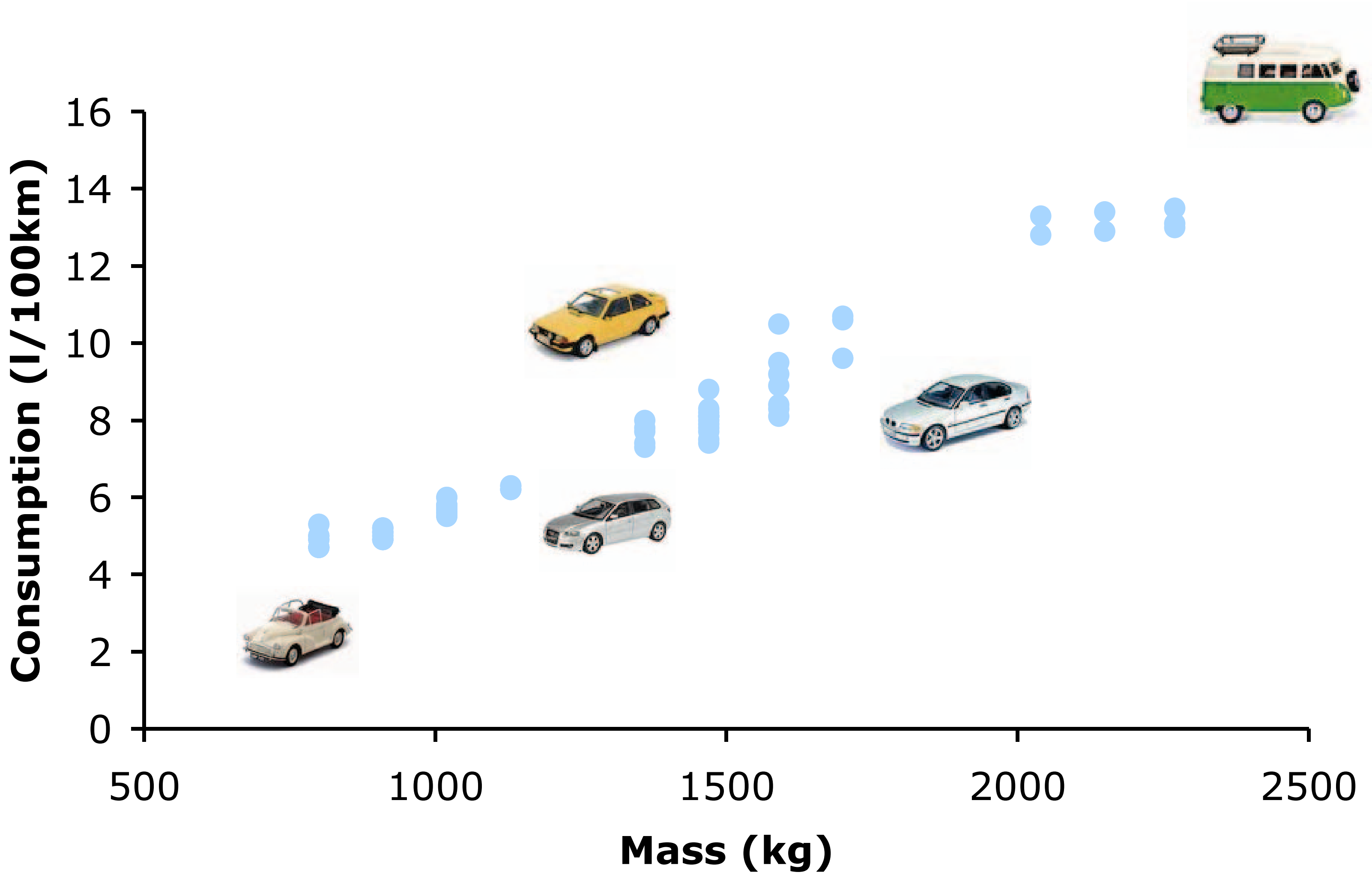
Clinic
of Zoo Animals, Exotic Pets and Wildlife

42

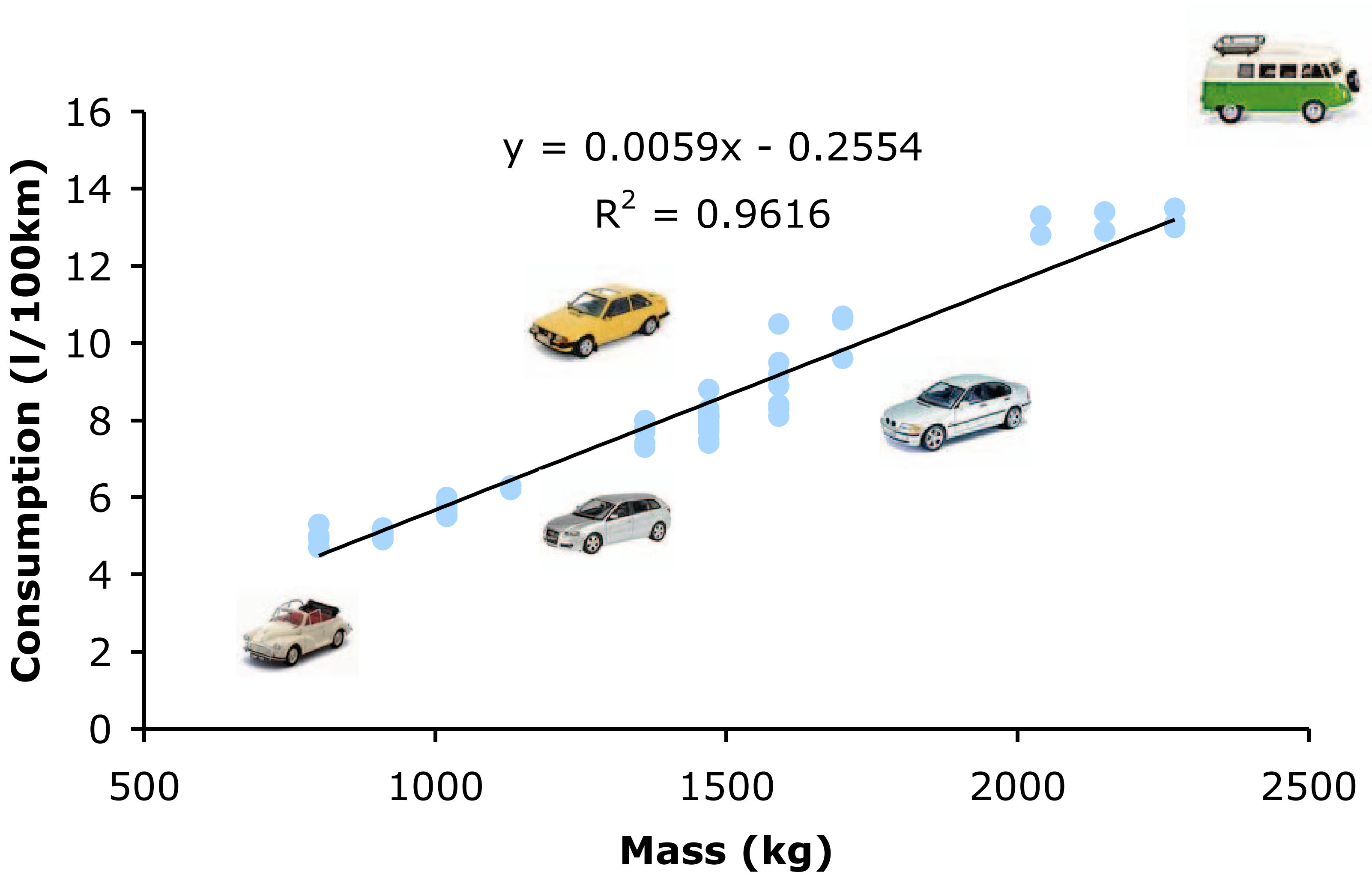
D. Adams: Hitchhiker's Guide to the Galaxy

0.75

Max Kleiber (1932)



Data from ADAC (2007)



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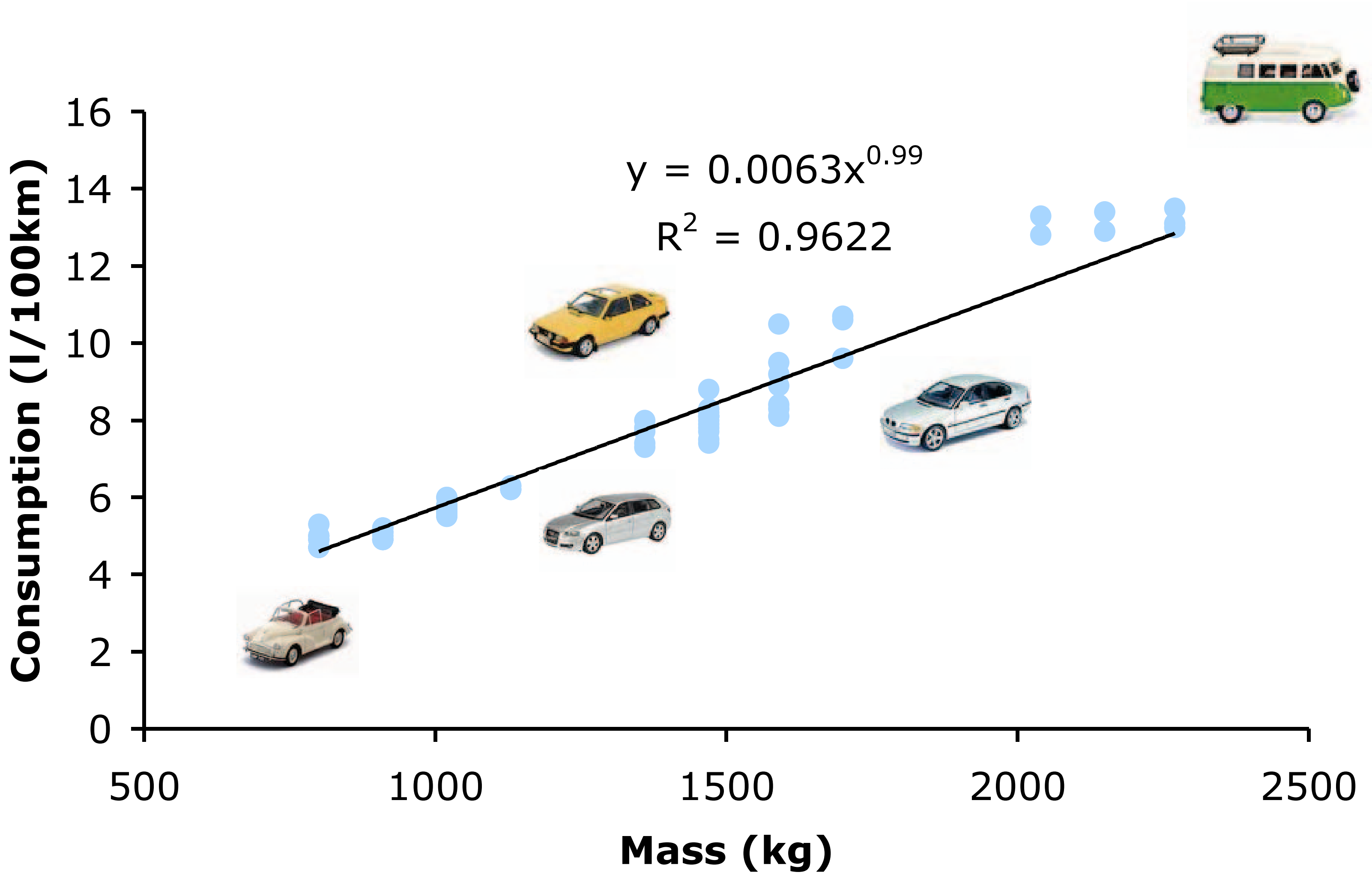
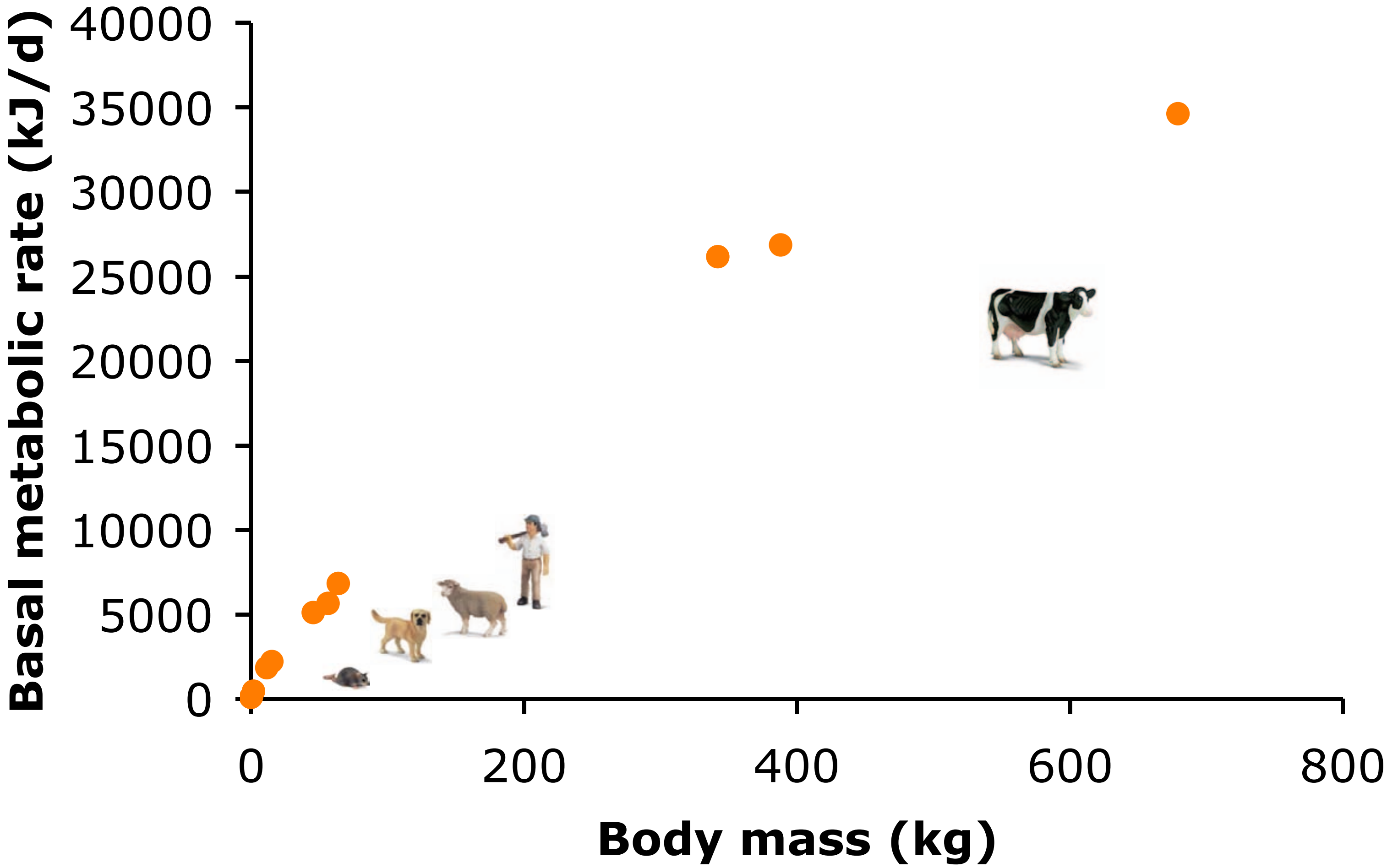
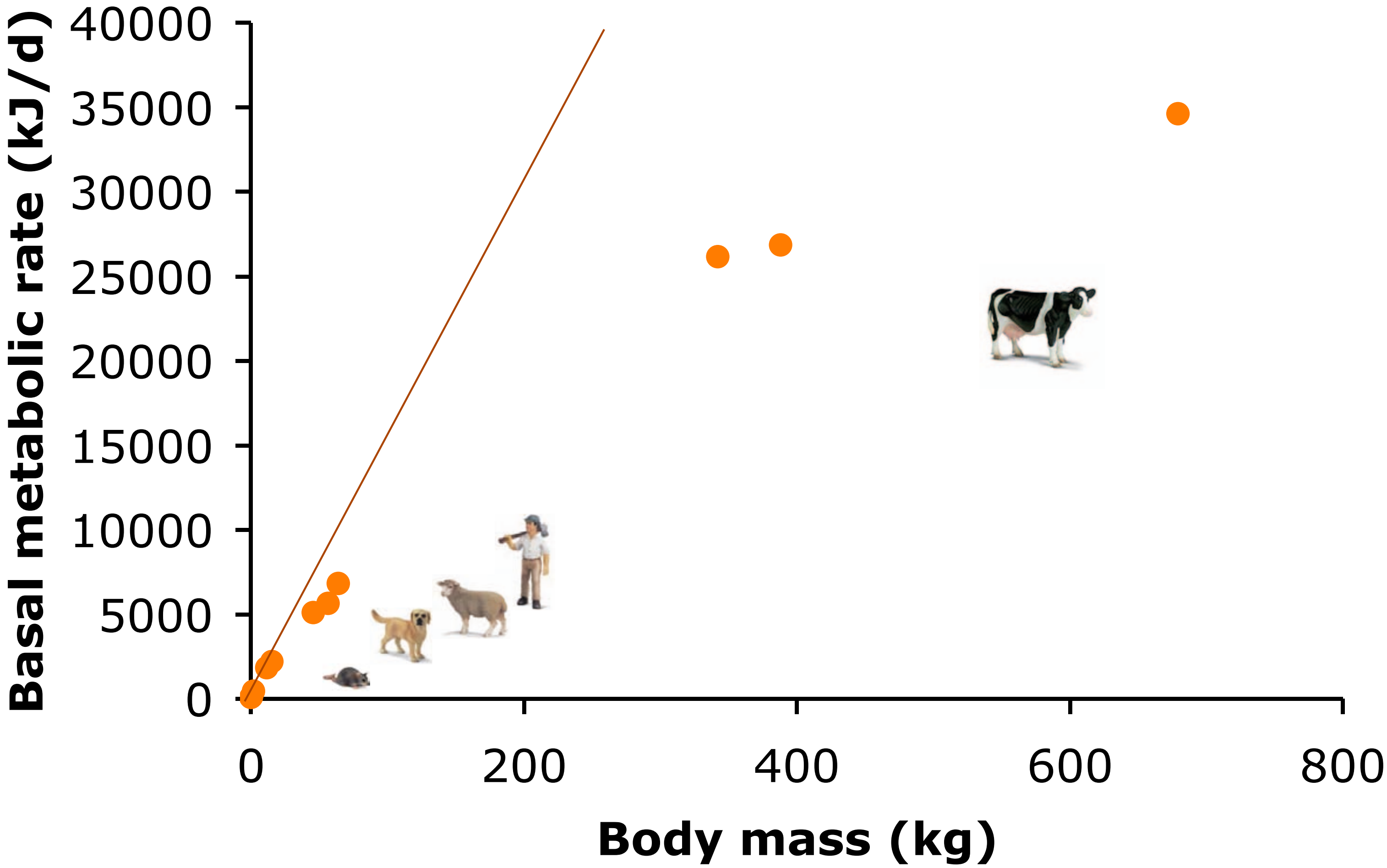


Data from ADAC (2007)

Kleiber (1932)



Kleiber (1932)



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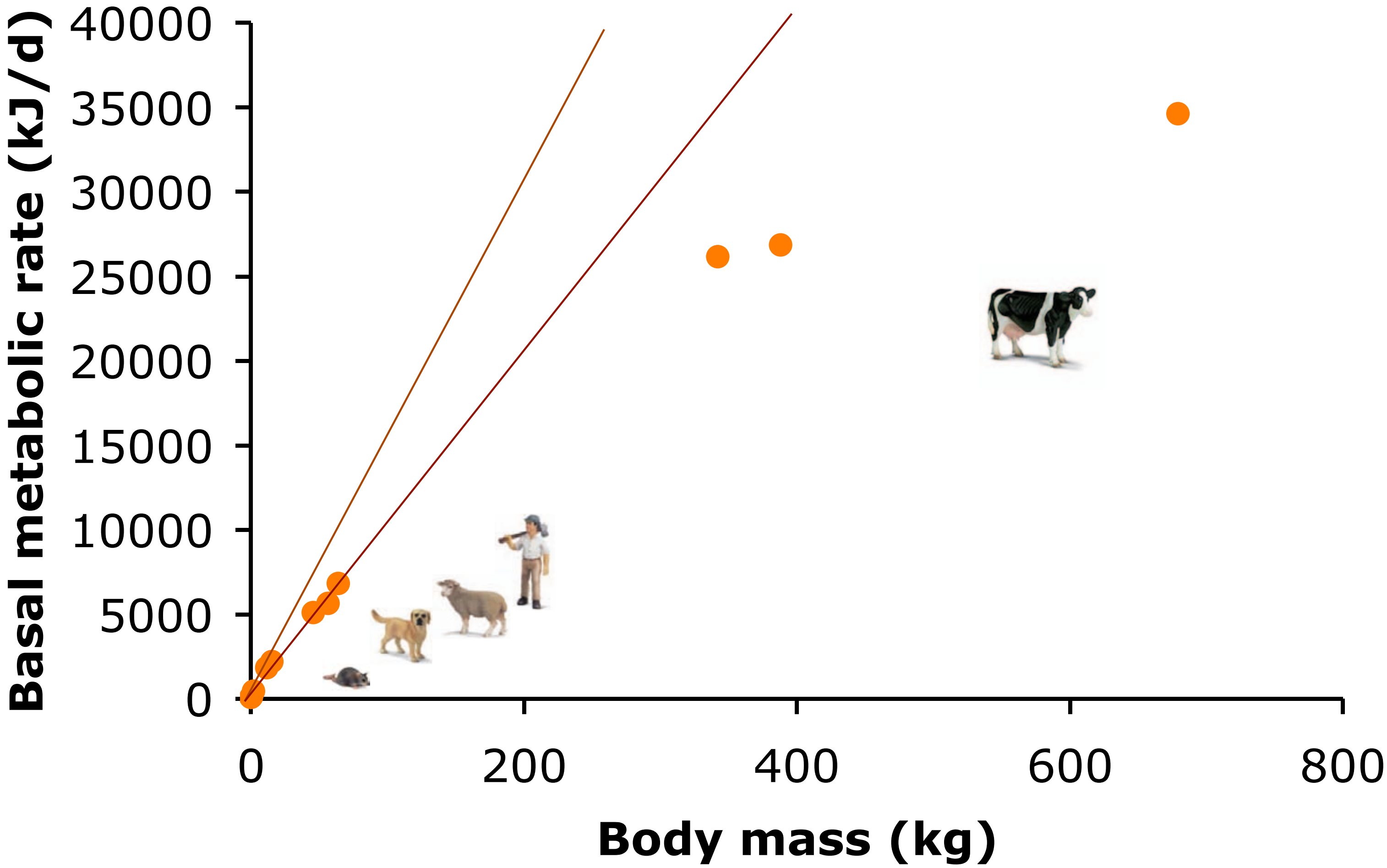

