

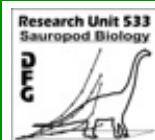


Beyond Jarman-Bell

how principles of digestive physiology can and cannot inform on ecological diversification

Marcus Clauss

Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of
Zurich, Switzerland
Guest lecture, Lyon 2015



University of
Zurich^{UZH}



Clinic
of Zoo Animals, Exotic Pets and Wildlife



Overview

Allometry basics

Working with allometries:

fallacies

curvature / composite allometries

Jarman-Bell: allometric (and other) reasoning in
large herbivore diversity

Phylogenetic statistics

Allometries as snapshots in evolutionary time –
'directed evolution'?



Allometry basics



Allometries

Morphological, physiological and life history variables scale with body mass.



Allometries

Morphological, physiological and life history variables scale with body mass.

Linear scaling: $y = a \text{ BM}^{1.0}$ or $\log y = \log a + 1.0 \log \text{BM}$

Allometric scaling: $y = a \text{ BM}^b$ or $\log y = \log a + b \log \text{BM}$



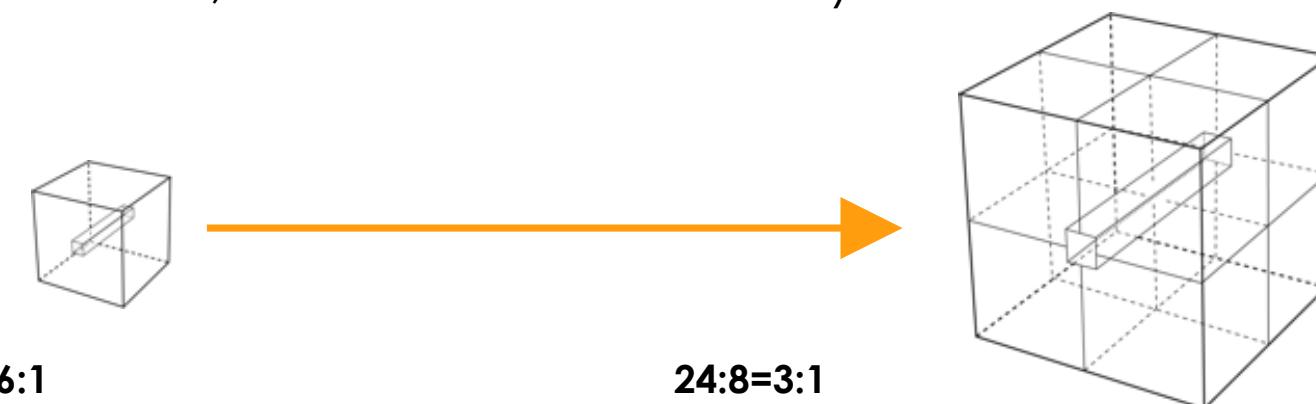
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Allometric scaling: $y = a \text{ BM}^b$ or $\log y = \log a + b \log \text{BM}$

(allometric scaling mostly explained by geometry – e.g. surface-volume shifts, distribution networks etc.)





Allometries

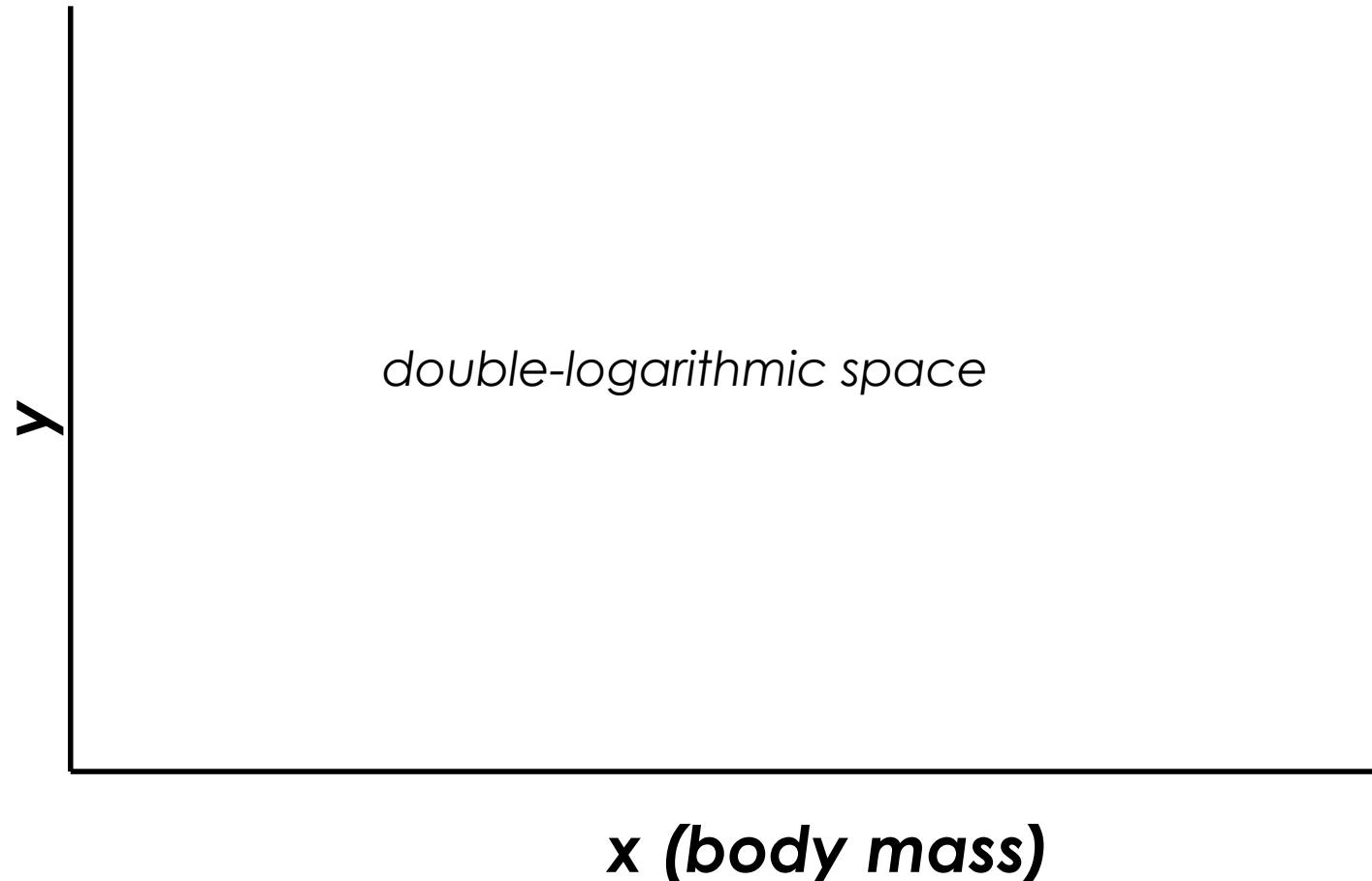
Morphological, physiological and life history variables scale with body mass.