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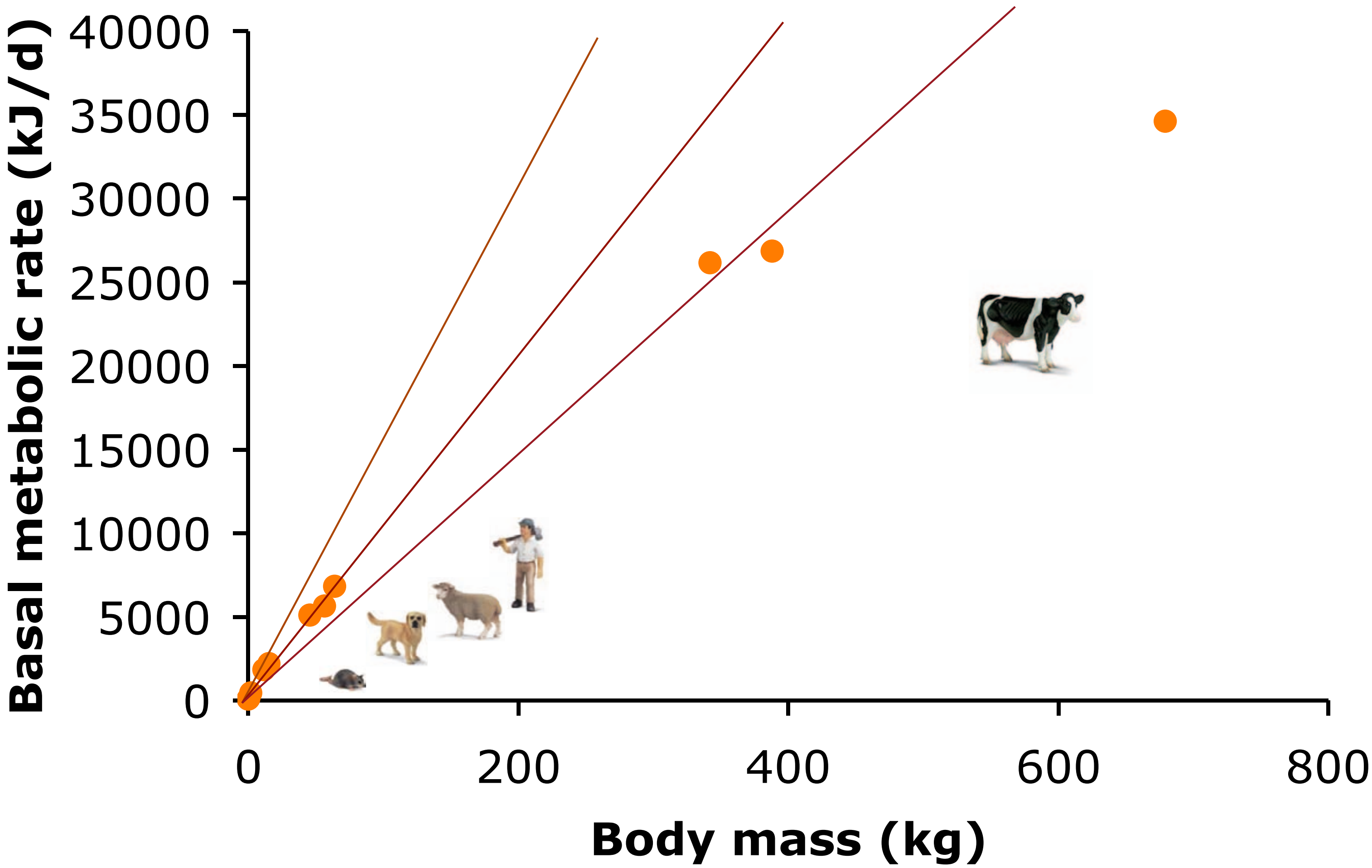

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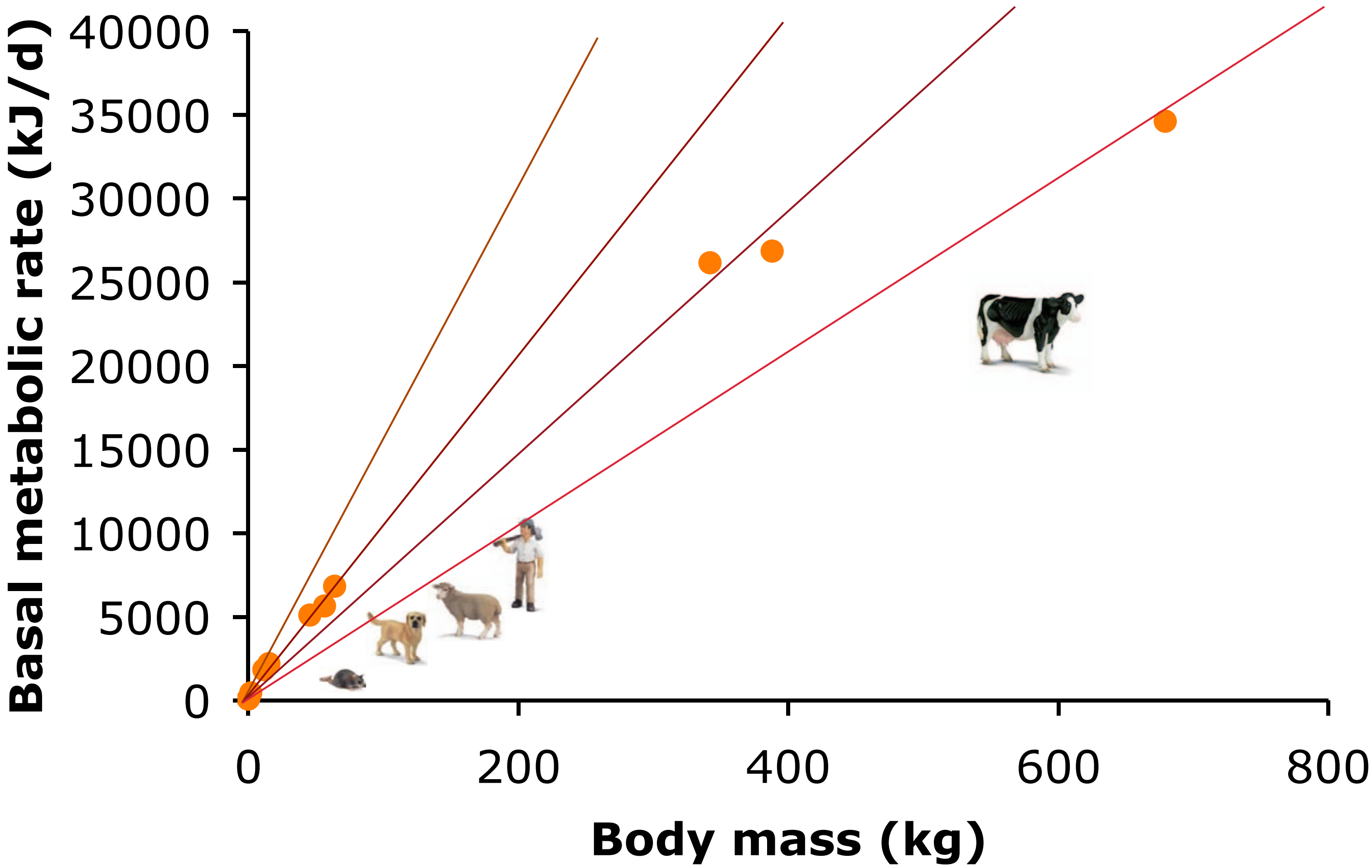

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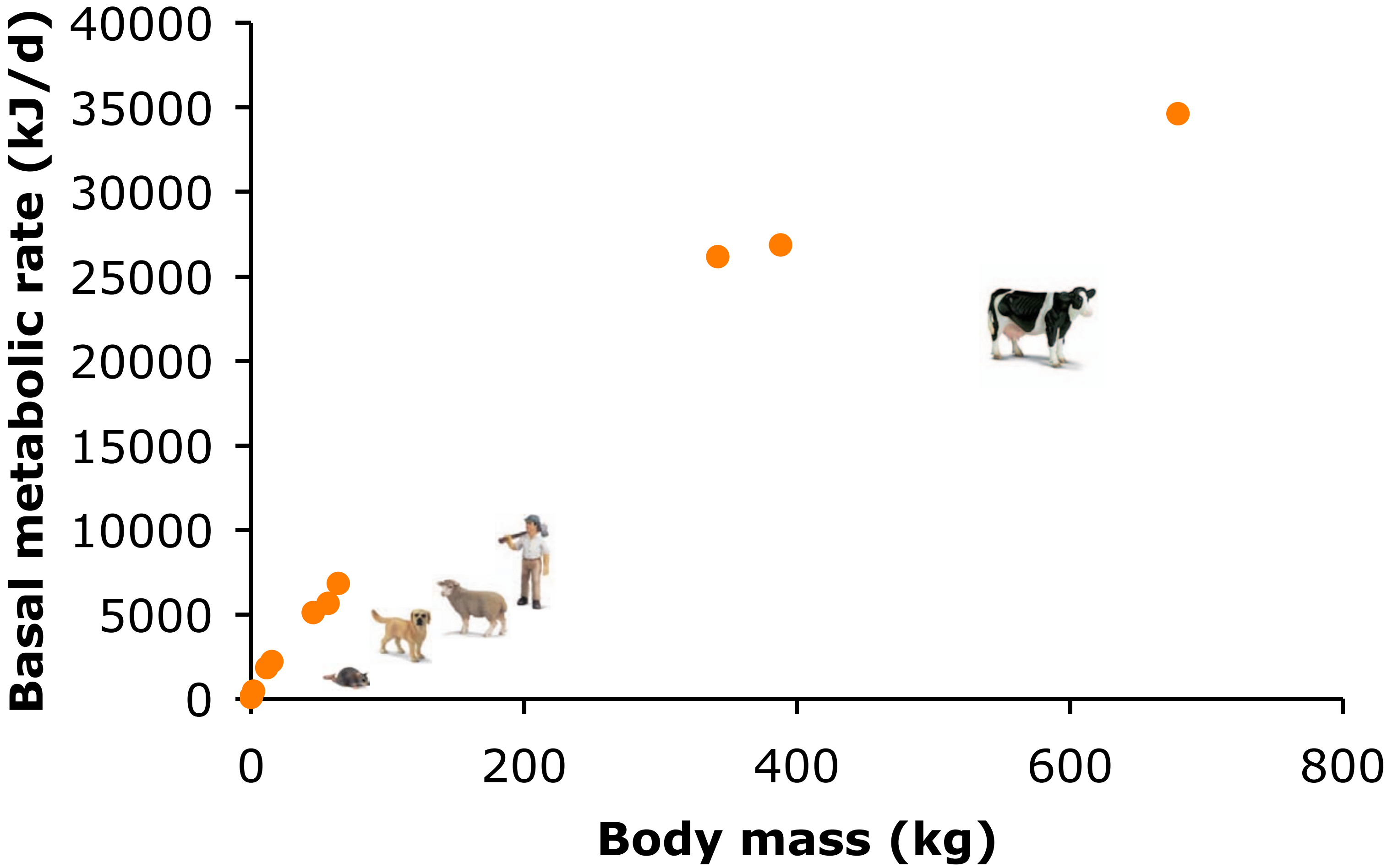

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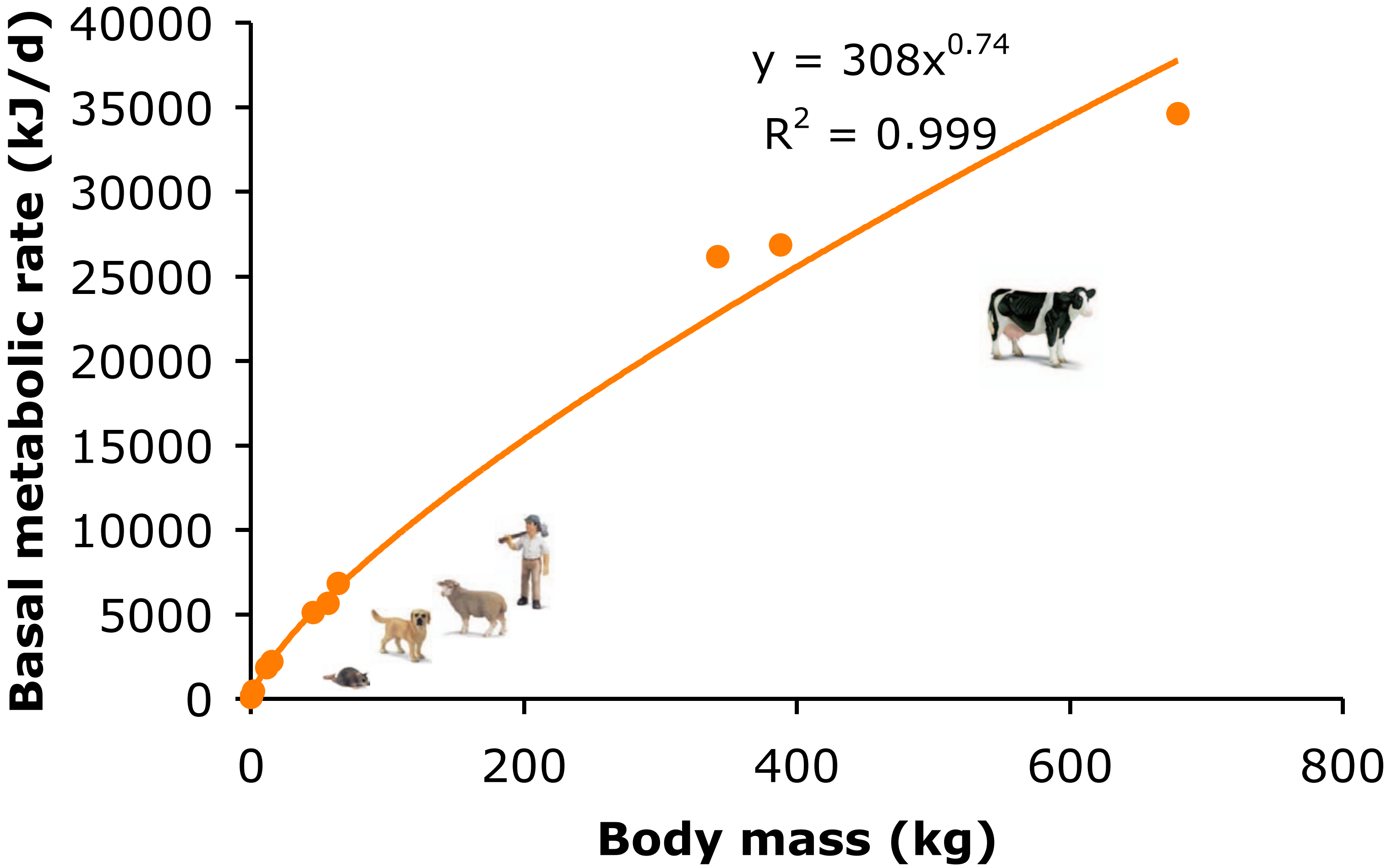

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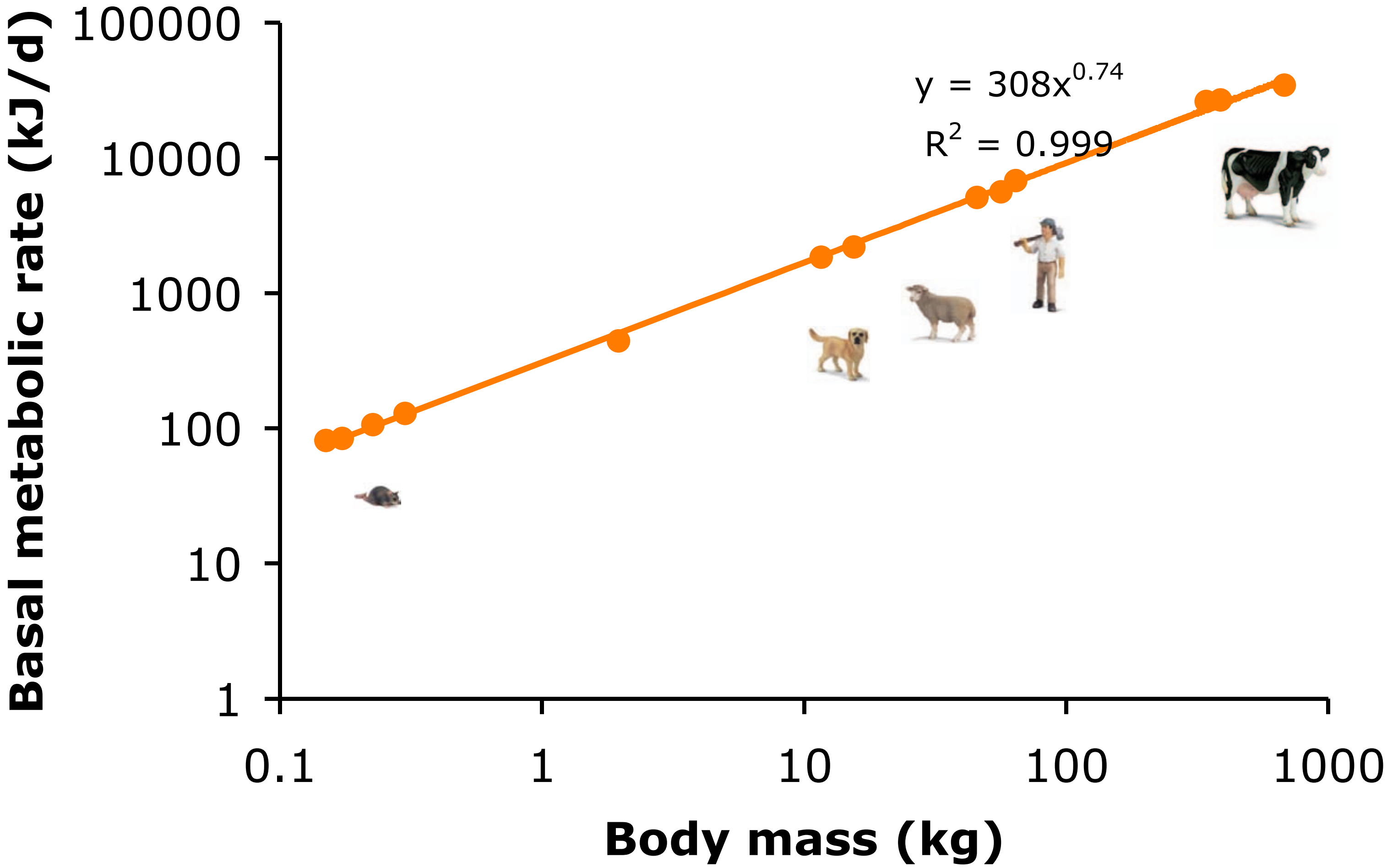

Allometry

$$\textit{Target parameter} = a * \textit{body mass}^{b}$$

$$Z = a * BM^{b}$$

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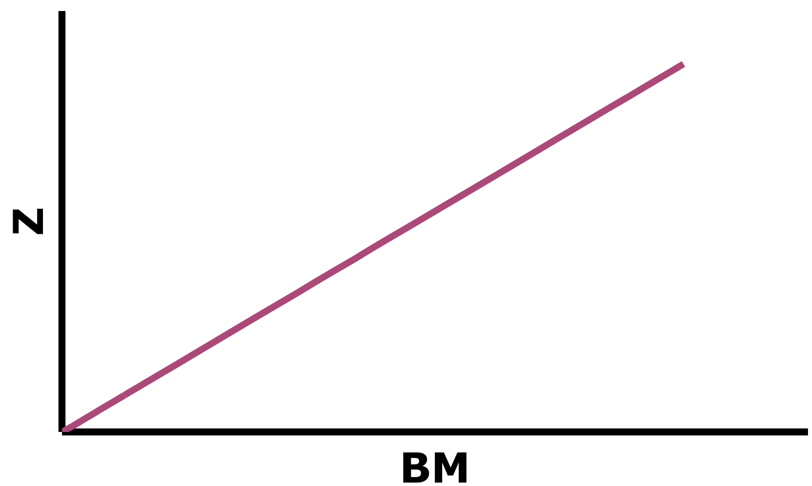

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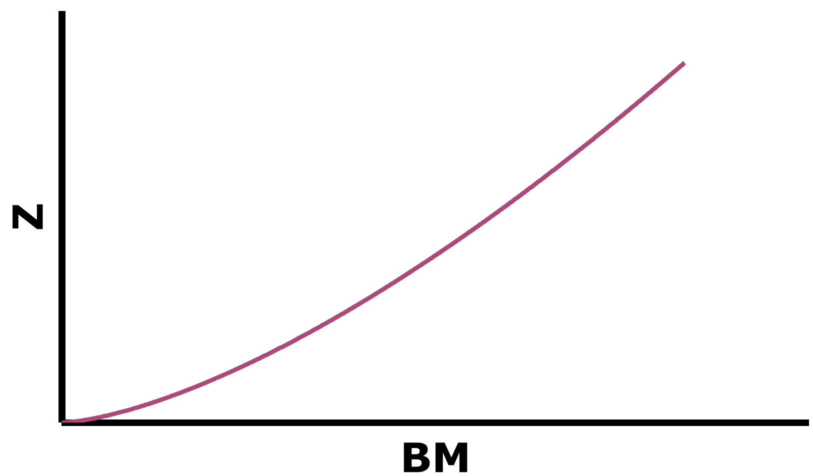
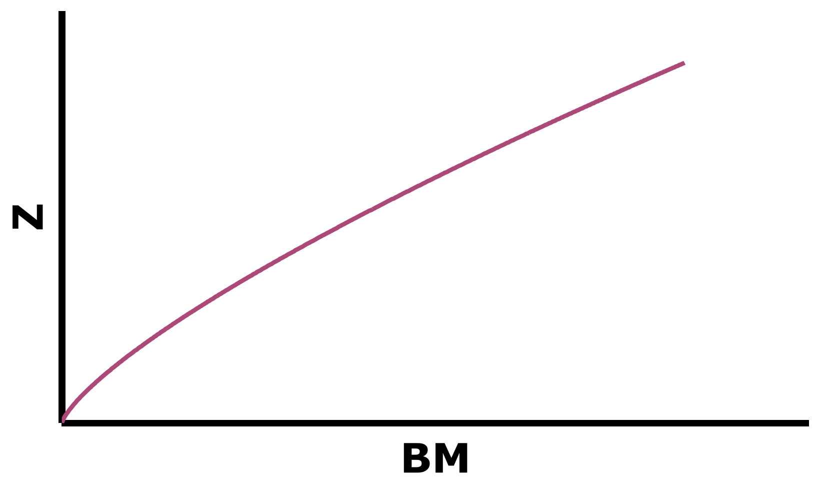


Allometry

*Target parameter = a * body mass*^{b}

$$Z = a * BM^b$$

b < 1

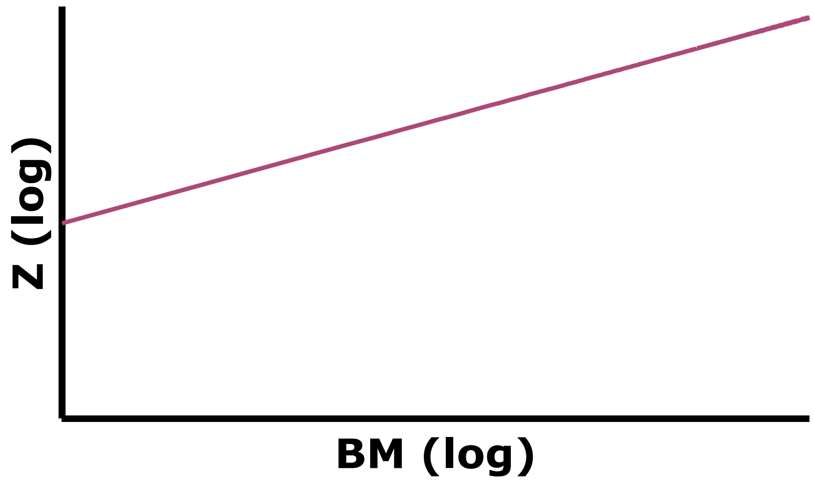


Allometry

*Target parameter = a * body mass*^{b}

$$\log(Z) = \log(a) + b\,\log(BM)$$

b < 1



Organ allometry

$$\text{Liver (kg)} = 0.033\ BW^{0.87}$$

$$\text{Brain (kg)} = 0.011\ BW^{0.76}$$

$$\text{Blood (kg)} = 0.069\ BW^{1.02}$$

$$\text{Muscle (kg)} = 0.450\ BW^{1.00}$$

$$\text{Skeleton (kg)} = 0.061\ BW^{1.09}$$

$$\text{Integument (kg)} = 0.134\ BW^{0.92}$$

$$\text{Gut contents (kg)} = 0.093\ BW^{1.08}$$

(Parra 1978, Calder 1983)

Basal metabolic rate

- Energy production
  - in resting
  - awake
  - at thermoneutrality
  - „post-absorptive□(not digesting)

Rubner’s Surface Law (1883)

- The basal metabolism of an animal is determined by its energy losses to the environment.
- These losses are determined by the contact surface to the environment - i.e. the body surface.
- ***With increasing body mass the ratio of surface to volume decreases.***

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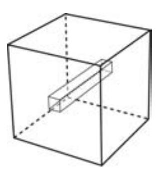

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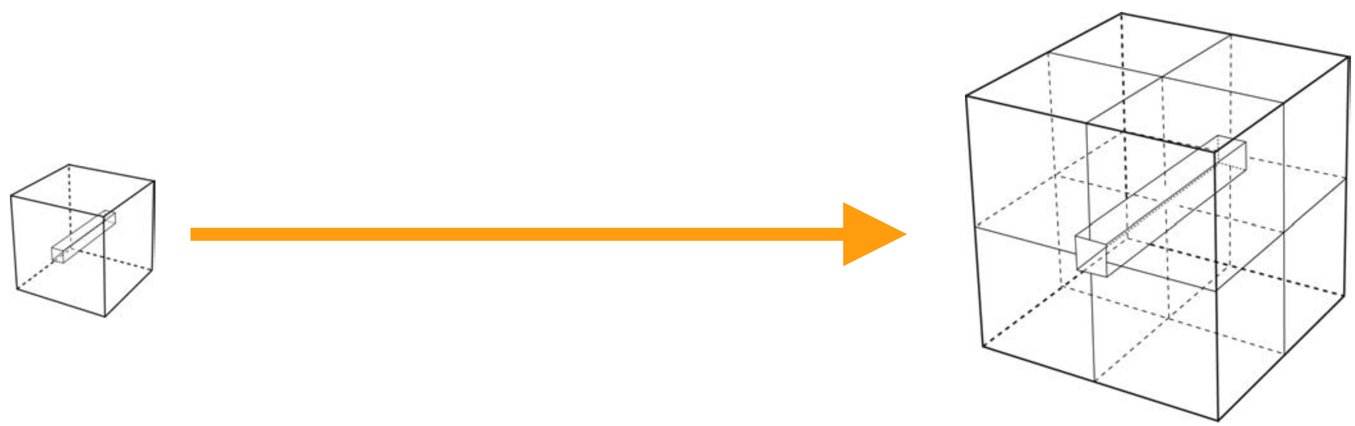

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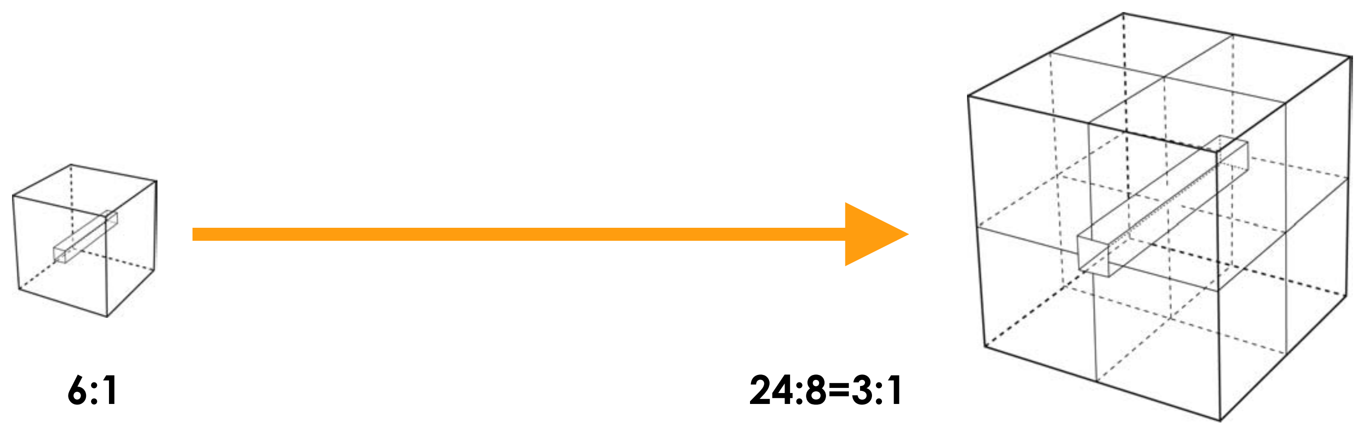
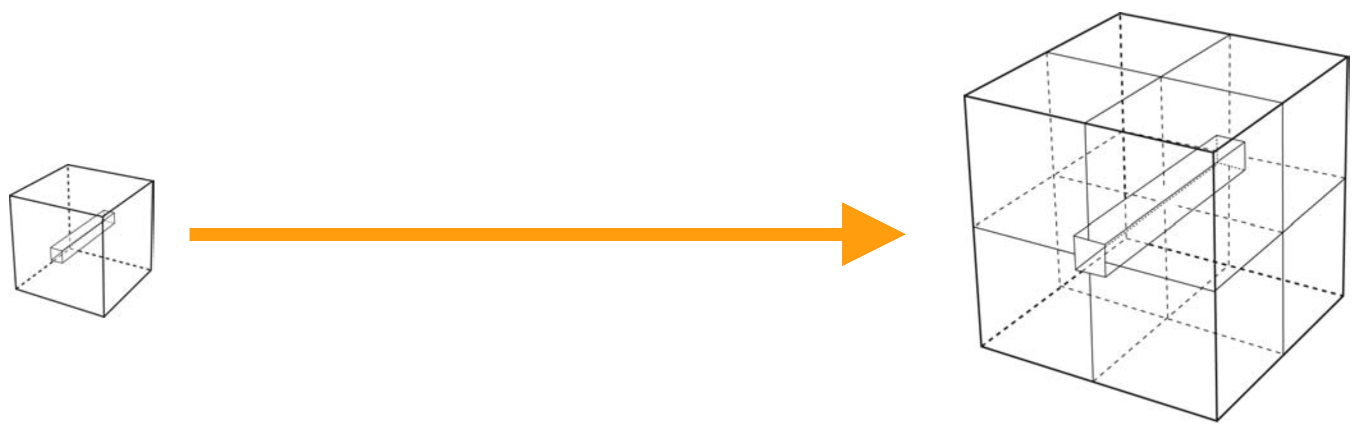


Rubner's Surface Law (1883)

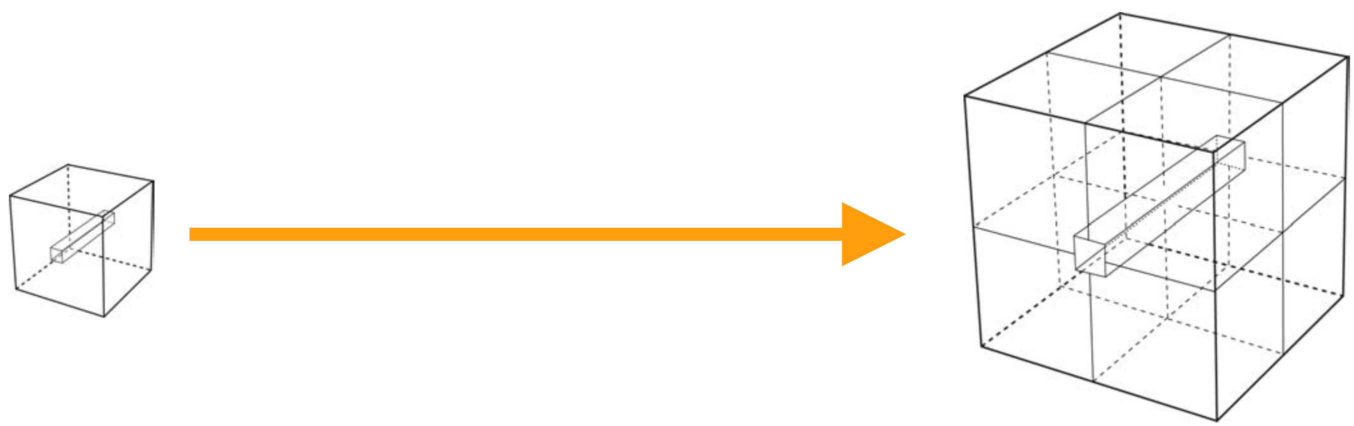
- The volume of a geometric body increases with $mass^{3/3} = mass^{1}$.
- The surface of a geometric body increases with $mass^{2/3} = mass^{0.67}$.
- The length of a geometric body increases with $mass^{1/3} = mass^{0.33}$.

- ***Basal metabolic rate should scale to $mass^{0.67}$.***



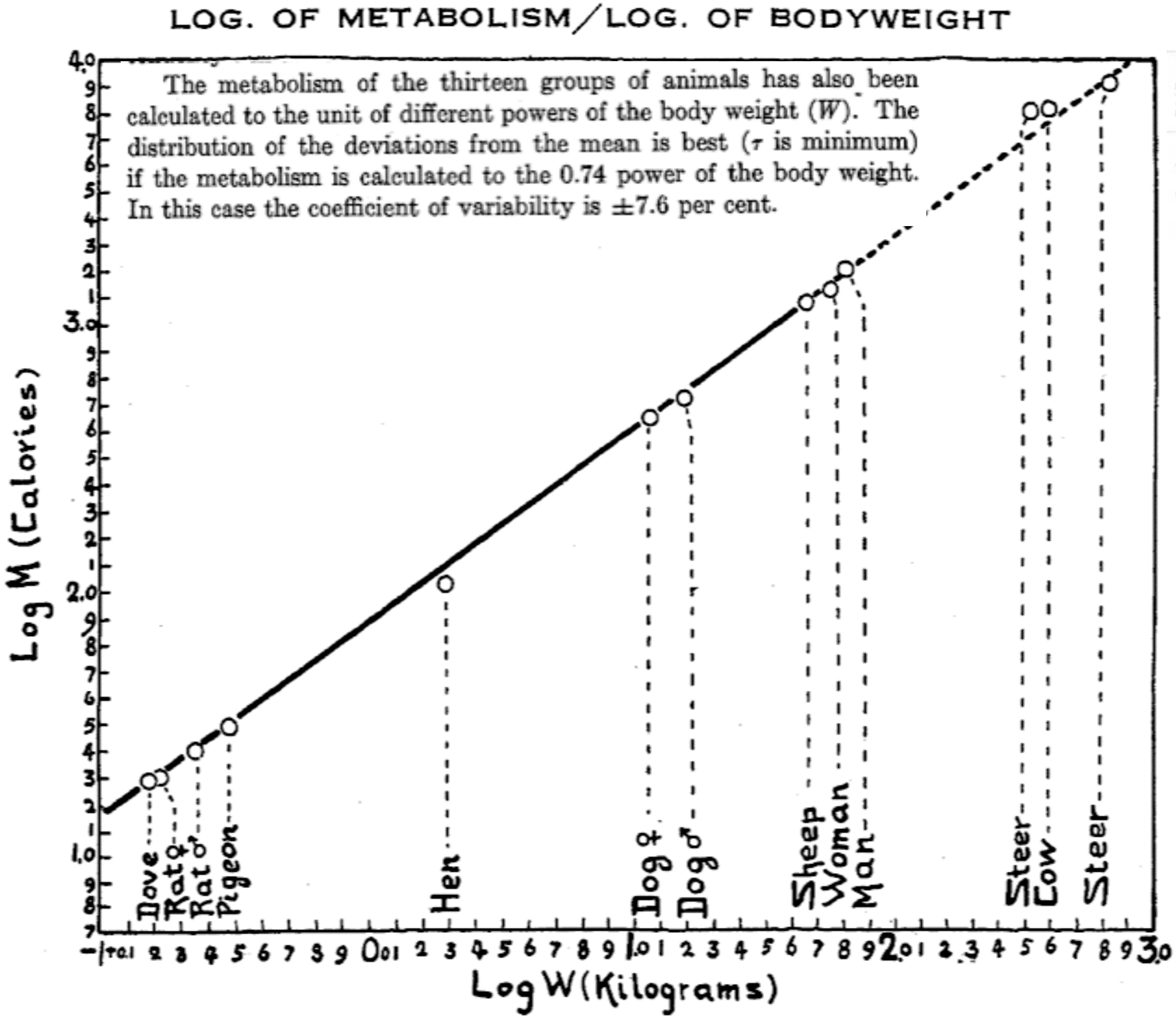
Rubner's Surface Law (1883)

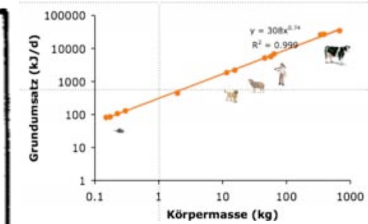
- If every cell of an elephant produced the same heat as a mouse cell, the elephant would be well done within a day.
- If every cell of a mouse produced the same heat as an elephant cell, the mouse would need a 20 cm-thick fur to maintain a constant body temperature.



0.67

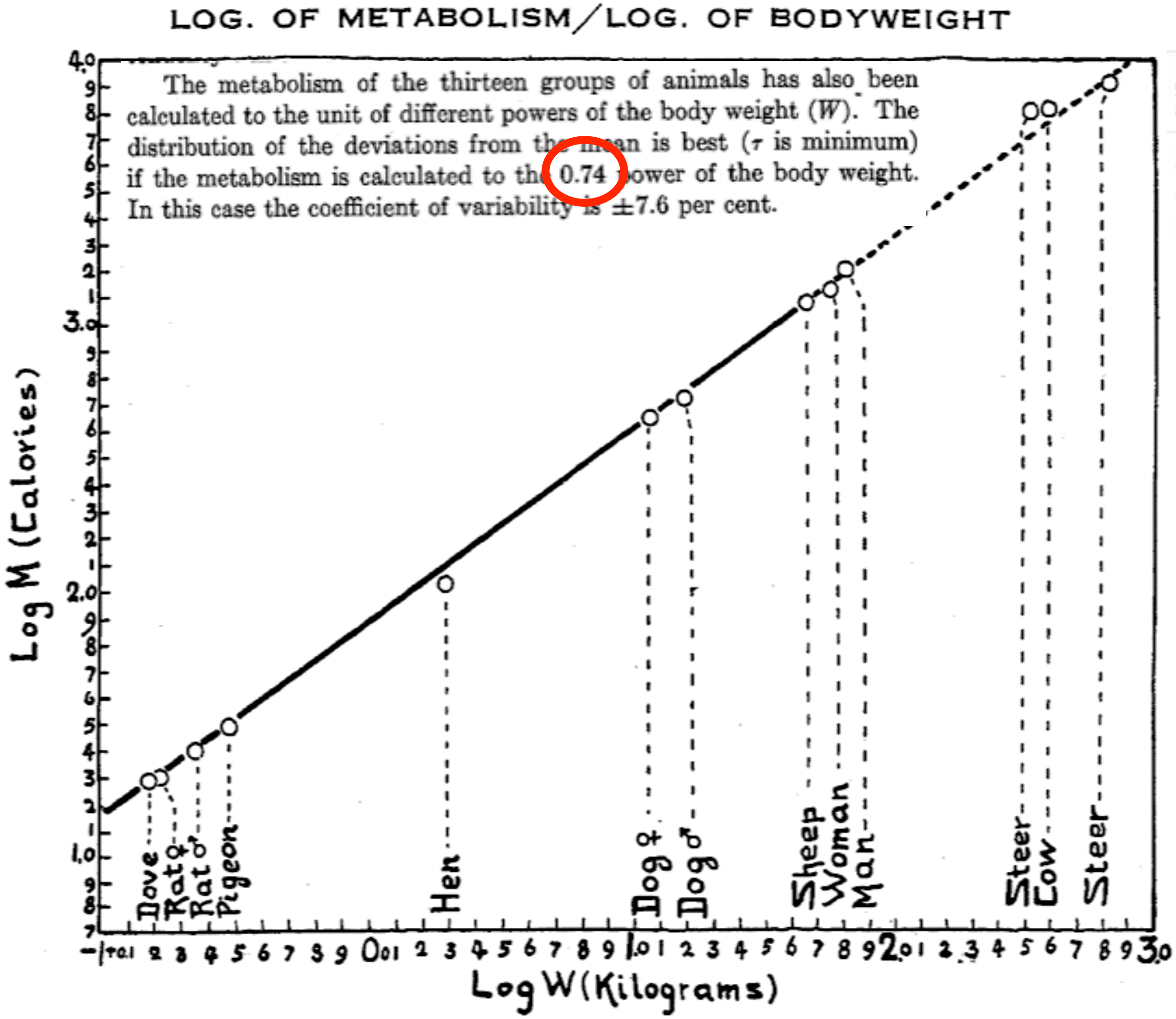
Kleiber (1932)

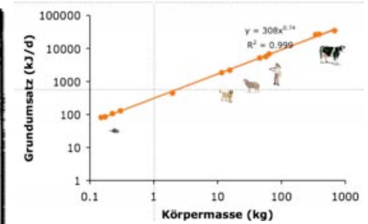




0.74

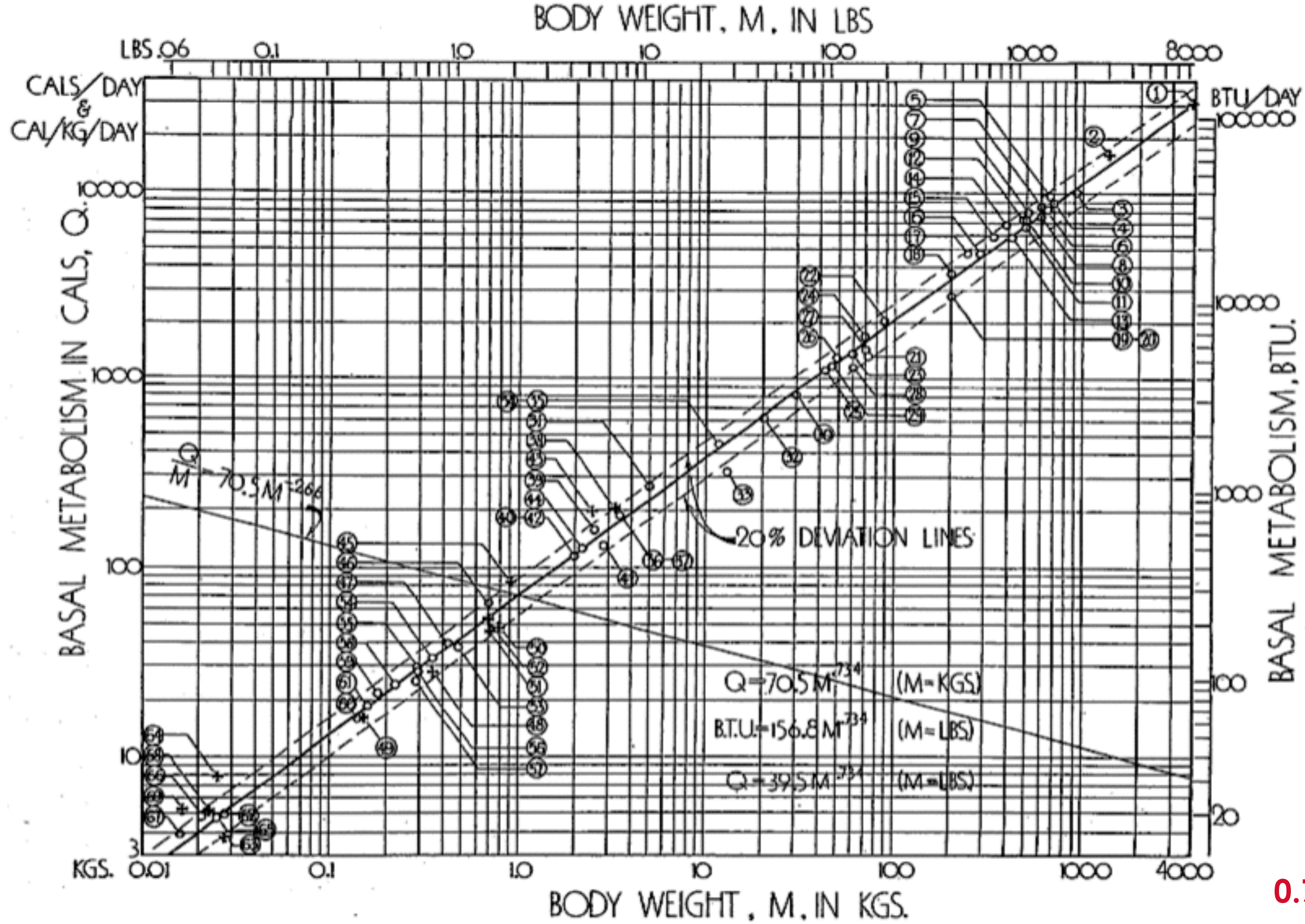
Kleiber (1932)