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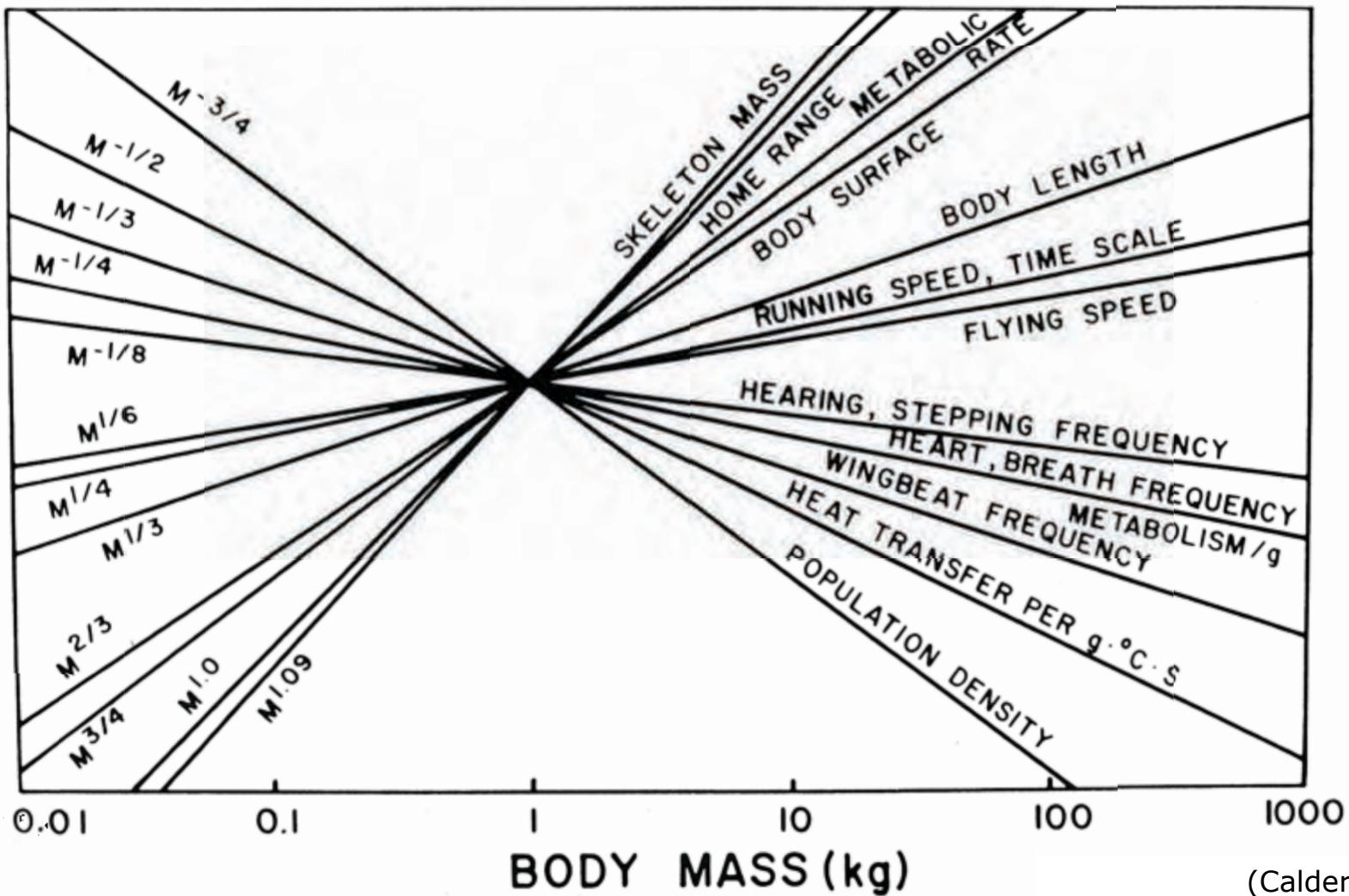
Morphological, physiological and life history variables scale with body mass.





Allometries

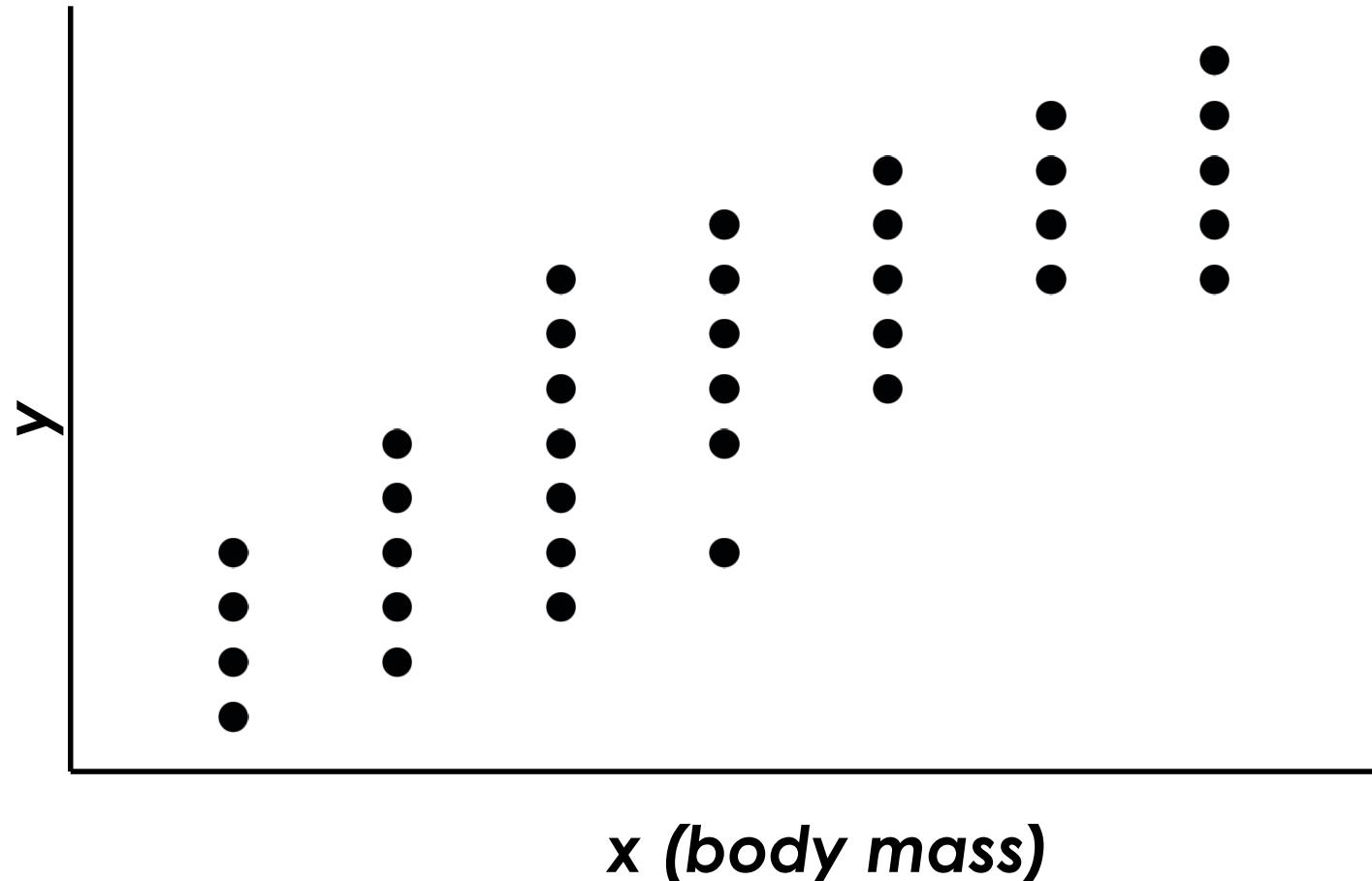
Morphological, physiological and life history variables scale with body mass.





Interpreting allometries

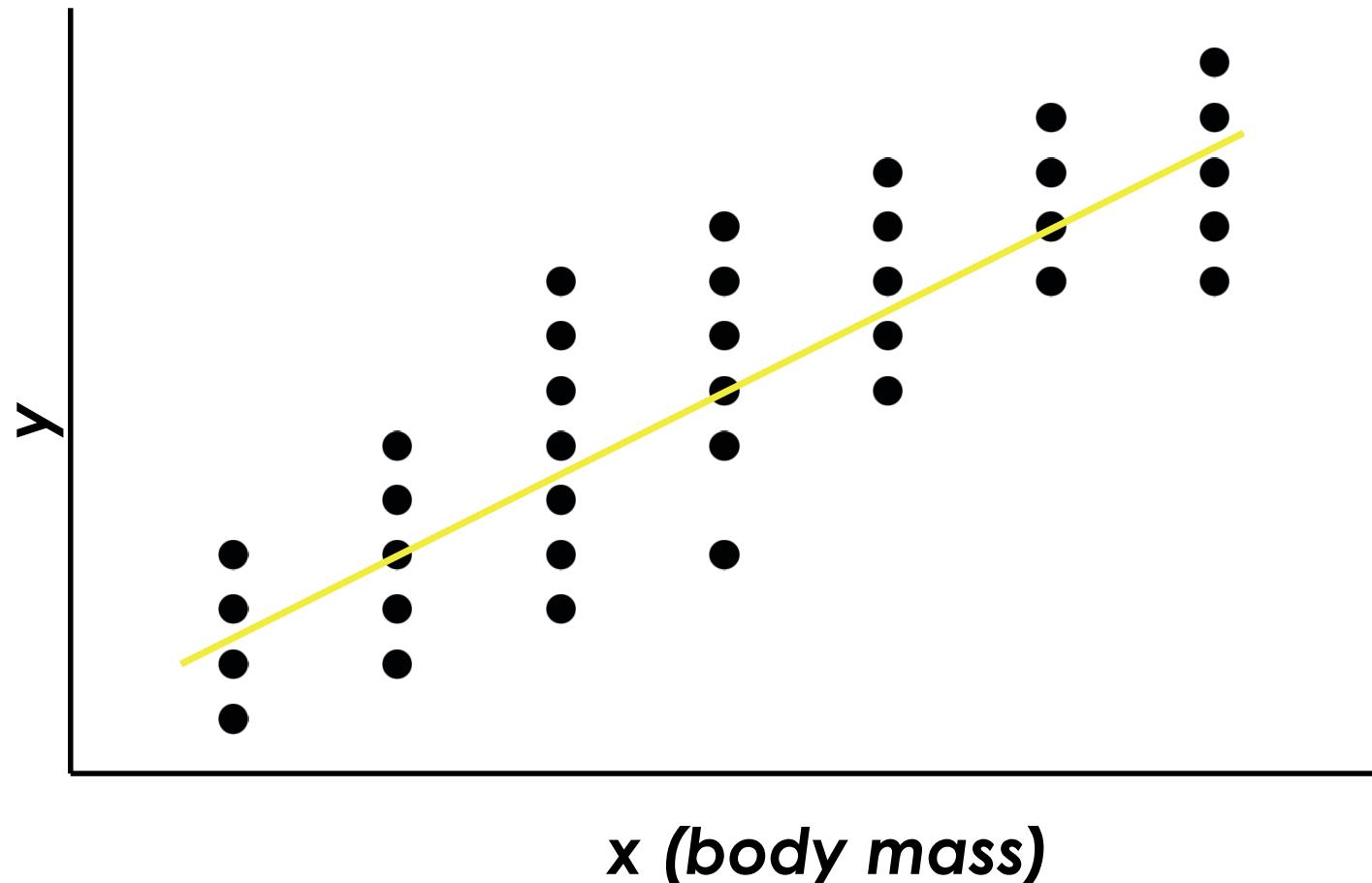
Morphological, physiological and life history variables scale with body mass.