0.74

Brody (1945): Mouse-to-Elephant-Curve



0.73

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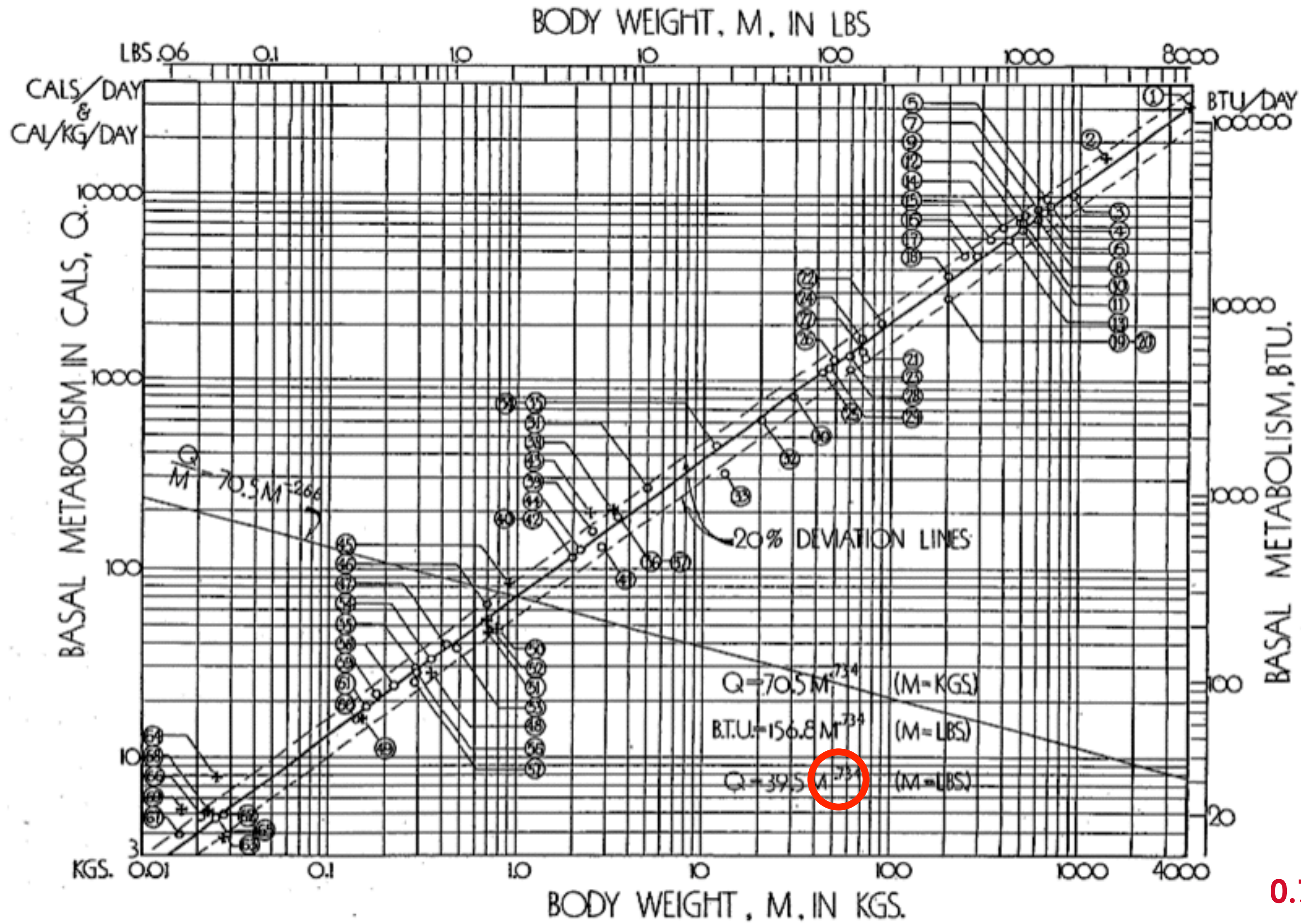
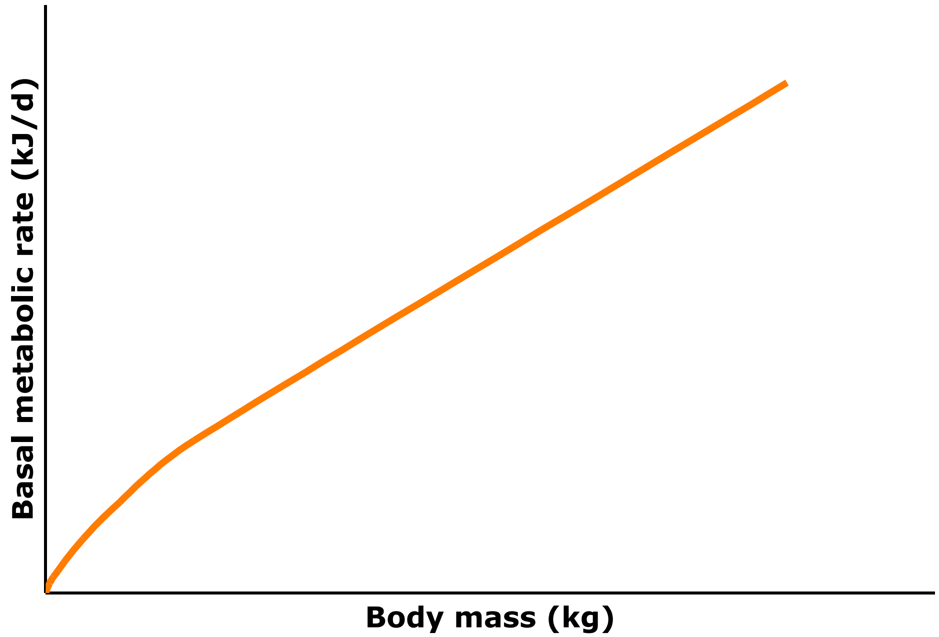


0.73

Calculation of BMR (kJ/d) in vertebrates

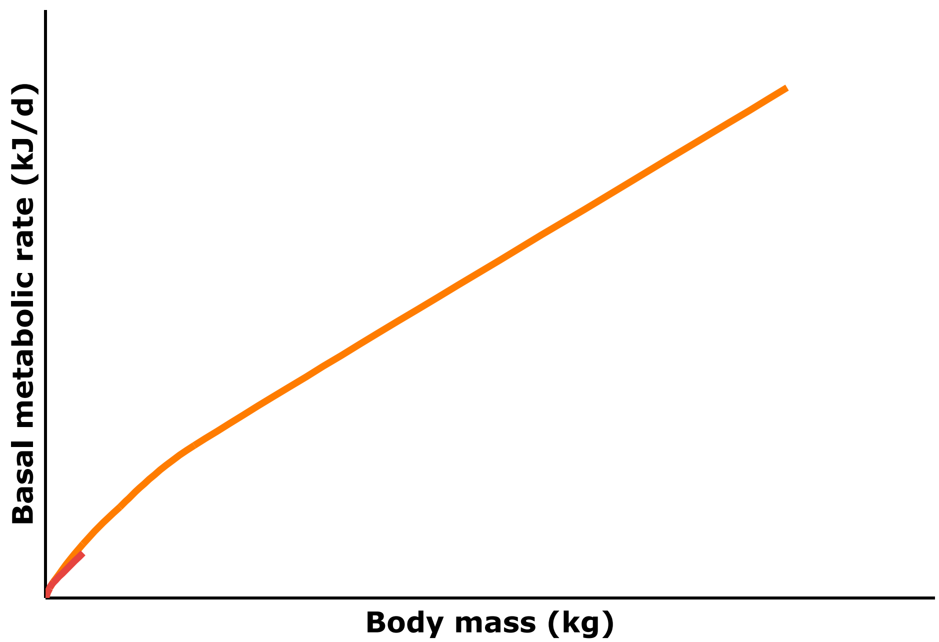
Calculation of BMR (kJ/d) in vertebrates

- mammals: $293\ BM^{0.75}$



Calculation of BMR (kJ/d) in vertebrates

- mammals: $293\ BM^{0.75}$
- birds: $335\ BM^{0.67}$



Calculation of BMR (kJ/d) in vertebrates

- mammals: $293\ BM^{0.75}$
- birds: $335\ BM^{0.67}$
- reptiles (30°C): $28\ BM^{0.77}$

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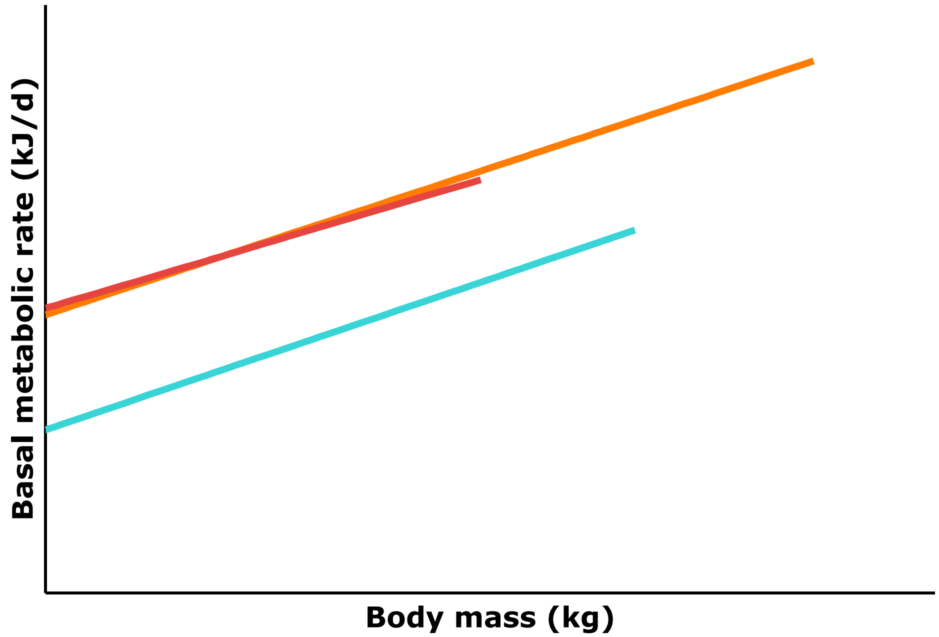
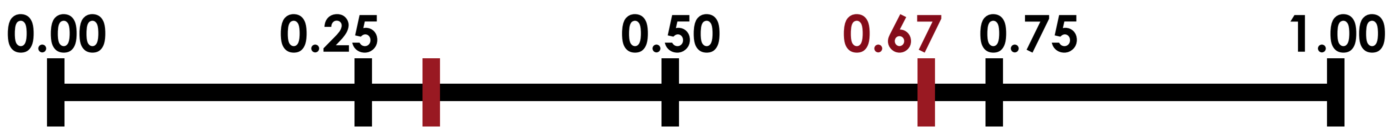


0.67 or 0.75 ?



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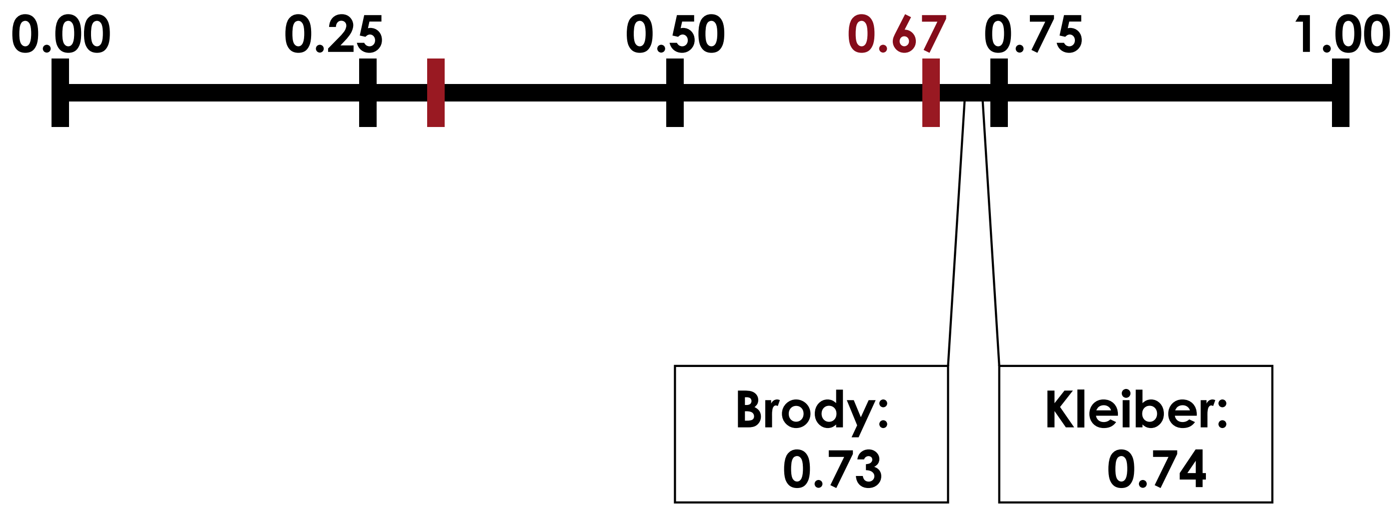

Why 0.75 ?

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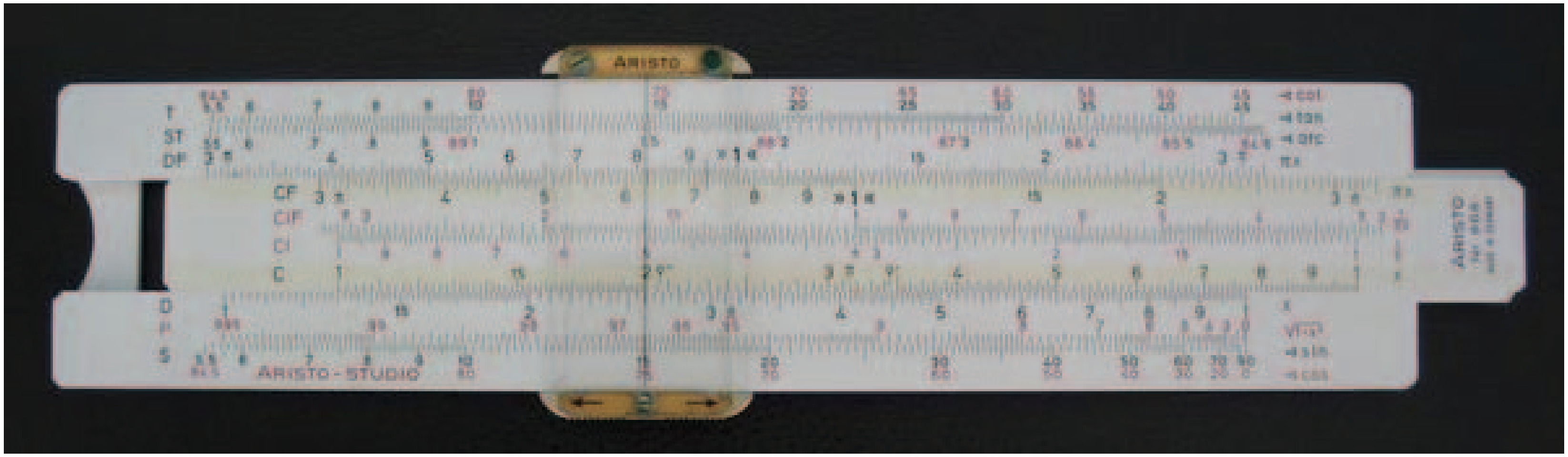


Why 0.75 ?

„The widespread use and acceptance of Kleiber‘s exponent can probably be attributed to a remarkably tight regression fit (r^2=0.999; n=13). To put this r^2 in perspective, we randomly selected 250000 groups of 13 species from a list of 391 species compiled by Heusner (including Kleiber's data). Each group had a mass range of 3-4 orders of magnitude. Of the 250000 regressions, only four had an r^2 greater than 0.9980 and none an r^2 greater than 0.9990. The strength of Kleiber's exponent therefore seems to stem from an exceedingly fortuitous selection of data.“

(White & Seymour 2003)

0.67 or 0.75 ?

Functional Ecology 2004
18, 257–282

FORUM

The predominance of quarter-power scaling in biology

V. M. SAVAGE,*‡† J. F. GILLOOLY,§ W. H. WOODRUFF,*‡ G. B. WEST,*‡ A. P. ALLEN,§ B. J. ENQUIST¶ and J. H. BROWN*§

**The Santa Fe Institute, 1399 Hyde Park Road., Santa Fe, NM 87501 USA, ‡Los Alamos National Laboratory, Los Alamos, NM 87545 USA, §Department of Biology, The University of New Mexico, Albuquerque, NM 87131 USA, and ¶Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA*

Mammalian basal metabolic rate is proportional to body mass$^{2/3}$

4046–4049 | PNAS | **April 1, 2003** | vol. 100 | no. 7

Craig R. White* and Roger S. Seymour

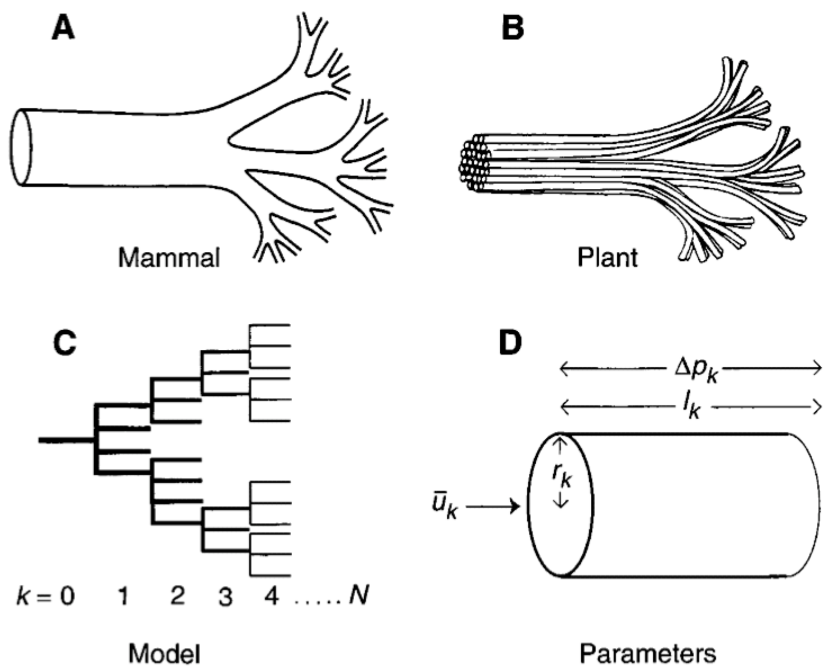
Department of Environmental Biology, University of Adelaide, Adelaide 5005, Australia

0.67 or 0.75 ?

SCIENCE • VOL. 276 • 4 APRIL 1997

A General Model for the Origin of Allometric Scaling Laws in Biology

Geoffrey B. West, James H. Brown,* Brian J. Enquist



0.67 or 0.75 ?

Functional Ecology 2004
18, 283–289

FORUM

Is West, Brown and Enquist's model of allometric scaling mathematically correct and biologically relevant?

J. KOZŁOWSKI*† and M. KONARZEWSKI‡
**Institute of Environmental Sciences, Jagiellonian University, Gronostajowa 7, 30–387 Krakow, Poland, and*
‡Institute of Biology, University of Bialystok, Swierkowa 20B, 15–950 Bialystok, Poland

Functional Ecology 2005
19, 735–738

FORUM

Yes, West, Brown and Enquist's model of allometric scaling is both mathematically correct and biologically relevant

J. H. BROWN,*†¶ GEOFFREY B. WEST†‡ and B. J. ENQUIST§
**Department of Biology, University of New Mexico, Albuquerque, NM 87131, USA, †Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, NM 87501, USA, ‡Theoretical Division, MS B285, Los Alamos National Laboratory, Los Alamos, NM 87545, USA, §Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA*

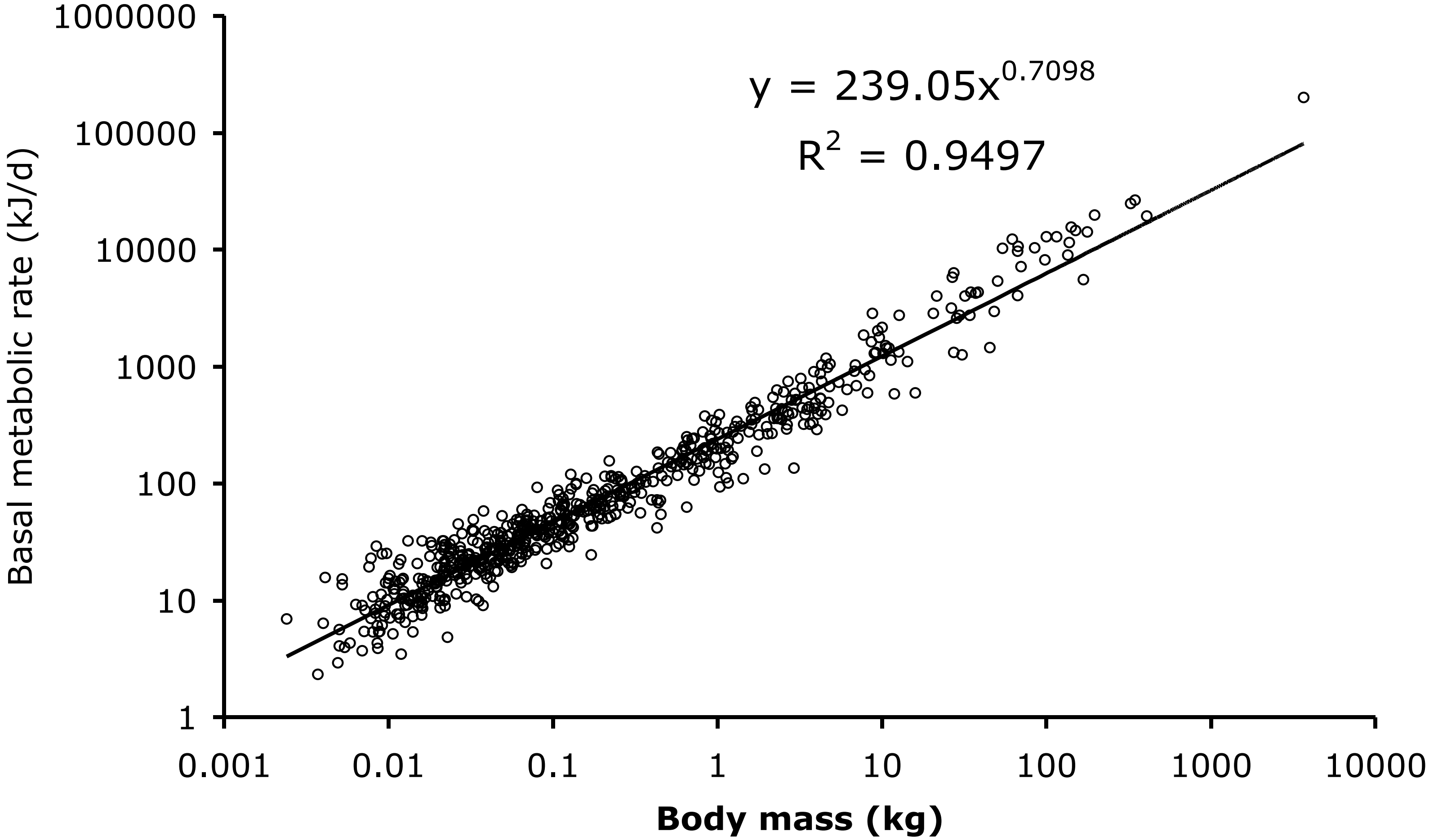
Functional Ecology 2005
19, 739–743

FORUM

West, Brown and Enquist's model of allometric scaling again: the same questions remain