Interpreting allometries

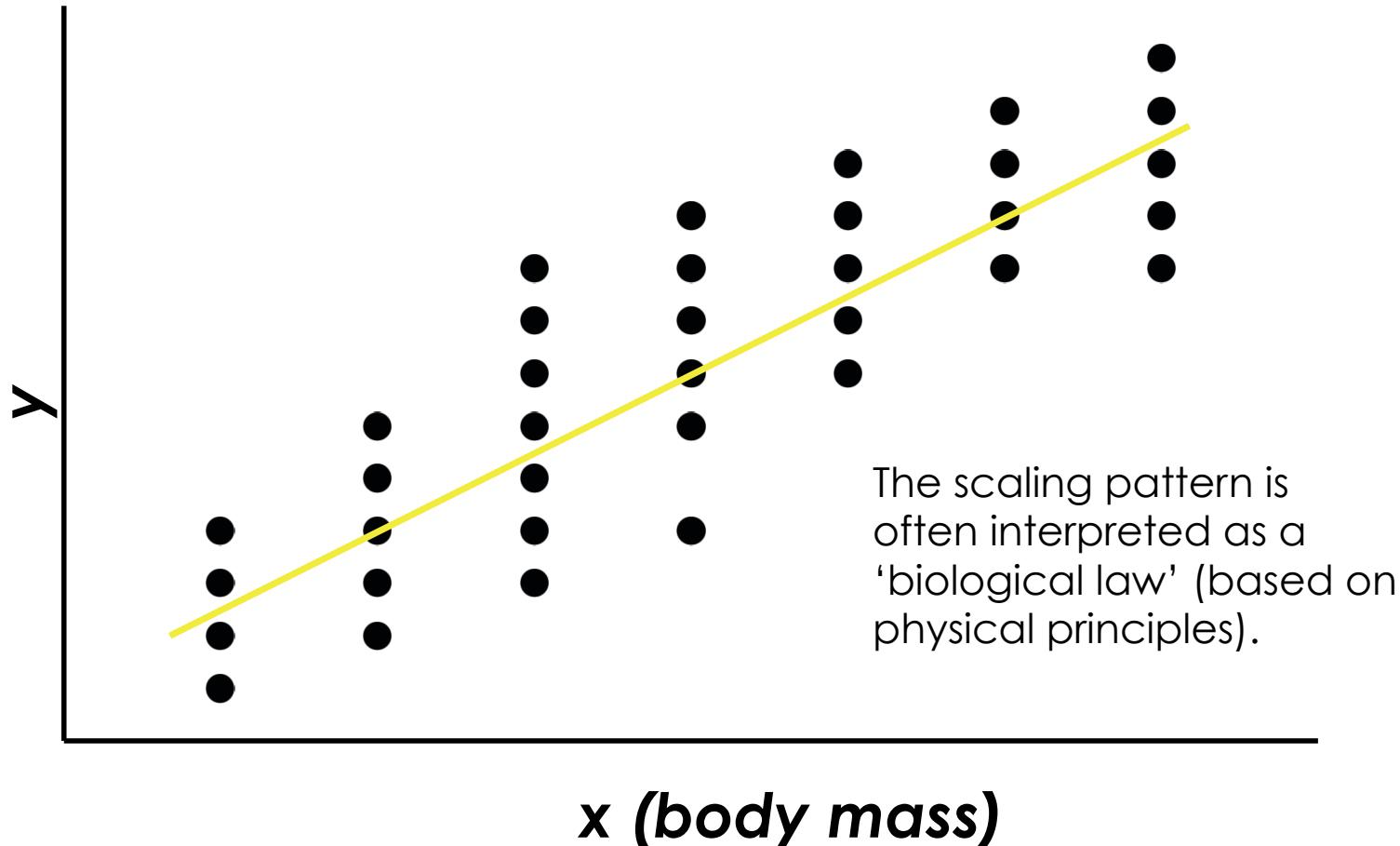
Morphological, physiological and life history variables scale with body mass.





Interpreting allometries

Morphological, physiological and life history variables scale with body mass.





Allometry fallacies



Using allometries: a call for caution



Using allometries: a call for caution

The probably most-often committed fallacy in ecophysiological manuscripts:

Metabolic rate = requirements
scale to $BM^{0.75}$



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This can be expressed in three different ways:



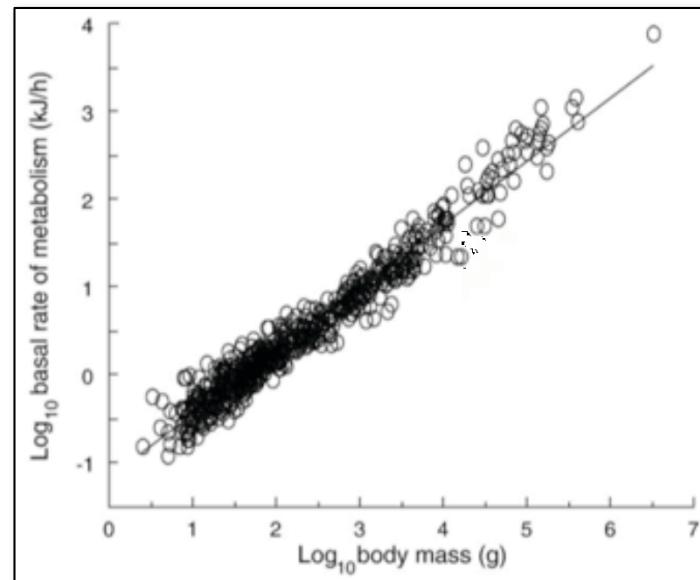
Using allometries: a call for caution

The probably most-often committed fallacy in ecophysiological manuscripts:

Metabolic rate = requirements
scale to $BM^{0.75}$

This can be expressed in three different ways:

1. larger animals have higher absolute requirements
(in joules (per day))





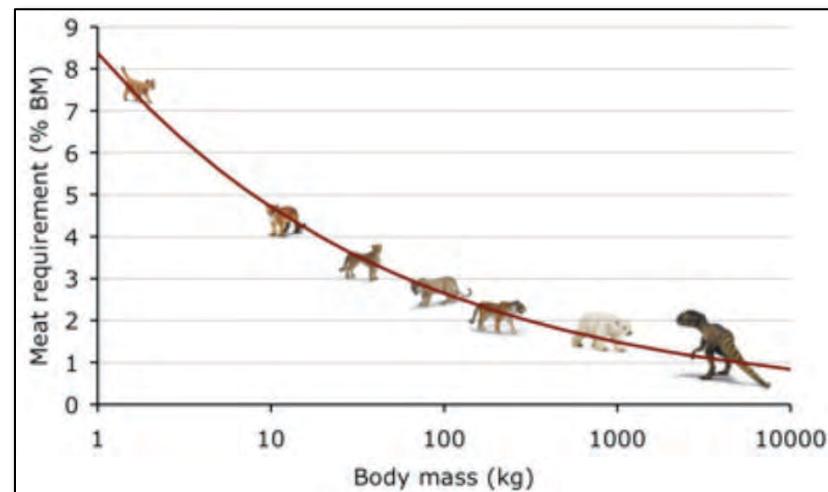
Using allometries: a call for caution

The probably most-often committed fallacy in ecophysiological manuscripts:

Metabolic rate = requirements
scale to $BM^{0.75}$

This can be expressed in three different ways:

2. a) smaller animals have higher 'mass-specific' requirements (in joules per kg (per day))





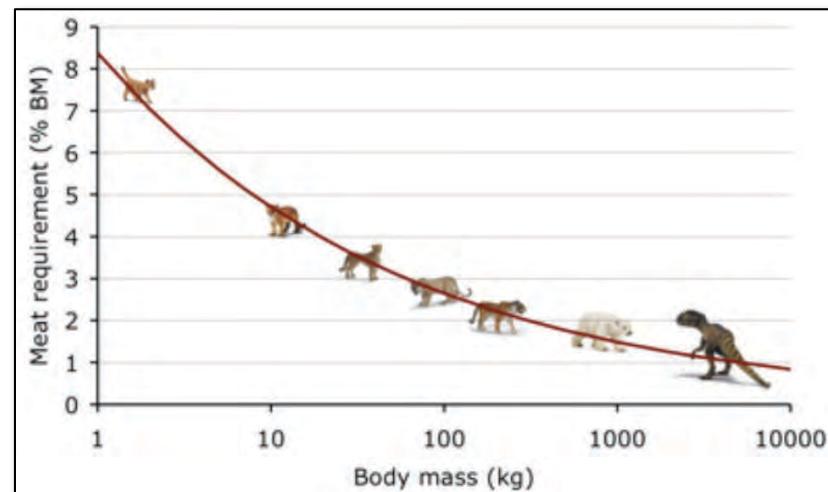
Using allometries: a call for caution

The probably most-often committed fallacy in ecophysiological manuscripts:

Metabolic rate = requirements
scale to $BM^{0.75}$

This can be expressed in three different ways:

2. b) larger animals have lower 'mass-specific' requirements (in joules per kg (per day))



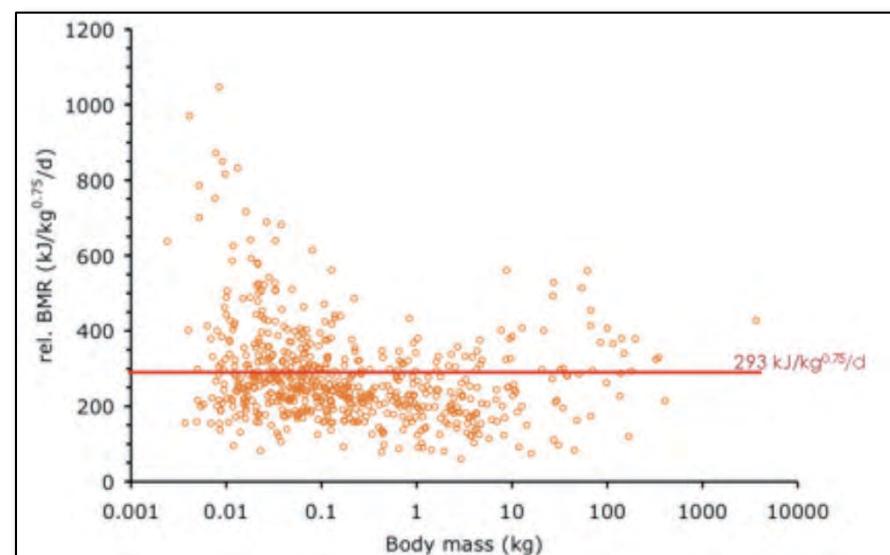


Using allometries: a call for caution

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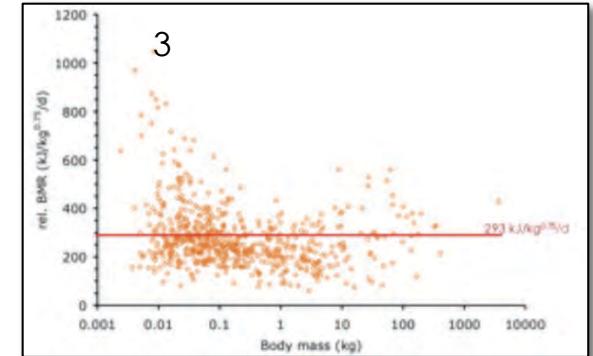
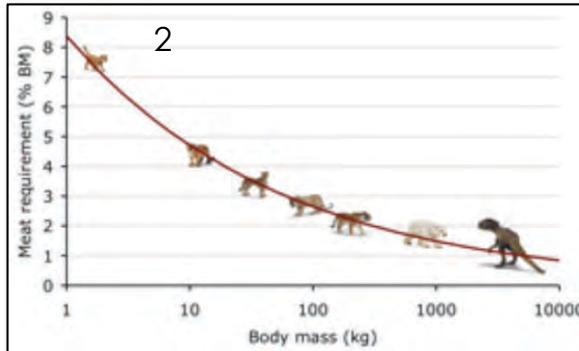
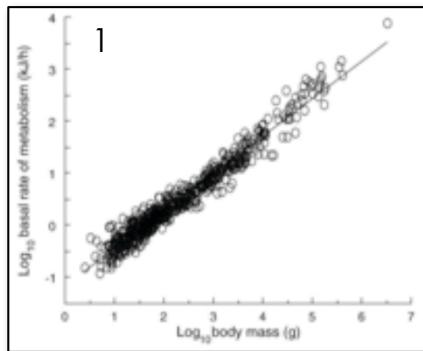
This can be expressed in three different ways:

3. all animals have the same requirements (in joules per $kg^{0.75}$ (per day))





Using allometries: a call for caution



1. larger animals have higher absolute requirements (in joules (per day))
2. larger animals have lower 'mass-specific' requirements (in joules per kg (per day))
3. all animals have the same requirements (in joules per kg^{0.75} (per day))

The choice of words very often depends on a rhetoric argument, as if 'higher' had any relevant meaning.



Using allometries: a call for caution

Any scaling can only be used as an argument if it is compared to another scaling !



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e.g.

“Larger animals have lower ‘mass-specific’ requirements – therefore they can use lower-quality food.”



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no comparison to other scaling!



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Any scaling can only be used as an argument if it is compared to another scaling !

e.g.

“Larger animals have lower ‘mass-specific’ requirements – therefore they can use lower-quality food.”

no comparison to other scaling!

Does intake also scale like requirements?
Does gut capacity scale like intake?



Using allometries: a call for caution

Any scaling can only be used as an argument if it is compared to another scaling !

Do not trust one-scaling statements.



Using allometries: a call for caution

A difference in the scaling of two characteristics has a promising potential to explain diversification and niche differentiation along a body size gradient!