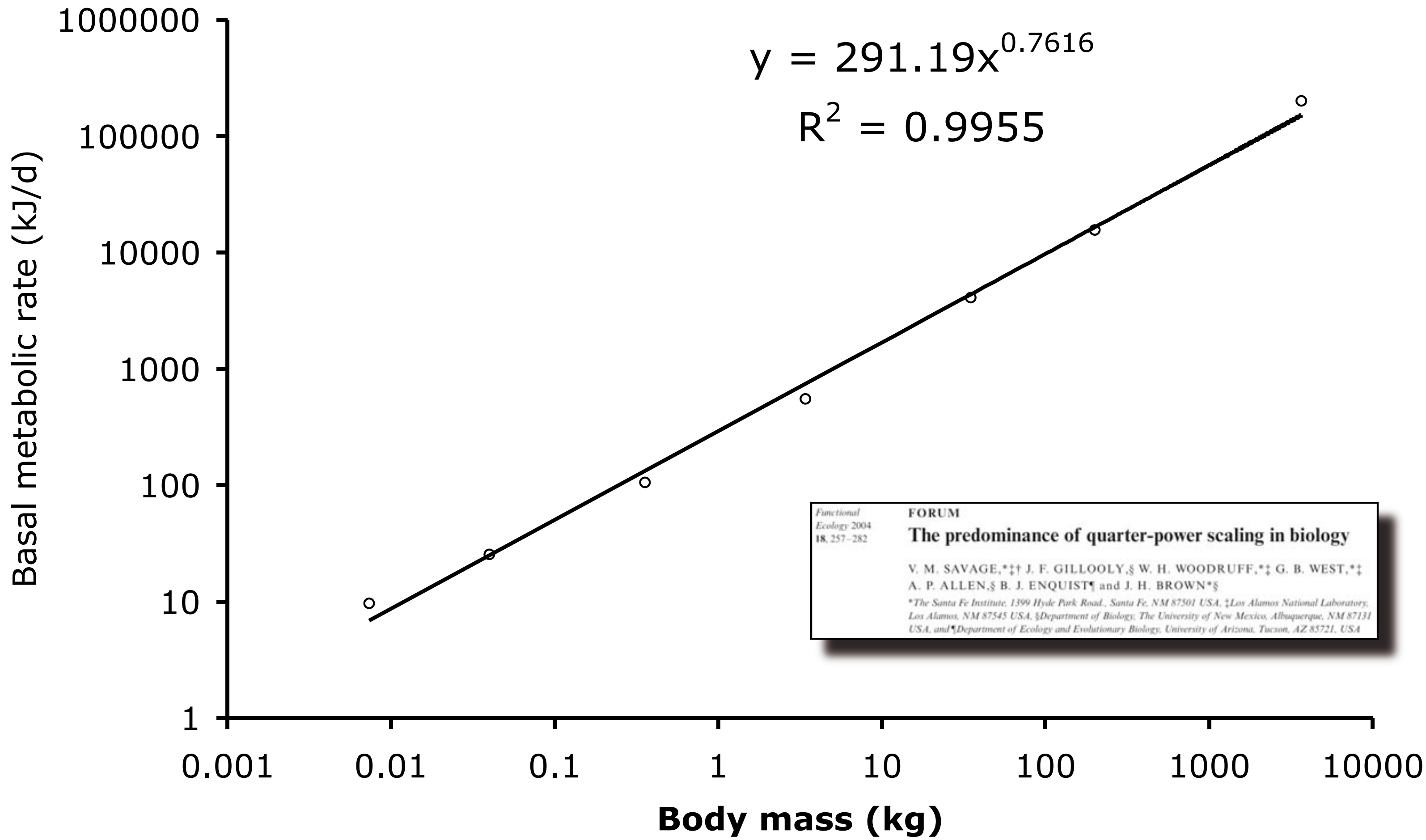
J. KOZŁOWSKI*‡ and M. KONARZEWSKI†
**Institute of Environmental Sciences, Jagiellonian University, Gronostajowa 3, 30–387 Krakow, Poland,*
†Institute of Biology, University of Bialystok, Swierkowa 20B, 15–950 Bialystok, Poland

Savage, West et al. (2004): 626 Species!



Data from Savage et al. (2004)

Savage, West et al. (2004): Body mass-“binning”!



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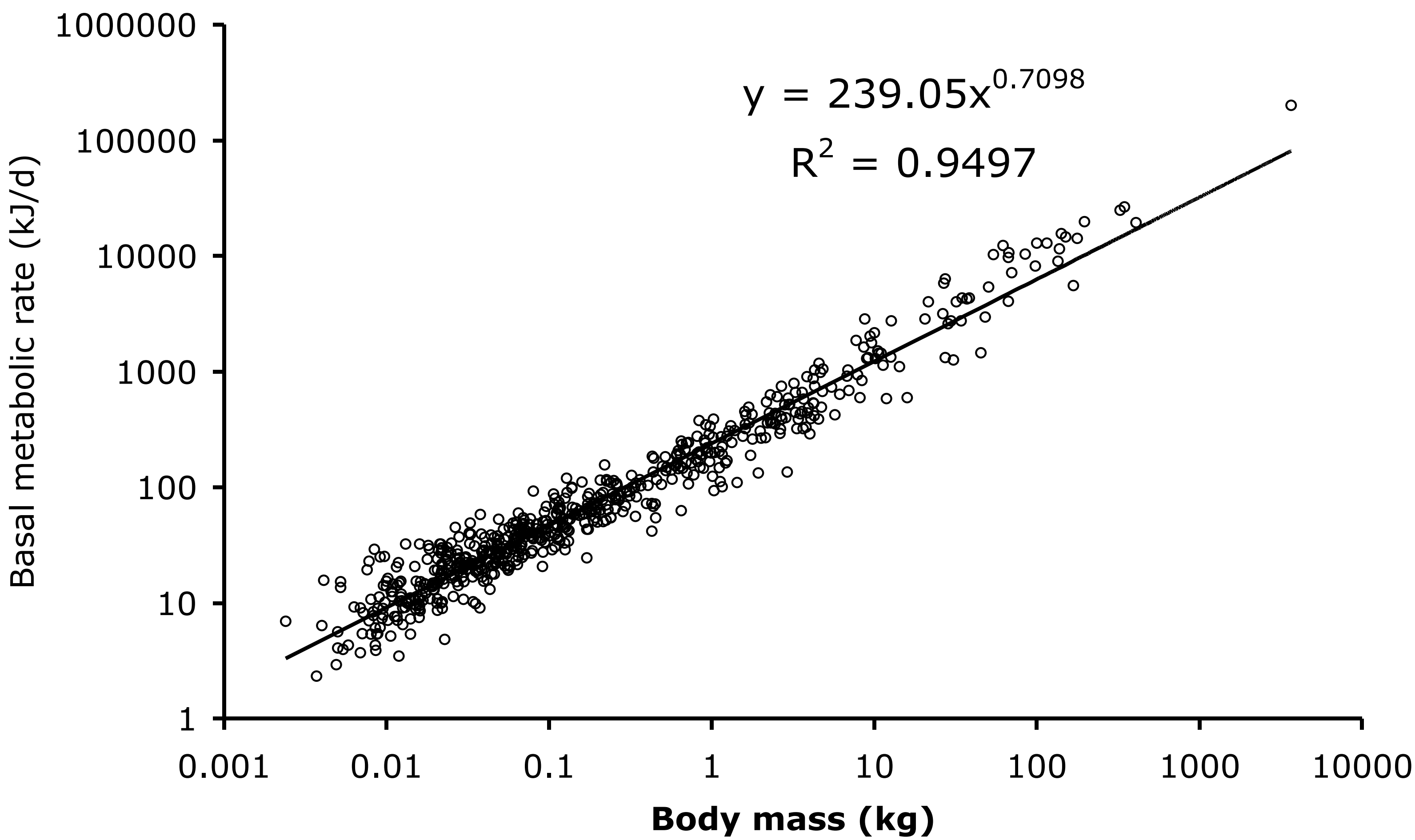

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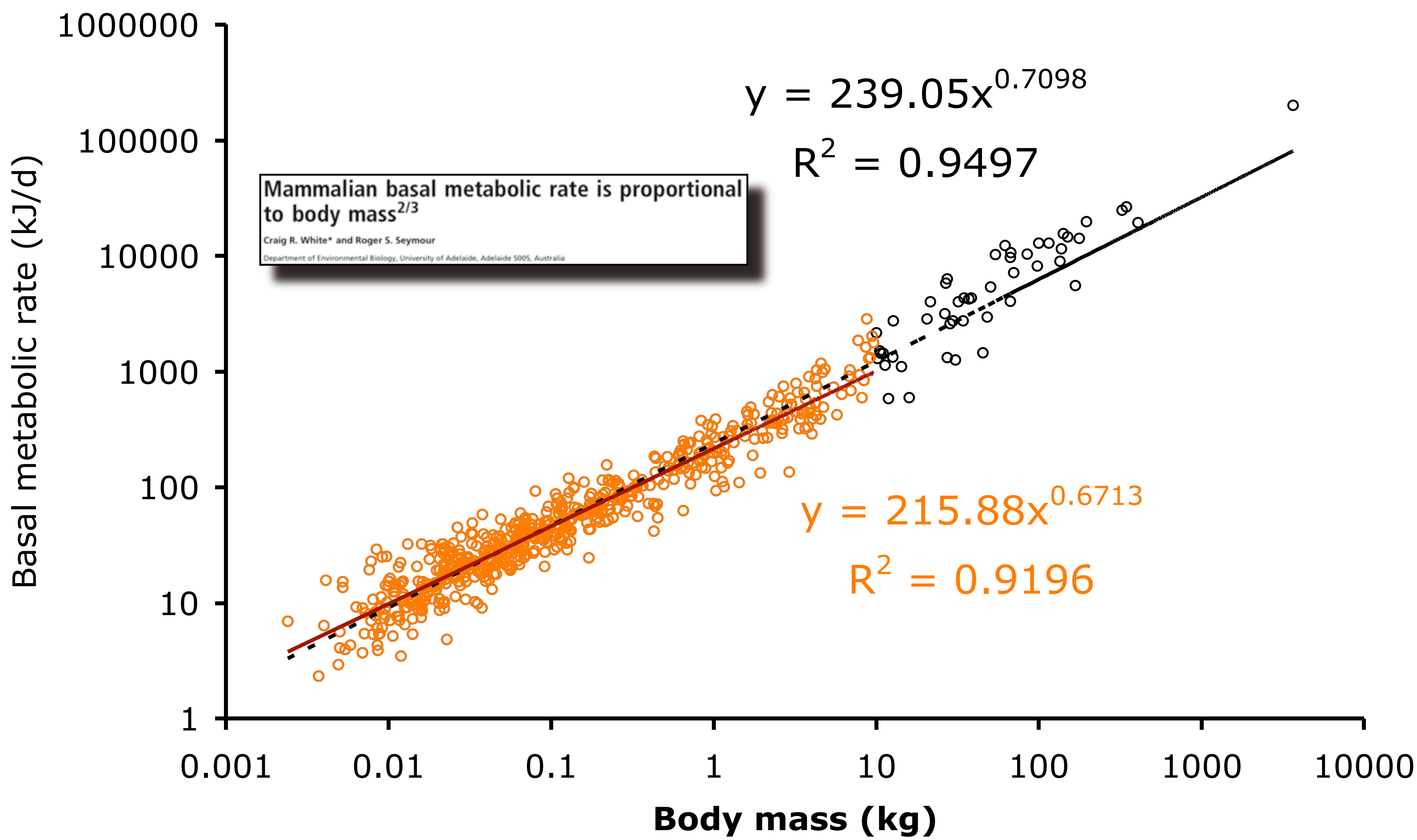
White & Seymour (2003): exclude large animals!



Data from Savage et al. (2004)

Basal metabolic rate

- Energy production
  - in resting
  - awake
  - at thermoneutrality
  - „post-absorptive“(not digesting)

White & Seymour (2003): exclude large animals!

- Large animals are mainly herbivores
- Large animals contain a high proportion of body mass as gut contents with an active but flora
- Large animals are rarely post-absorptive (even if a cow fasts for a day, it still has digesta in its rumen)

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$$t_{Elephant} = t_{Mouse} \left(KM_{Elephant}^{0.25} / KM_{Mouse}^{0.25}\right)$$

$$t_{Mouse} = 3 \text{ hours}$$

$$t_{Elephant} = 53 \text{ hours}$$

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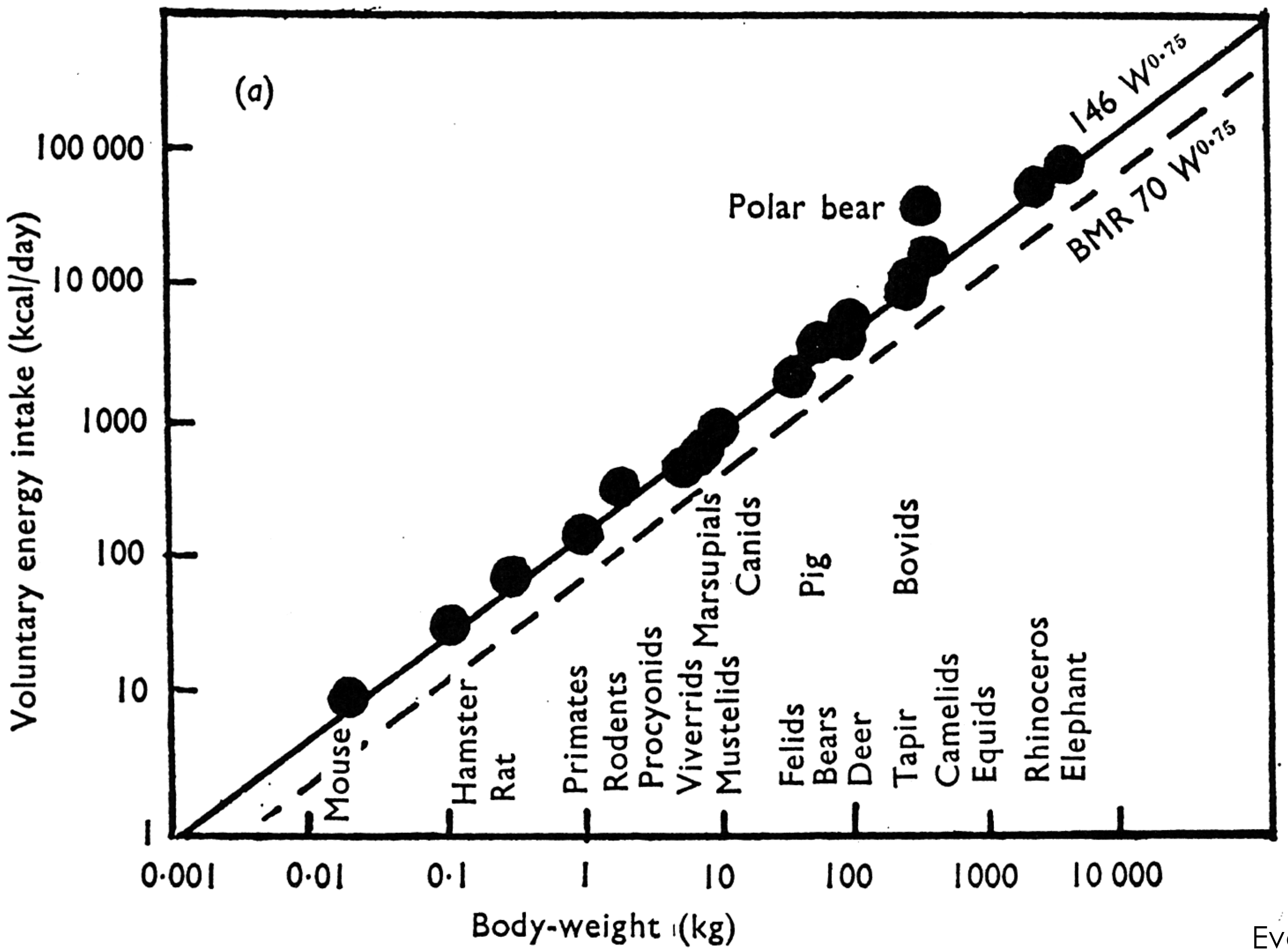
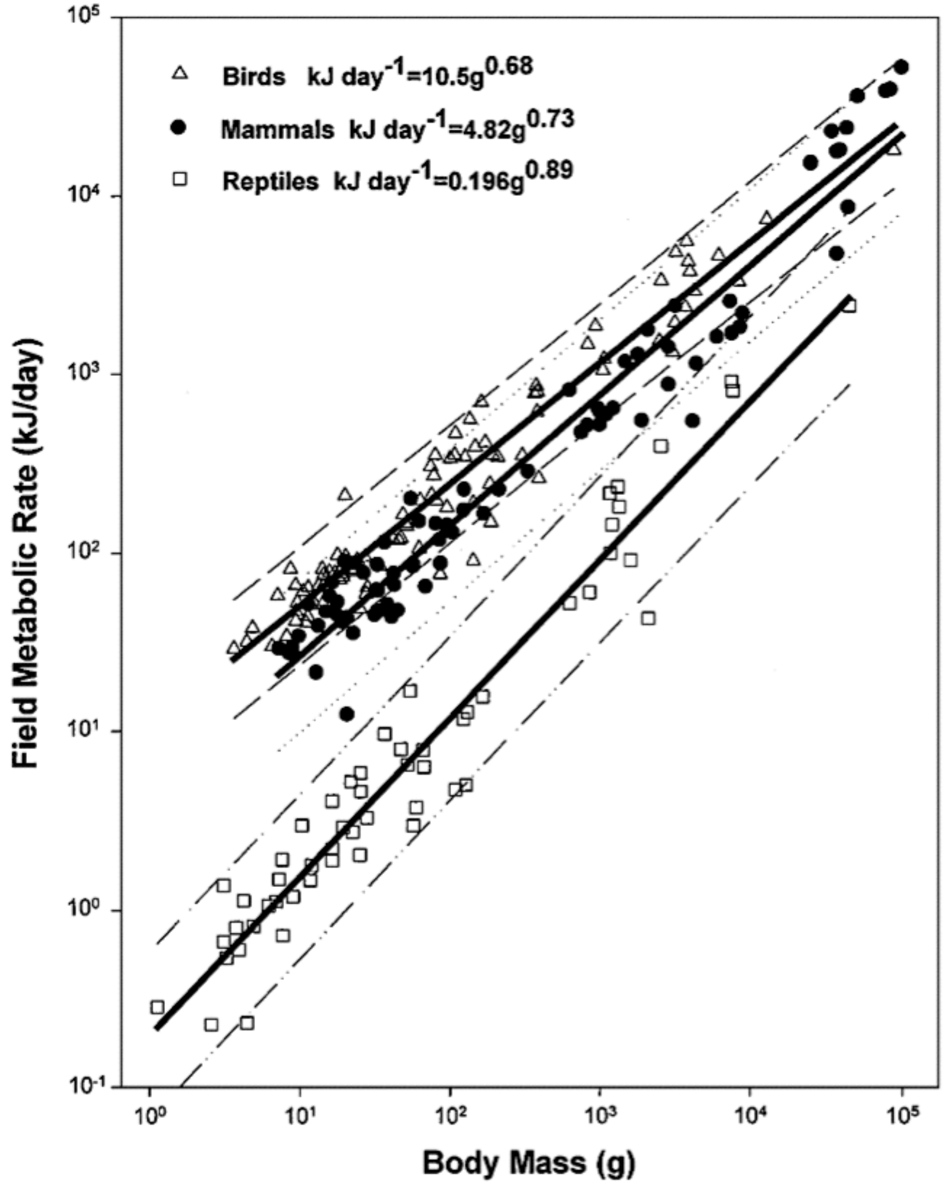
Voluntary food intake at the zoo



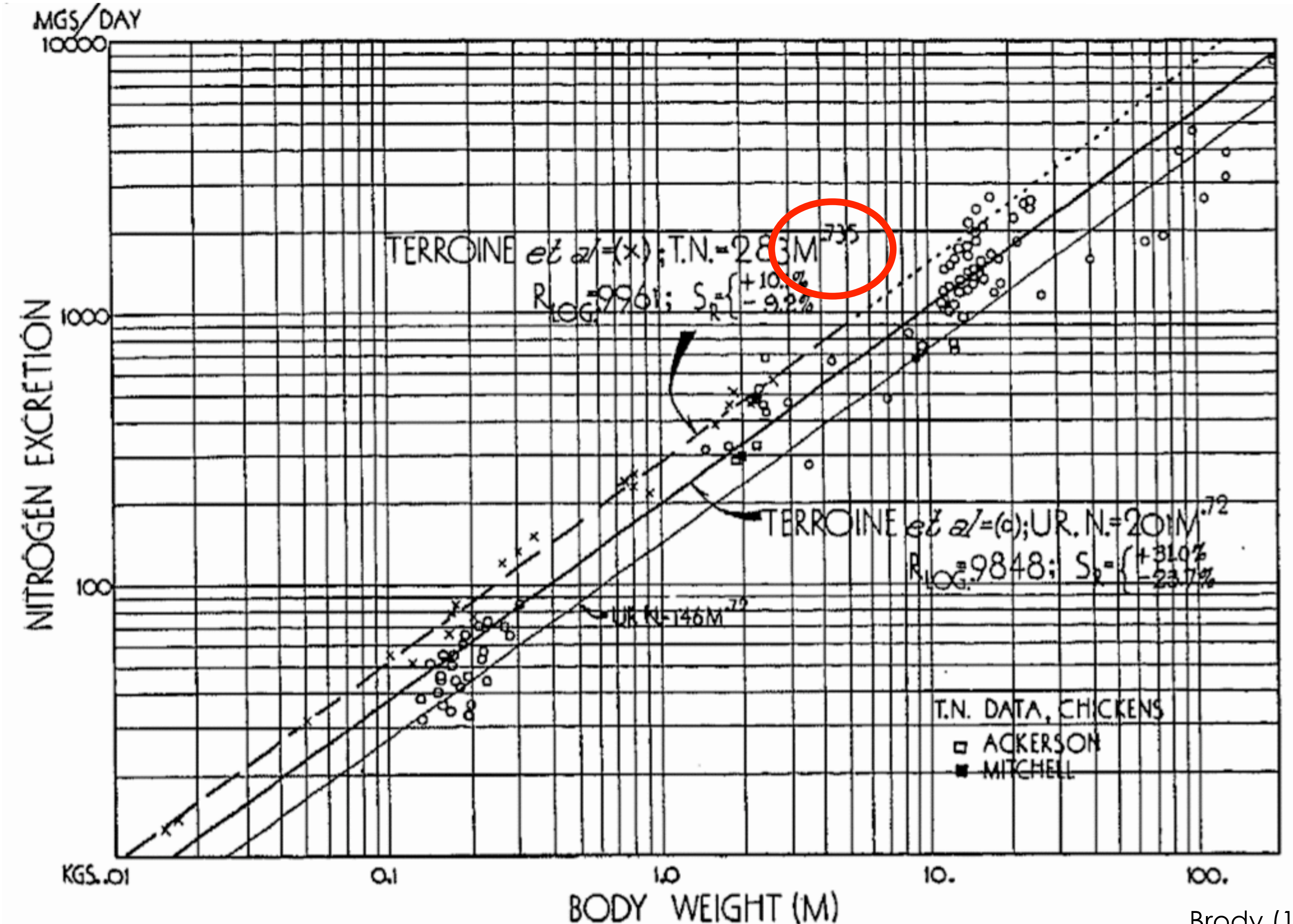
Evans & Miller (1968)

Energy expenditure in real life (field metabolic rate)



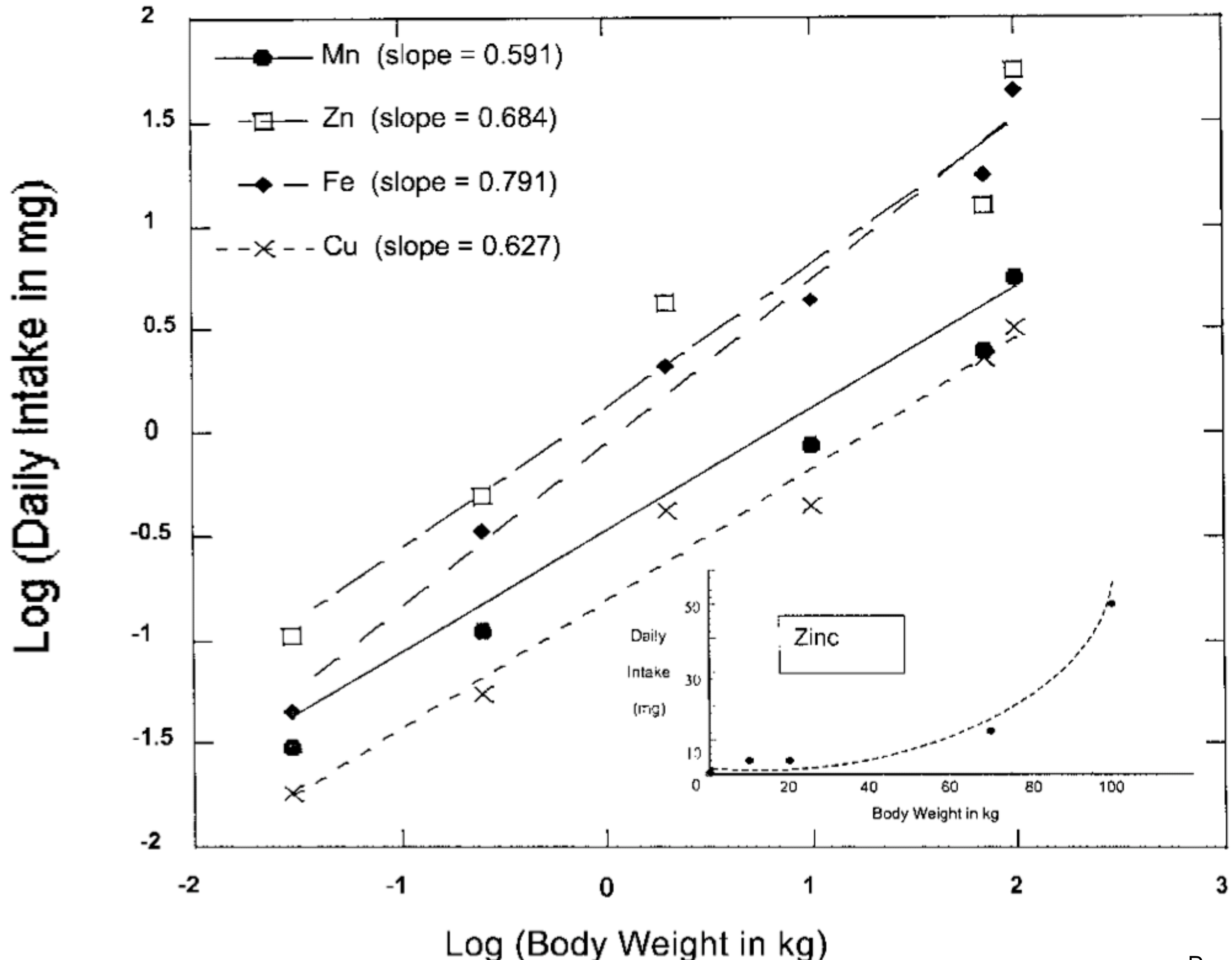
Nagy et al. (1999)

Endogenous protein losses



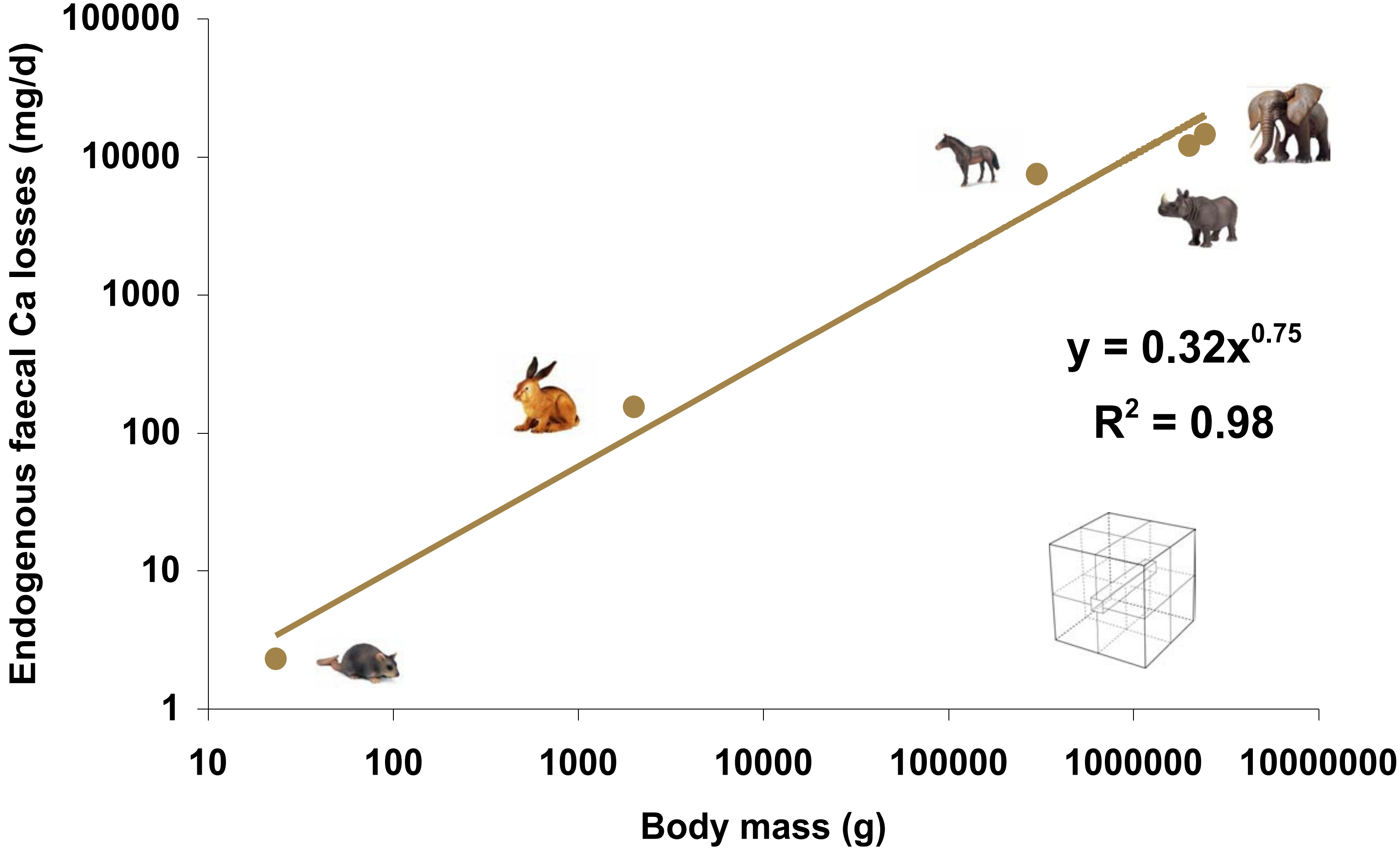
Brody (1945)

Mineral maintenance requirements



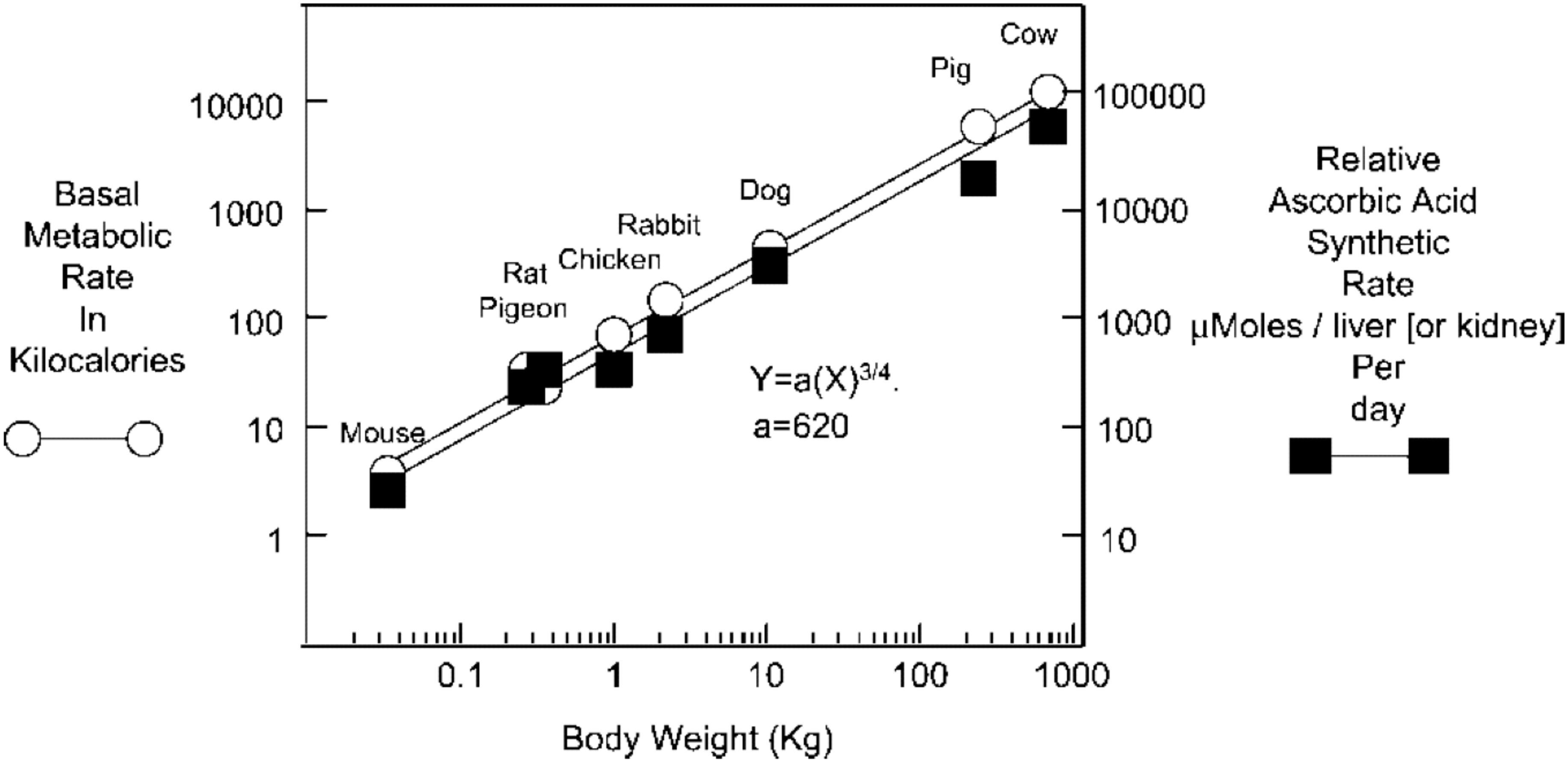
Rucker & Storm (2002)

Endogenous faecal calcium losses



Data from Kamphues et al. (1986), Shoe et al. (1992), Meyer & Coenen (2002), Clauss et al. (2003, 2005)

Endogenous vitamin C synthesis

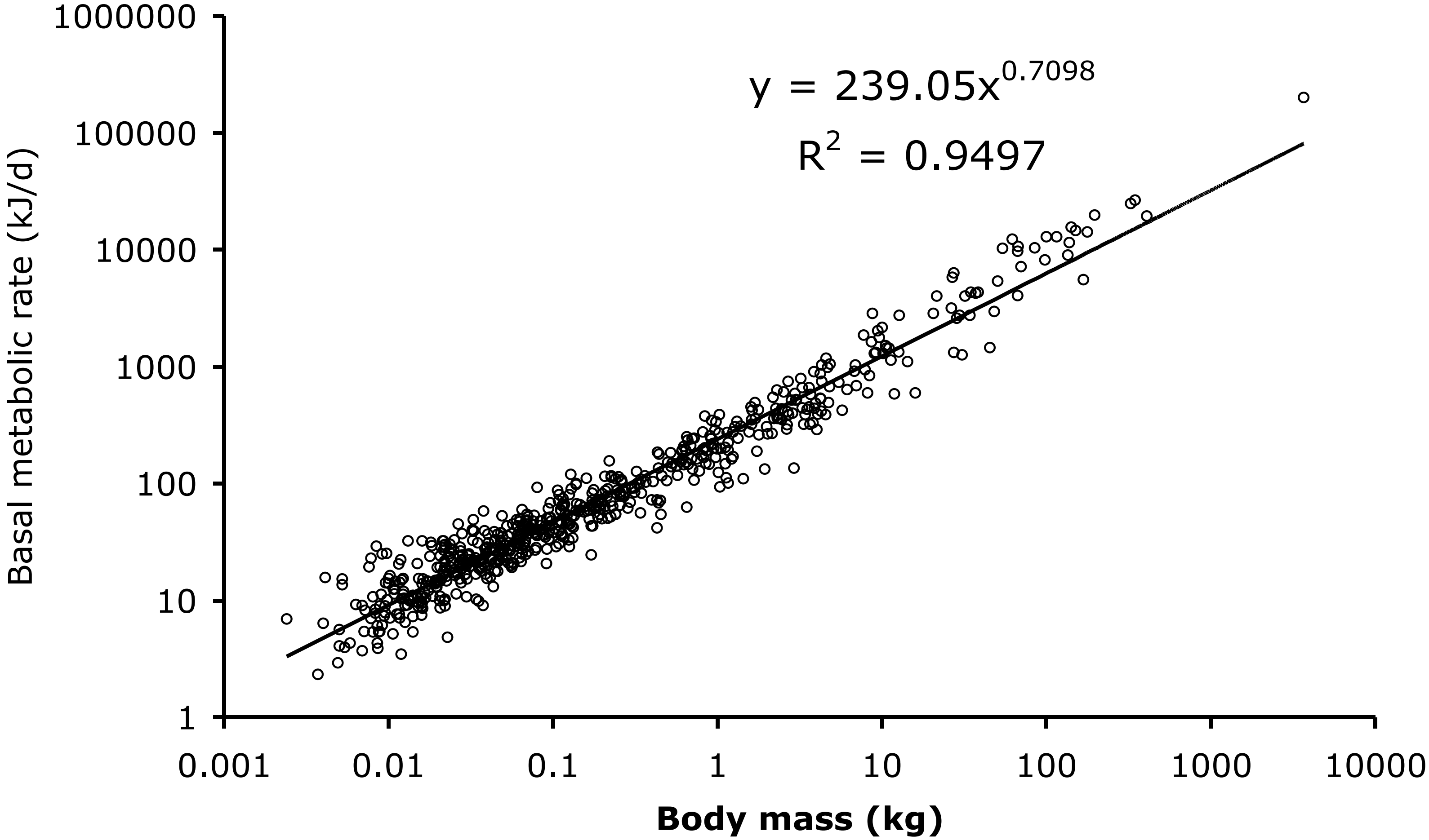


Rucker & Steinberg (2002)

Interim result

- A large number of parameters that have a connection to metabolism scale allometrically to body mass
  - with an exponent of about 0.67-0.75 (but also above or below this)

Good correlation but enormous variance!



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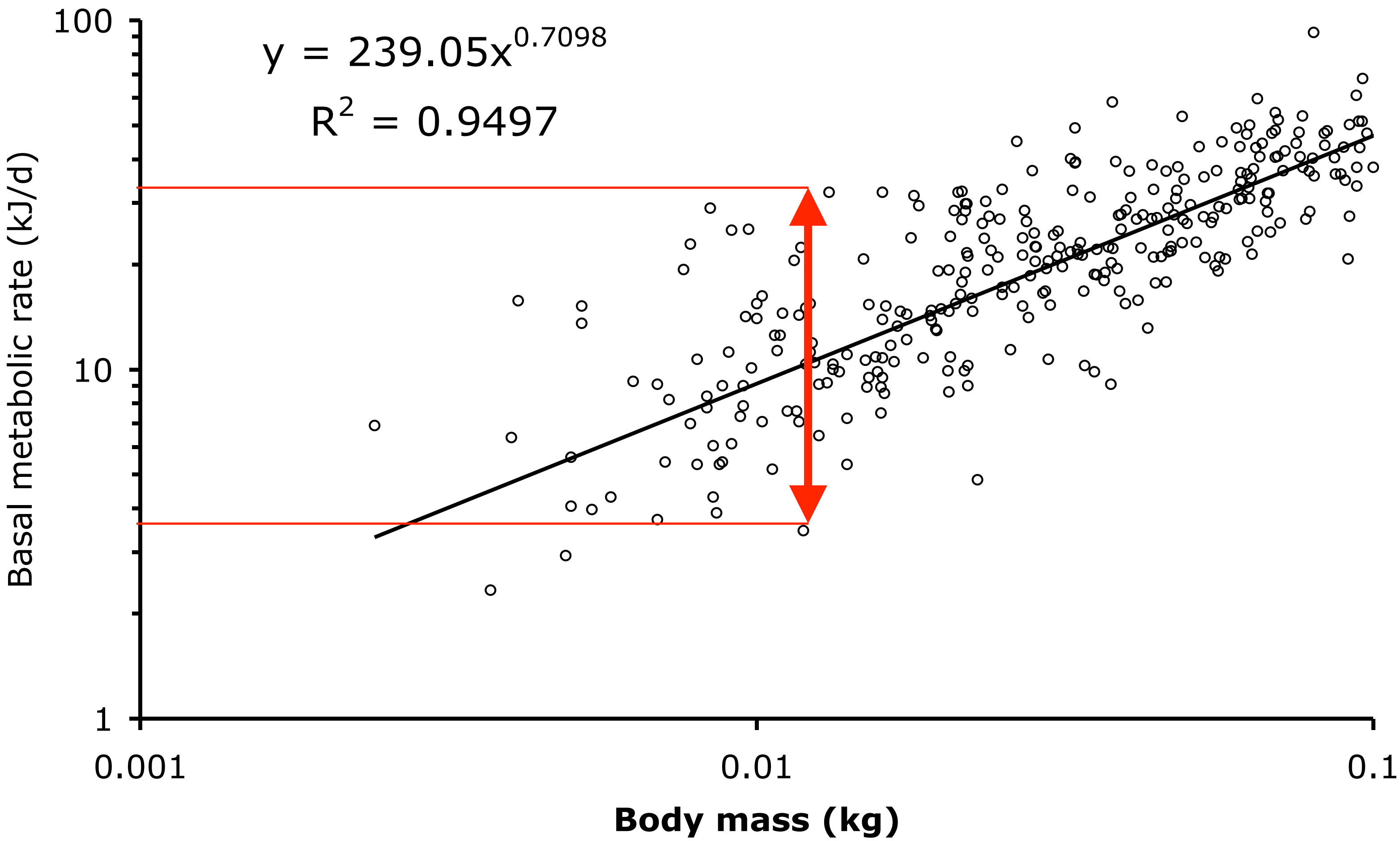

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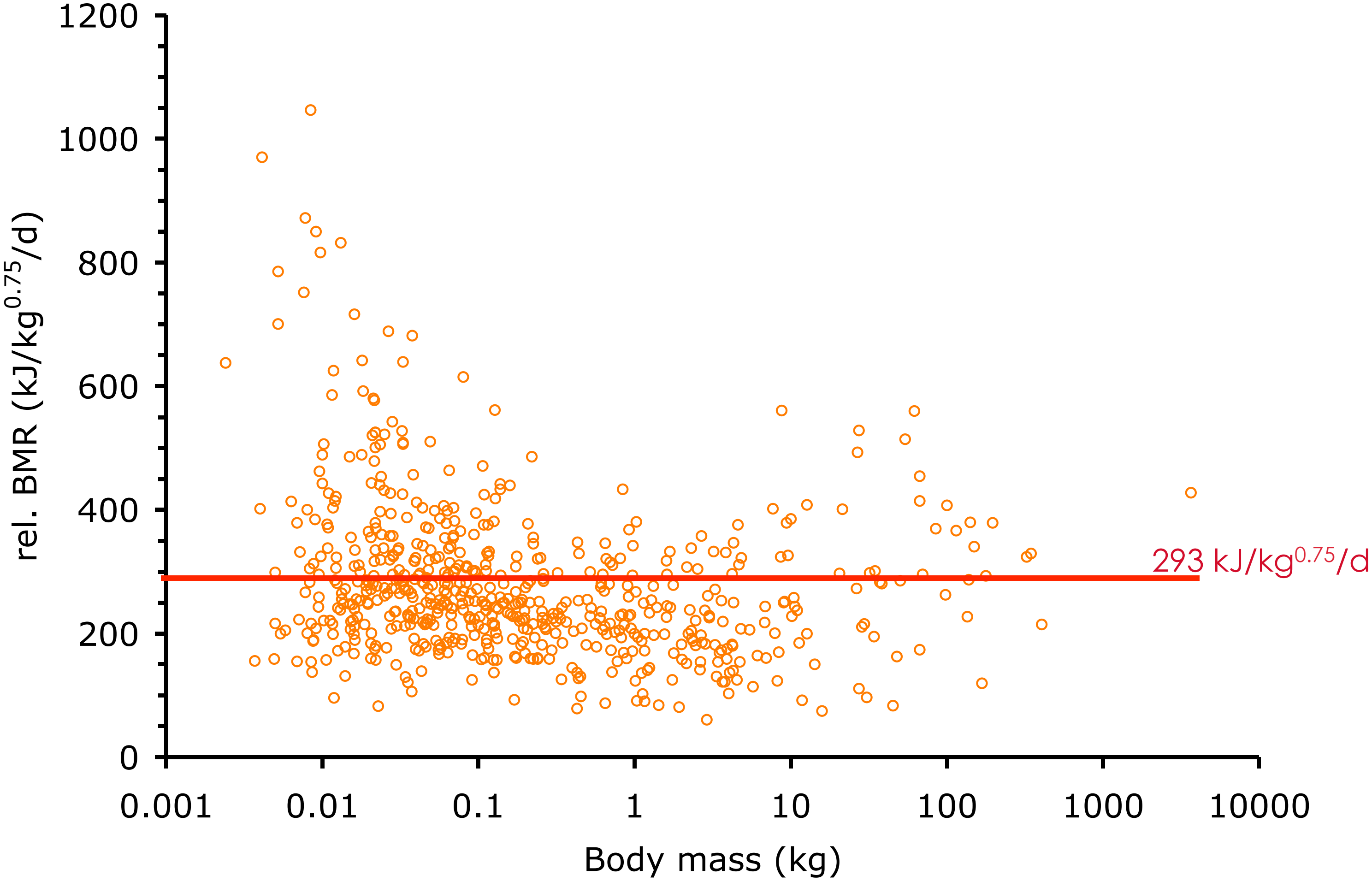
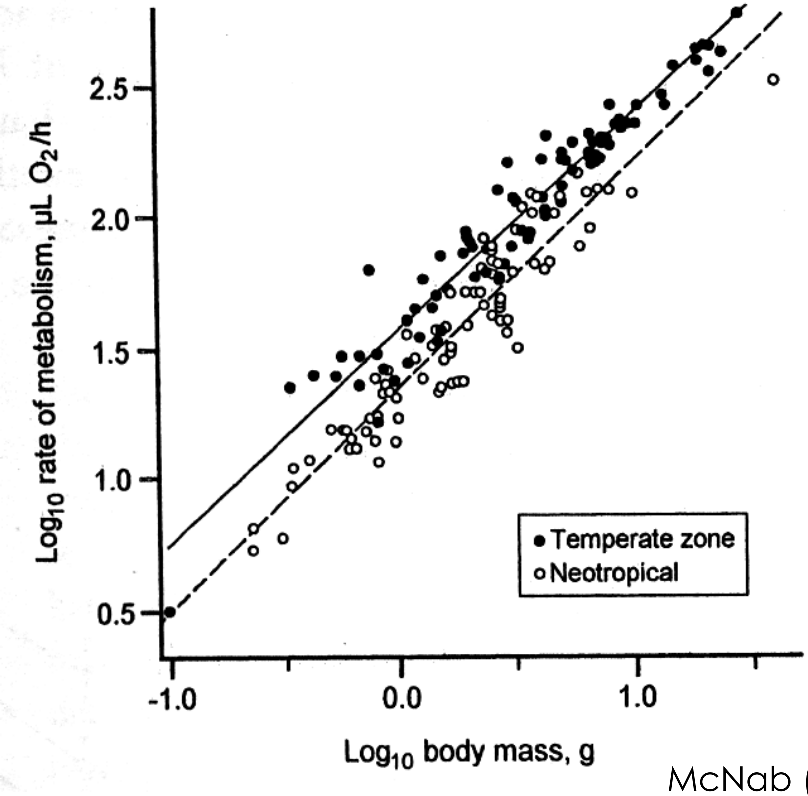


Data from Savage et al. (2004)

What determines the relative BMR?