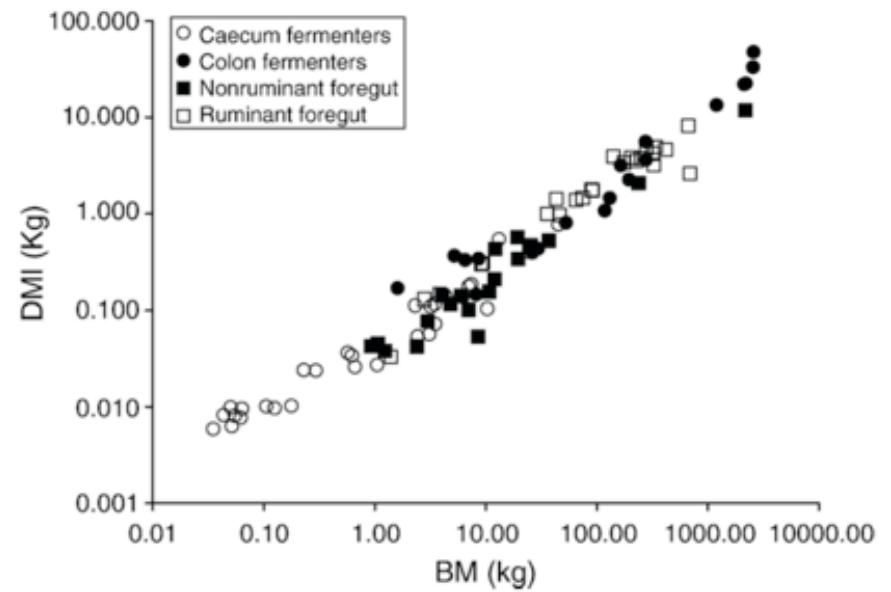
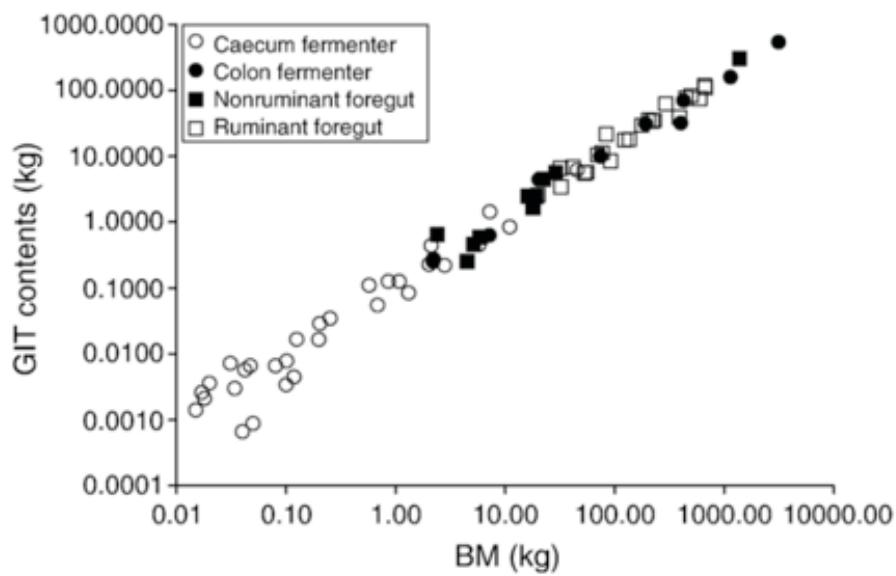
If $x \sim BM^{0.95}$ and $y \sim BM^{0.75}$, it follows that with increasing body size, the difference between x and y increases => a systematic shift in animal design along the BM gradient.
Larger animals have more x per y . This could allow them to use a different niche than smaller animals.



Curvature



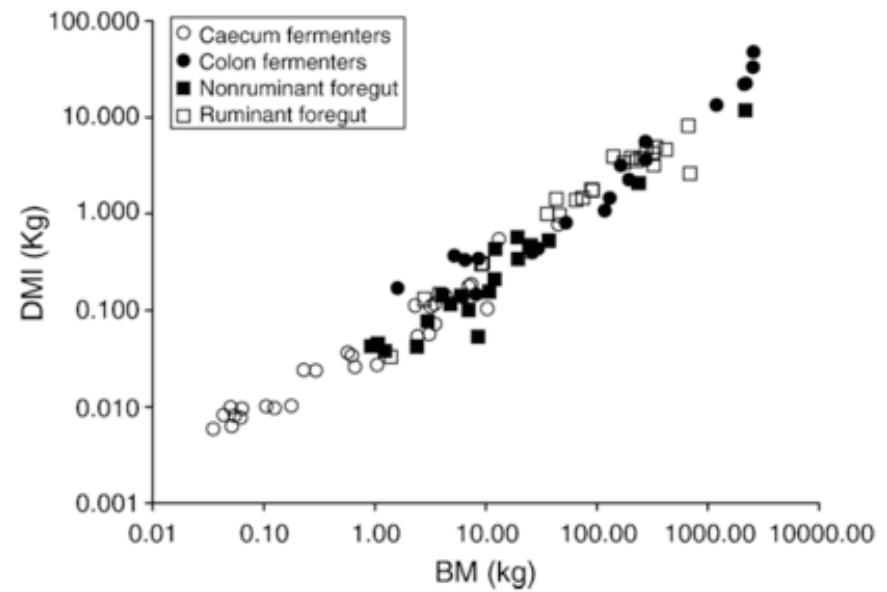
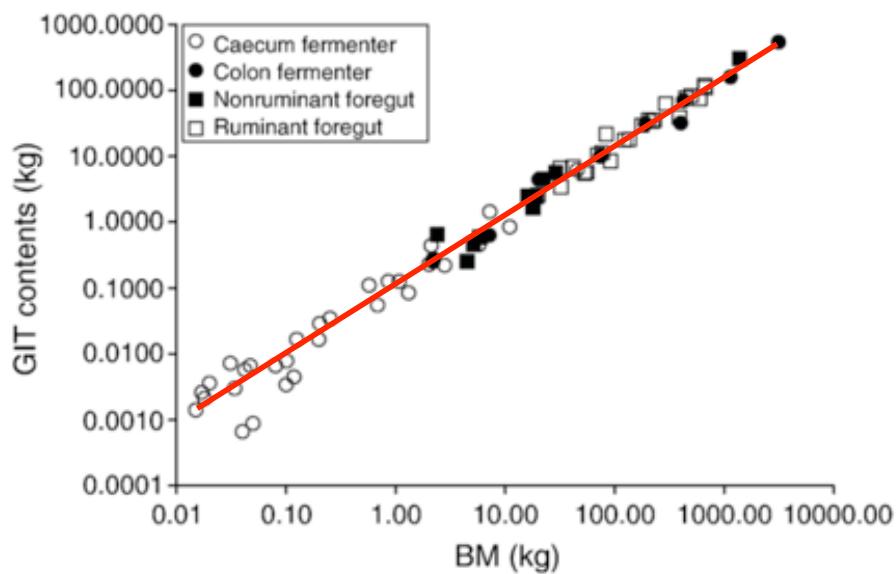
Straight line ... ?



from Clauss et al. (2007)