- Adaptation to climate zone: increase with latitude



McNab (2002)

What determines the relative BMR?

- Adaptation to climate zone: increase with latitude
- Adaptation to habitat:
  - increase in marine mammals

McNab (2002)

What determines the relative BMR?

- Adaptation to climate zone: increase with latitude
- Adaptation to habitat:
  - increase in marine mammals
  - decrease in subterranean mammals

McNab (2002)

What determines the relative BMR?

- Adaptation to climate zone: increase with latitude
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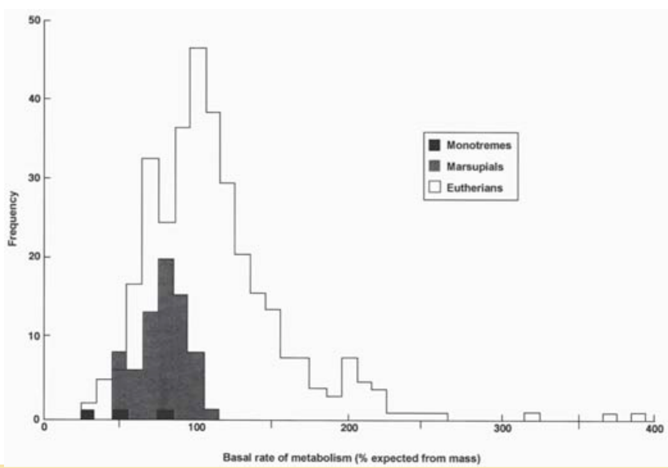
- Taxonomy: marsupials always lower than eutherians



McNab (2005)

What determines the relative BMR?

- Adaptation to climate zone: increase with latitude
- Adaptation to habitat:
  - increase in marine mammals
  - decrease in subterranean mammals
- Taxonomy: marsupials always lower than eutherians
- Adaptation to diet: higher the more digestible the food? (higher in carnivores)

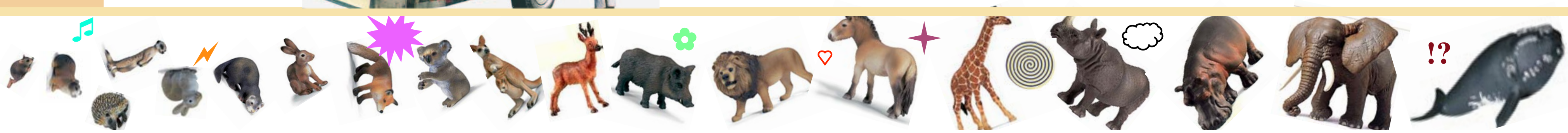
McNab (2002)

Interim result

- The relative BMR of different animal groups varies with various taxonomic, geographic, anatomical and physiological conditions.
- In order to recognize outliers, a knowledge of the fundamental allometric relationship is necessary.

The Acid Test and Allometry

CAN YOU PASS
THE ACID TEST ?



The Acid Test and Allometry

Lysergic acid diethylamide: its effects on a male Asiatic elephant

West et al. (1962) *Science* 138: 1100-1103

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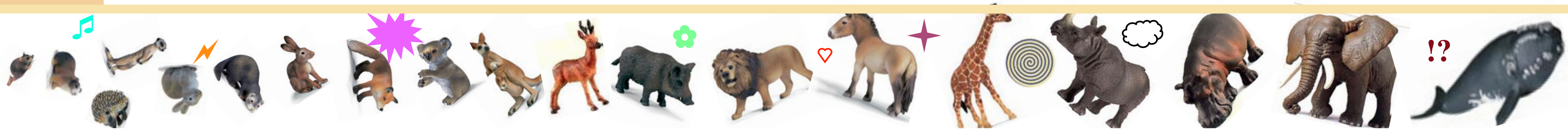

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Dose cat: 0.15 mg/kg

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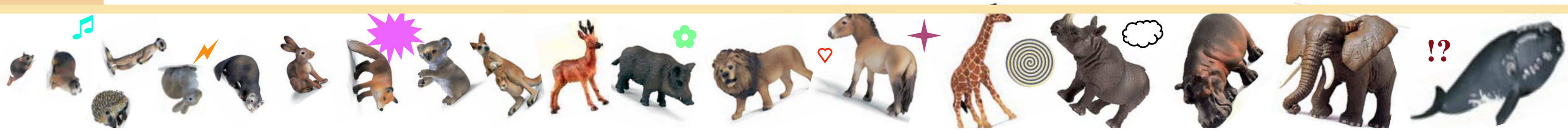

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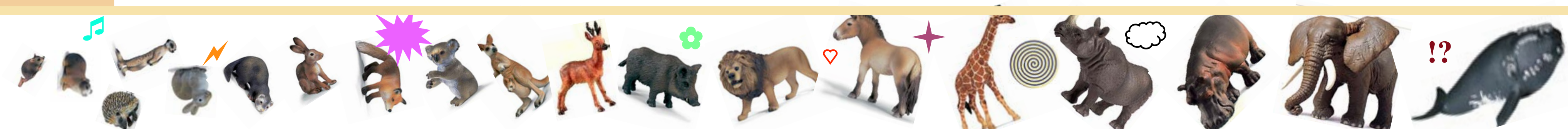
What dose of LSD is adequate for an elephant?

Dose cat: 0.15 mg/kg
3 kg => 0.45 mg total dose

Dose elephant: 0.10 mg/kg
2970 kg => 297 mg total dose



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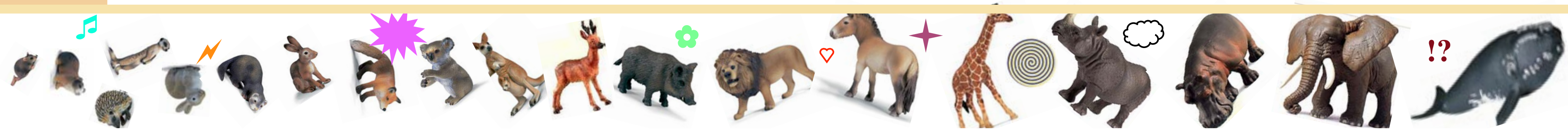

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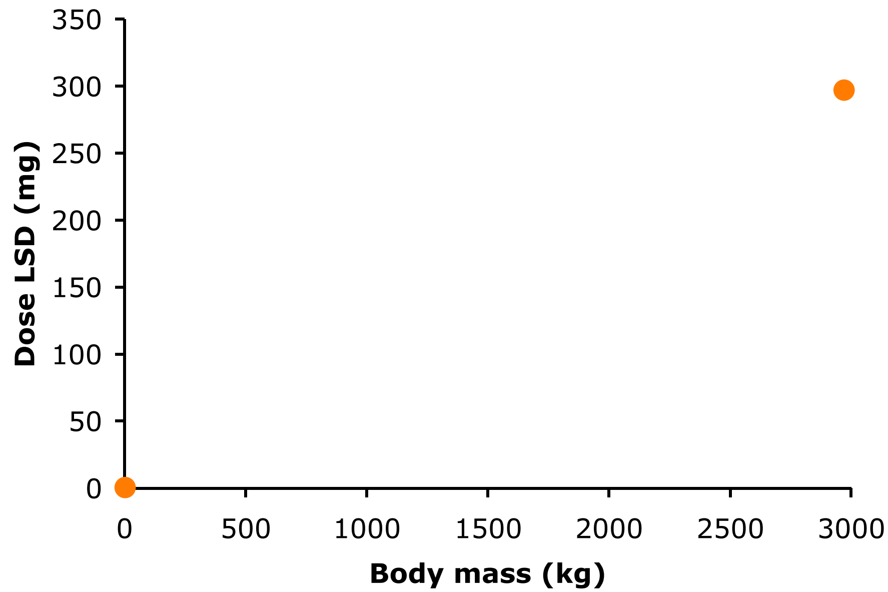

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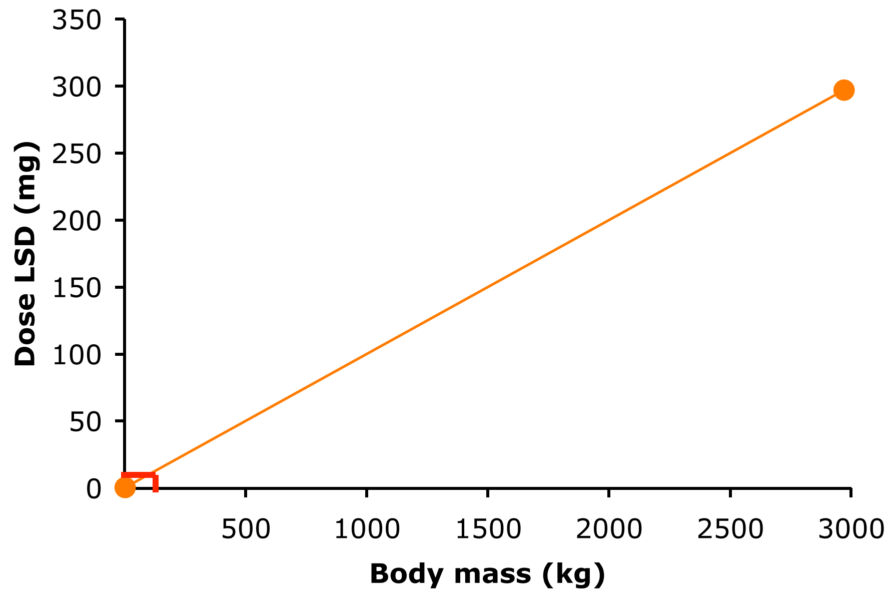
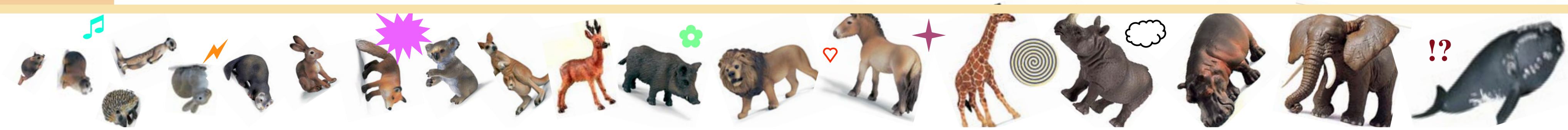
same logic: man
70kg => 7 mg total dose





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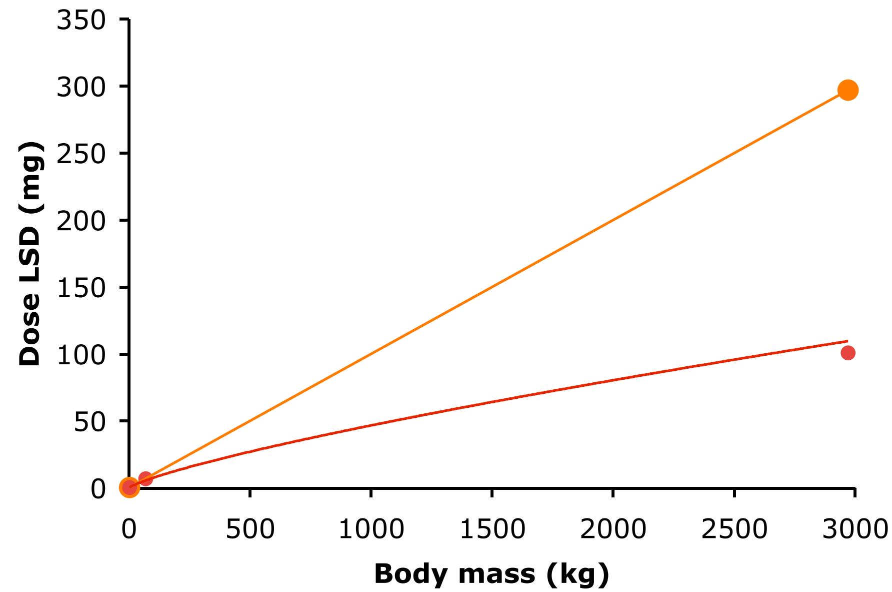
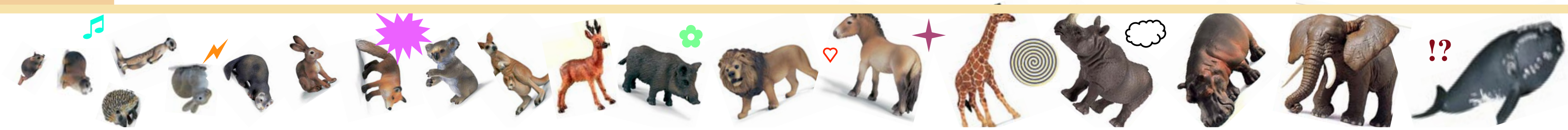
Dose cat: 0.45 mg/3 kg
=> 0.2 $mg/kg^{0.75}$

Dose man: 7mg/70kg
=> 0.3 $mg/kg^{0.75}$

Dose elephant: ca. 0.25 $mg/kg^{0.75}$
2970 kg => 101 mg total dose





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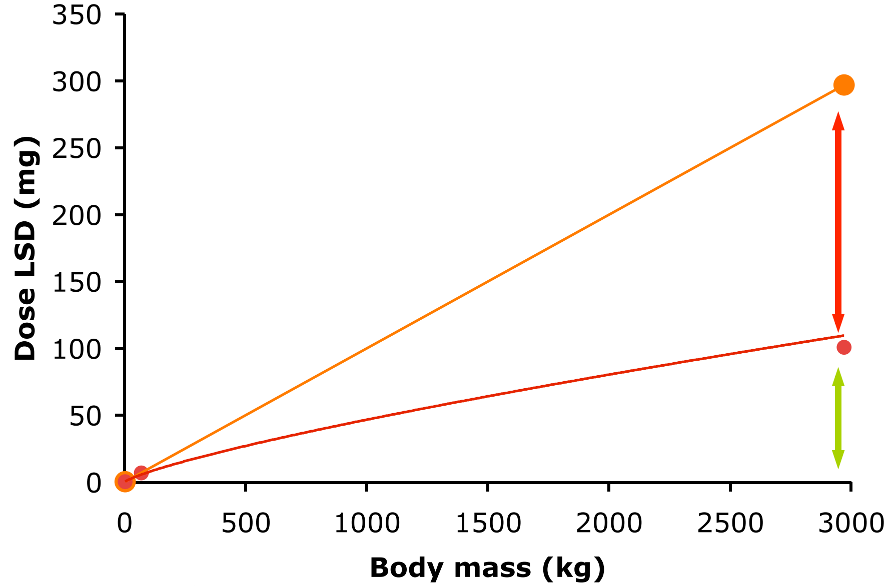
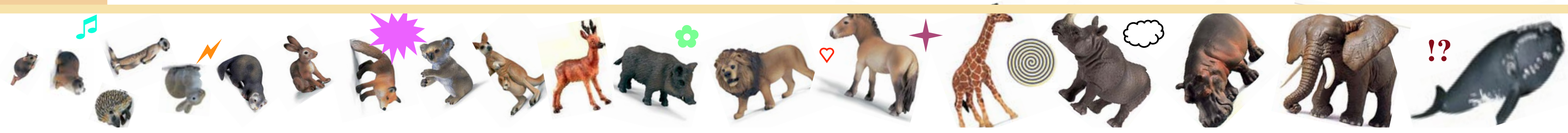




Organ allometry

$$\text{Liver (kg)} = 0.033\ BW^{0.87}$$

$$\text{Brain (kg)} = 0.011\ BW^{0.76}$$

$$\text{Blood (kg)} = 0.069\ BW^{1.02}$$

$$\text{Muscle (kg)} = 0.450\ BW^{1.00}$$

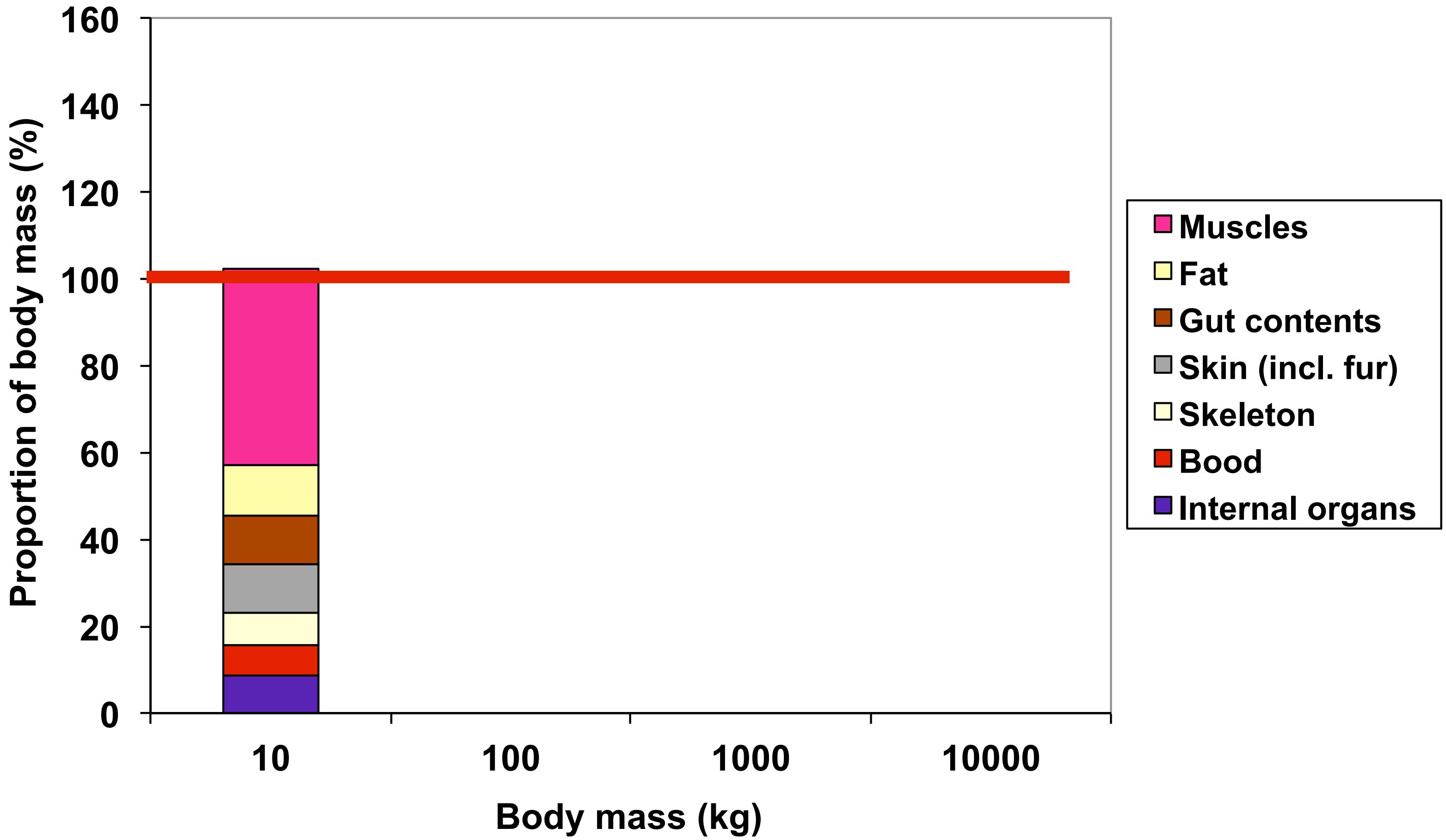
$$\text{Skeleton (kg)} = 0.061\ BW^{1.09}$$