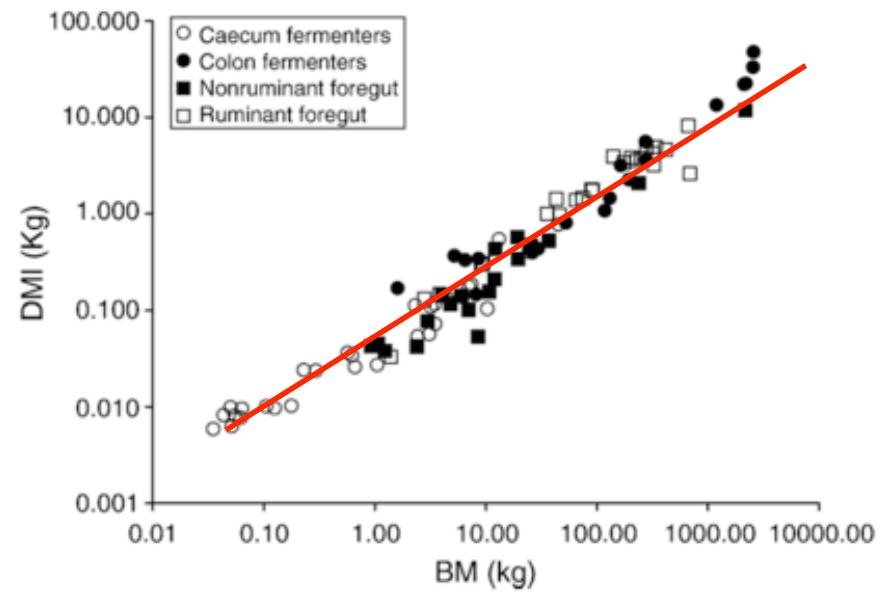
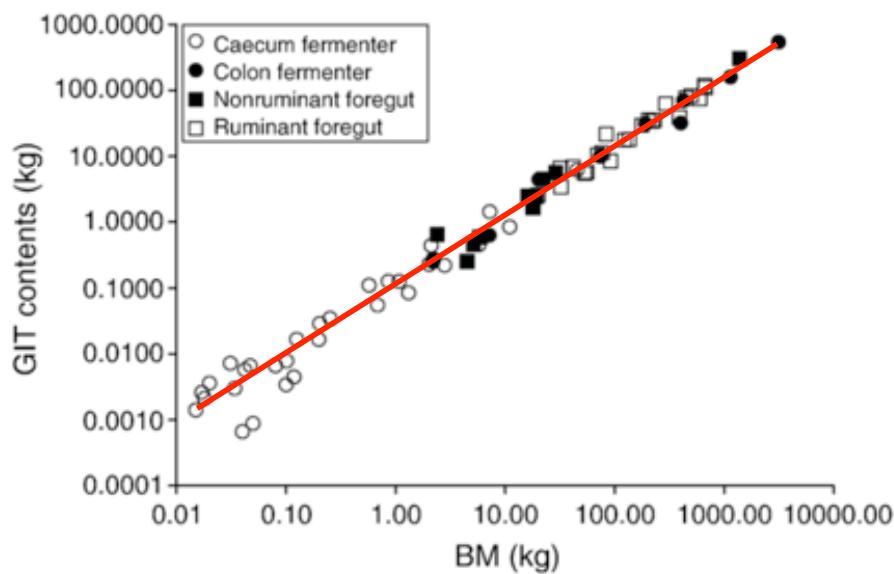
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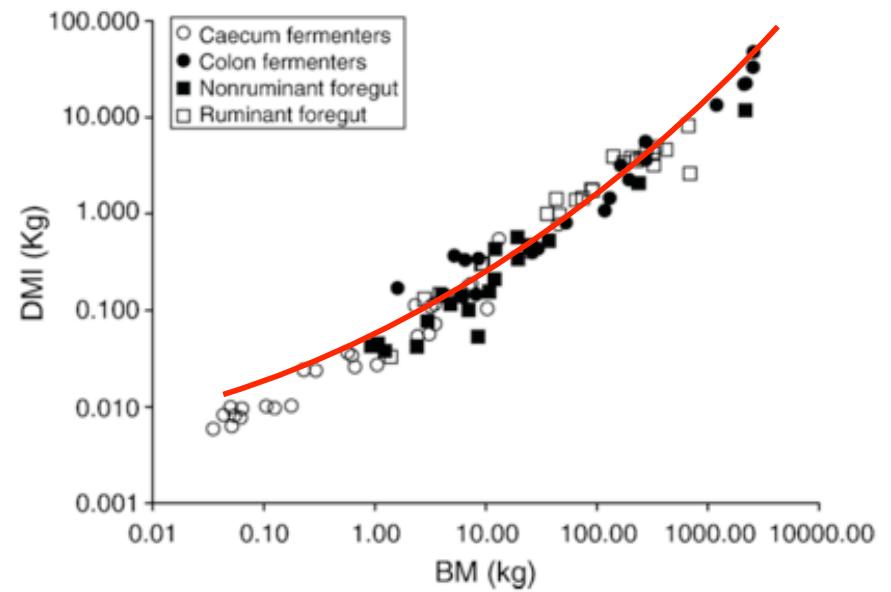
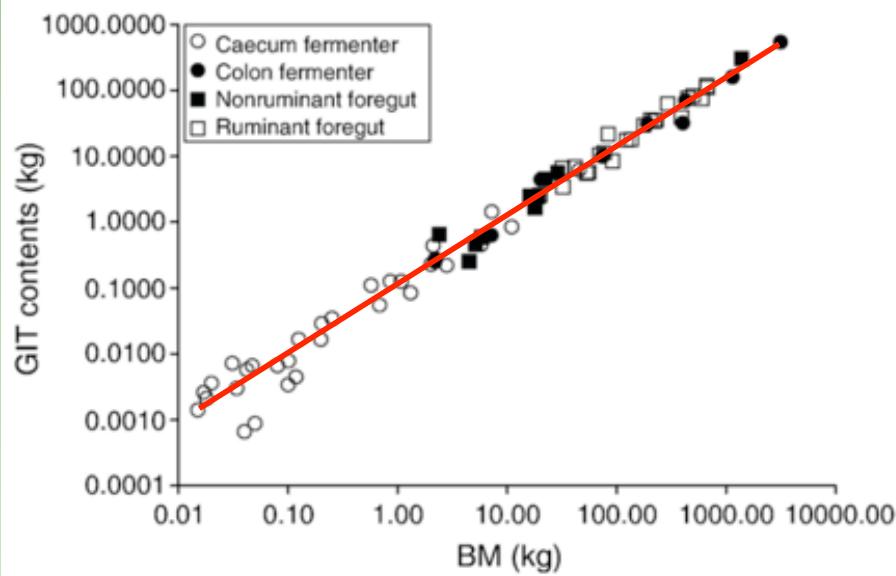
Straight line ... ?



from Clauss et al. (2007)