$$\text{Integument (kg)} = 0.134\ BW^{0.92}$$

$$\text{Gut contents (kg)} = 0.093\ BW^{1.08}$$

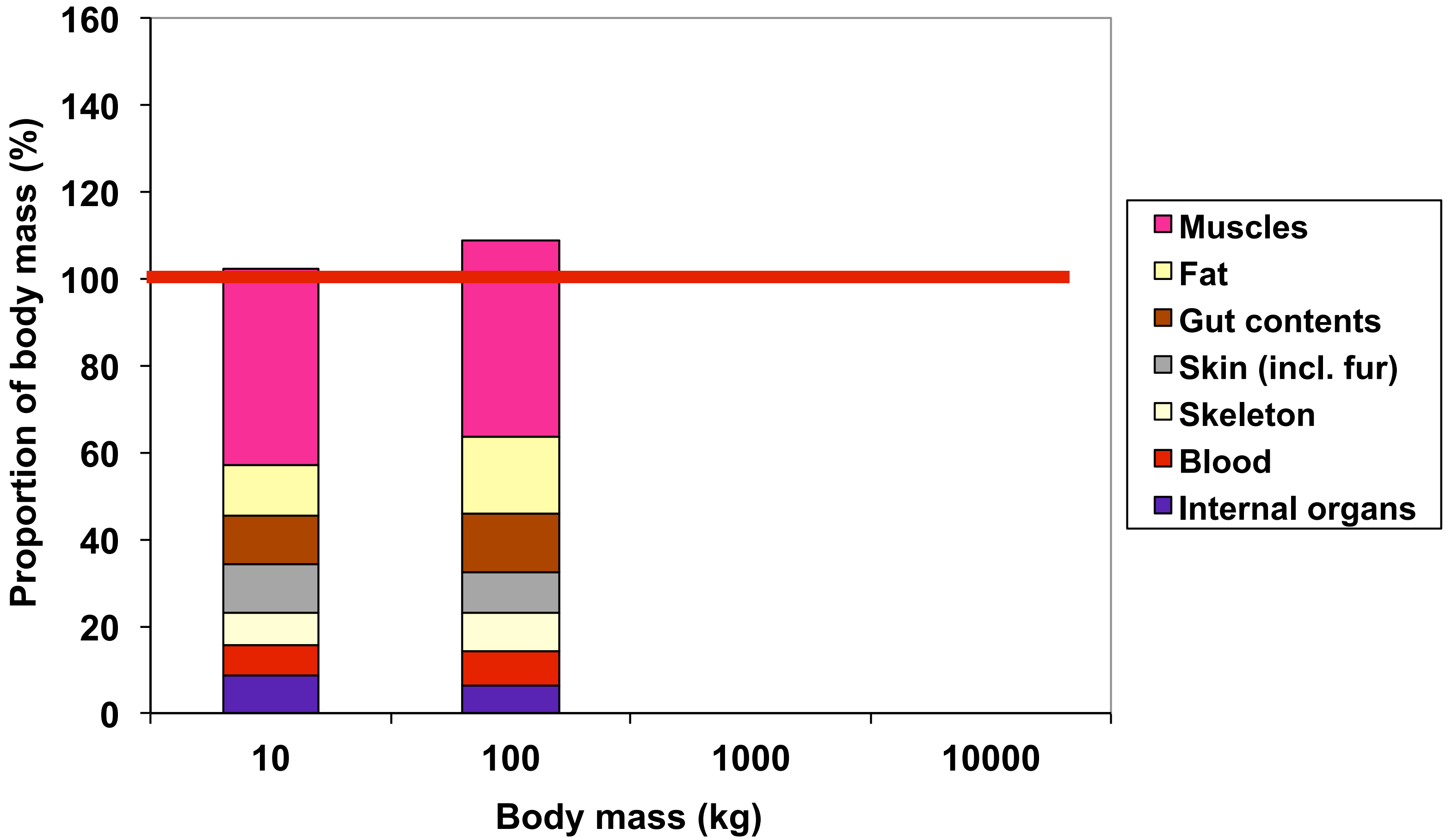
(Parra 1978, Calder 1983)

Allometry of body composition



from Hummel and Clauss (2010)

Allometry of body composition



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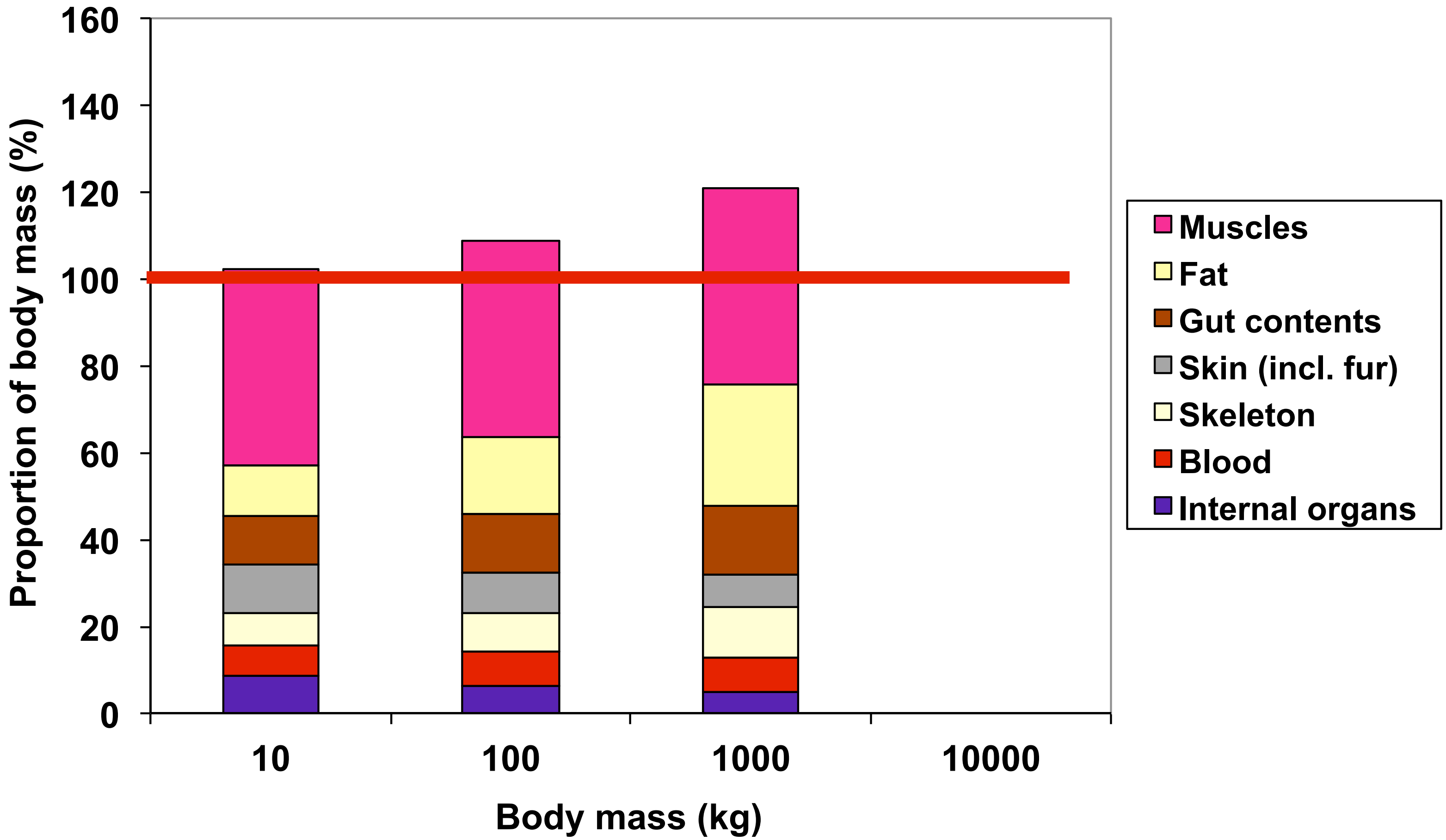

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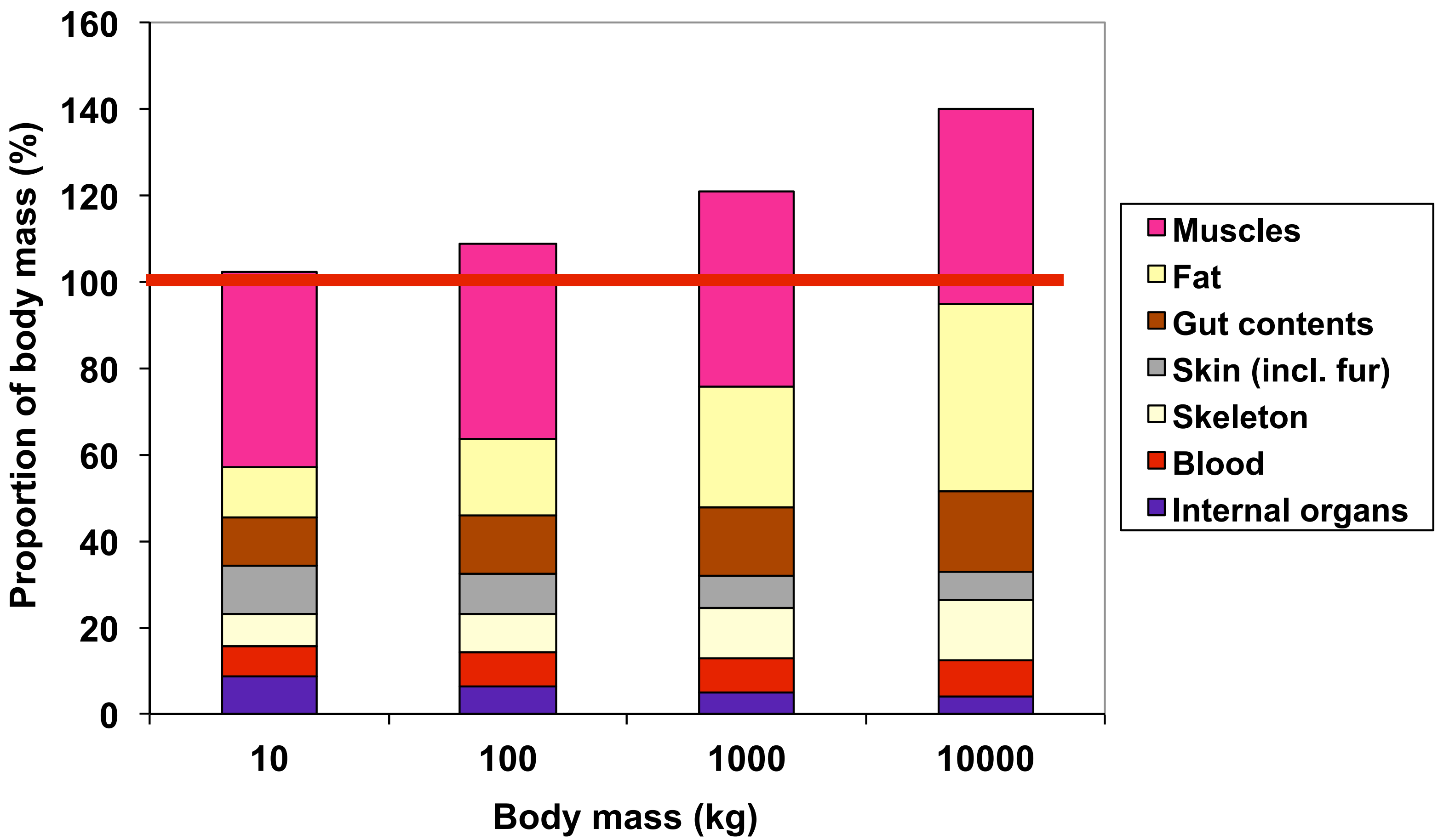


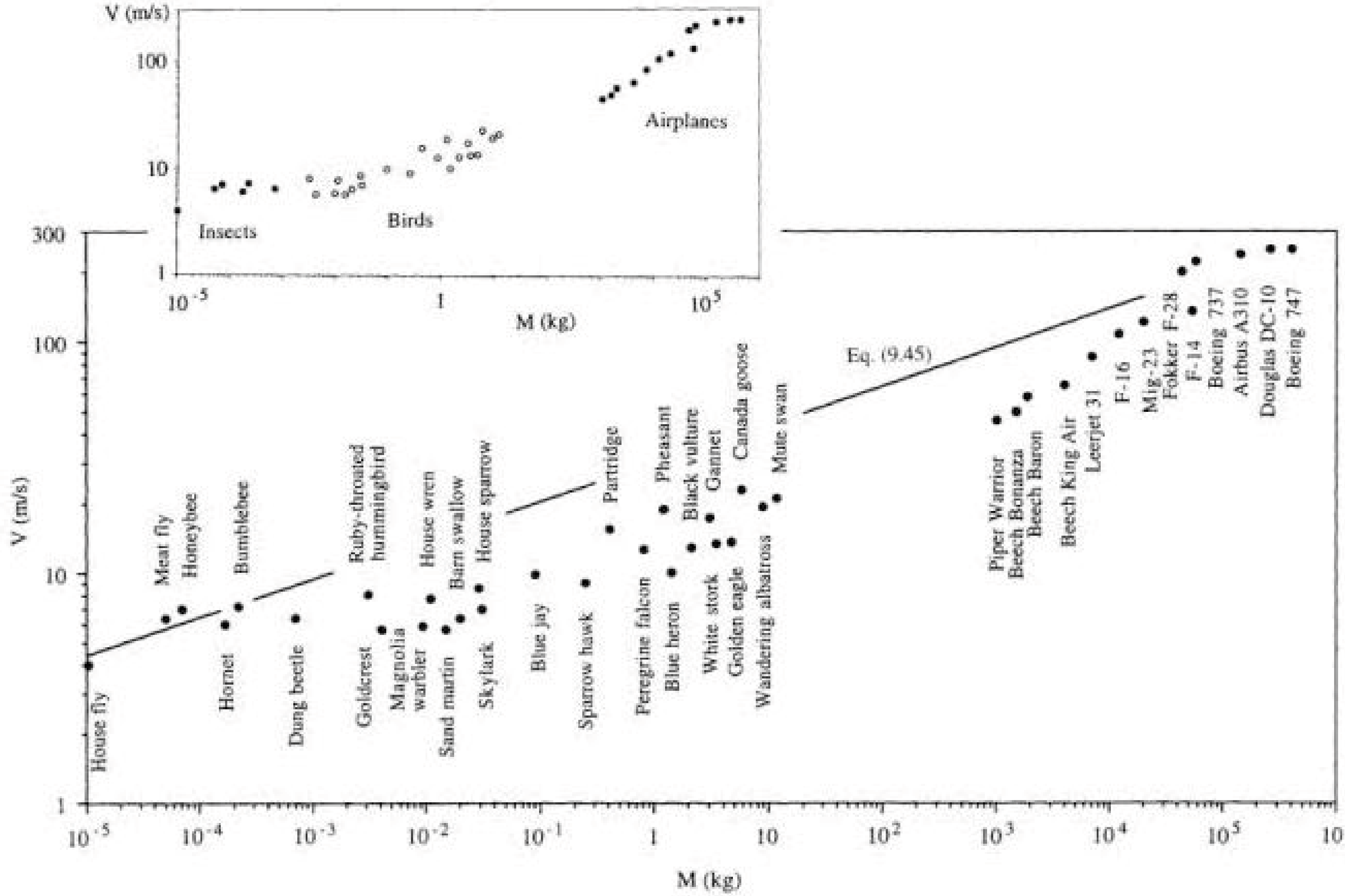
from Hummel and Clauss (2010)

Interim results

- The reliability of allometric predictions depends on whether the species in question is within the body size range from which the equation was derived, or beyond it.

Summary

- (Empirical) allometric functions with body mass are abundant in biology.
- The explanation of these functions is mostly under debate (but the debate is interesting!).
- The knowledge of these functions allows the identification of outliers and thus facilitates insight into functional and ecological correlations.
- For the calculation of dosages for species for which no data exists one should use an allometric approach.
- The reliability of allometric predictions depends on whether the species in question is within the body size range from which the equation was derived, or beyond it.

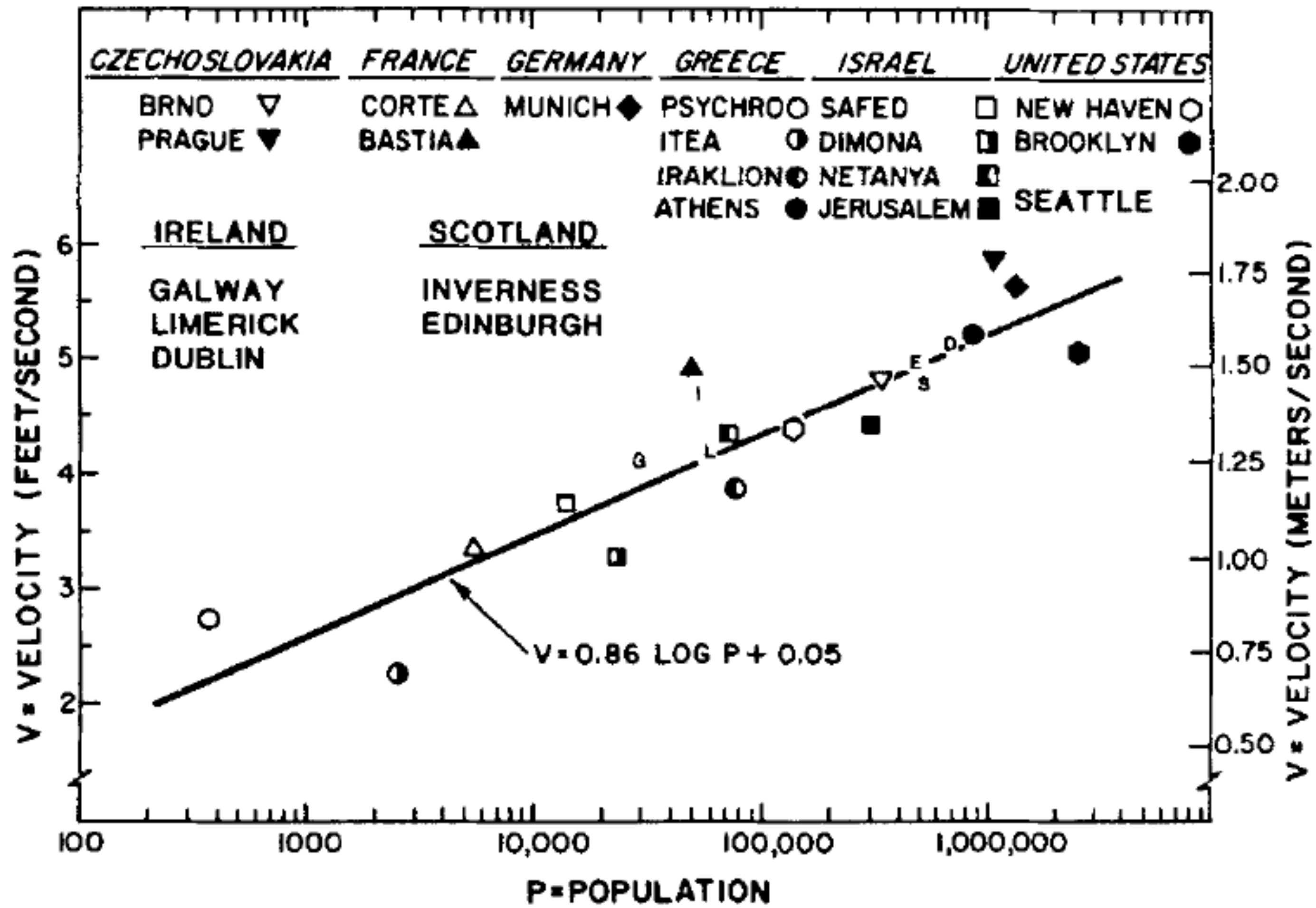


V (m/s)
100
10
1
10^{-5}
1
10^{5}
M (kg)
Insects
Birds
Airplanes
300
100
10
1
V (m/s)
10^{-5}
10^{-4}
10^{-3}
10^{-2}
10^{-1}
1
10
10^{2}
10^{3}
10^{4}
10^{5}
10
M (kg)
Eq. (9.45)
House fly
Meat fly
Honeybee
Hornet
Bumblebee
Dung beetle
Ruby-throated hummingbird
Goldcrest
Magnolia warbler
House wren
Sand martin
Barn swallow
House sparrow
Skylark
Blue jay
Sparrow hawk
Partridge
Peregrine falcon
Pheasant
Blue heron
Black vulture
White stork
Gannet
Golden eagle
Canada goose
Wandering albatross
Mute swan
Piper Warrior
Beech Bonanza
Beech Baron
Beech King Air
Learjet 31
F-16
Mig-23
Fokker F-28
F-14
Boeing 737
Airbus A310
Douglas DC-10
Boeing 747

THE PACE OF LIFE: REVISITED *

Marc H. BORNSTEIN

International Journal of Psychology 14 (1979) 83–90



Growth, innovation, scaling, and the pace of life in cities

Luís M. A. Bettencourt*†, José Lobo‡, Dirk Helbing§, Christian Kühnert§, and Geoffrey B. West*¶

PNAS | April 24, 2007 | vol. 104 | no. 17 | 7301–7306

Table 1. Scaling exponents for urban indicators vs. city size

Y	β	95% CI	Adj-R^2	Observations	Country–year
New patents	1.27	[1.25,1.29]	0.72	331	U.S. 2001
Inventors	1.25	[1.22,1.27]	0.76	331	U.S. 2001
Private R&D employment	1.34	[1.29,1.39]	0.92	266	U.S. 2002
"Supercreative" employment	1.15	[1.11,1.18]	0.89	287	U.S. 2003
R&D establishments	1.19	[1.14,1.22]	0.77	287	U.S. 1997
R&D employment	1.26	[1.18,1.43]	0.93	295	China 2002
Total wages	1.12	[1.09,1.13]	0.96	361	U.S. 2002
Total bank deposits	1.08	[1.03,1.11]	0.91	267	U.S. 1996
GDP	1.15	[1.06,1.23]	0.96	295	China 2002
GDP	1.26	[1.09,1.46]	0.64	196	EU 1999–2003
GDP	1.13	[1.03,1.23]	0.94	37	Germany 2003
Total electrical consumption	1.07	[1.03,1.11]	0.88	392	Germany 2002
New AIDS cases	1.23	[1.18,1.29]	0.76	93	U.S. 2002–2003
Serious crimes	1.16	[1.11, 1.18]	0.89	287	U.S. 2003
Total housing	1.00	[0.99,1.01]	0.99	316	U.S. 1990
Total employment	1.01	[0.99,1.02]	0.98	331	U.S. 2001
Household electrical consumption	1.00	[0.94,1.06]	0.88	377	Germany 2002
Household electrical consumption	1.05	[0.89,1.22]	0.91	295	China 2002
Household water consumption	1.01	[0.89,1.11]	0.96	295	China 2002
Gasoline stations	0.77	[0.74,0.81]	0.93	318	U.S. 2001
Gasoline sales	0.79	[0.73,0.80]	0.94	318	U.S. 2001
Length of electrical cables	0.87	[0.82,0.92]	0.75	380	Germany 2002
Road surface	0.83	[0.74,0.92]	0.87	29	Germany 2002

Data sources are shown in *SI Text*. CI, confidence interval; Adj-R^2, adjusted R^2; GDP, gross domestic product.

[redacted]