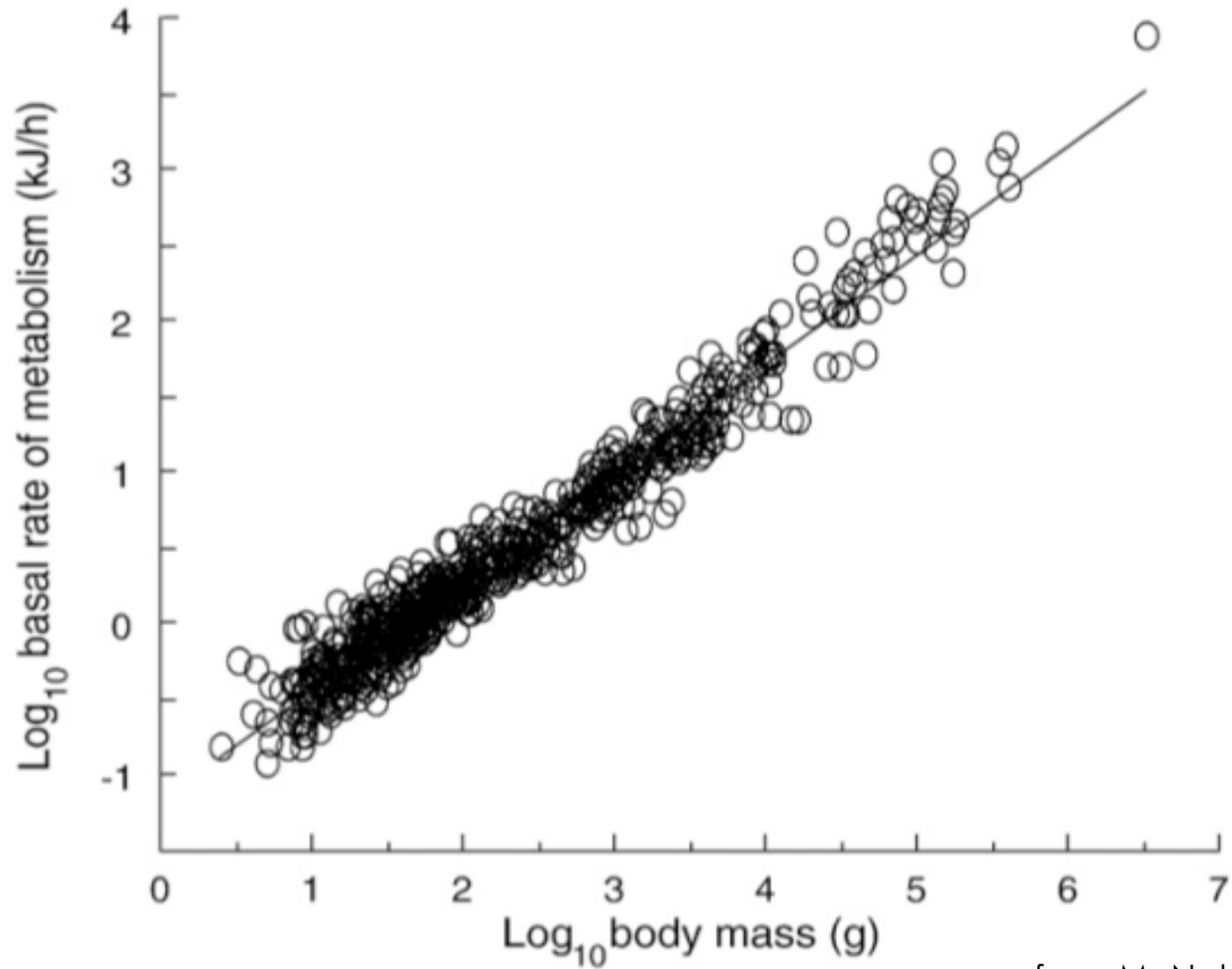
Straight line ... or curvature?



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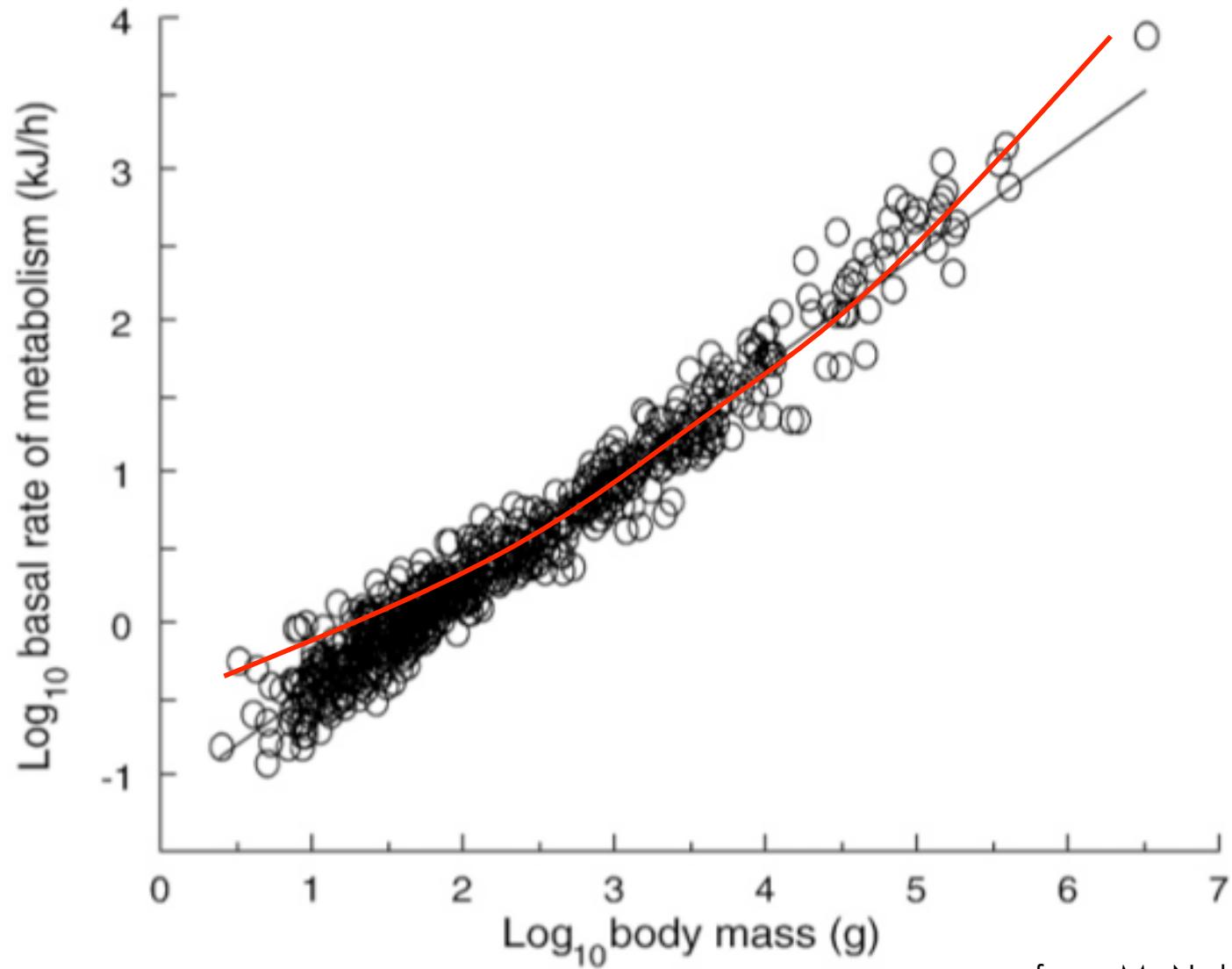
Straight line ... or curvature?



from McNab (2008)



Straight line ... or curvature?



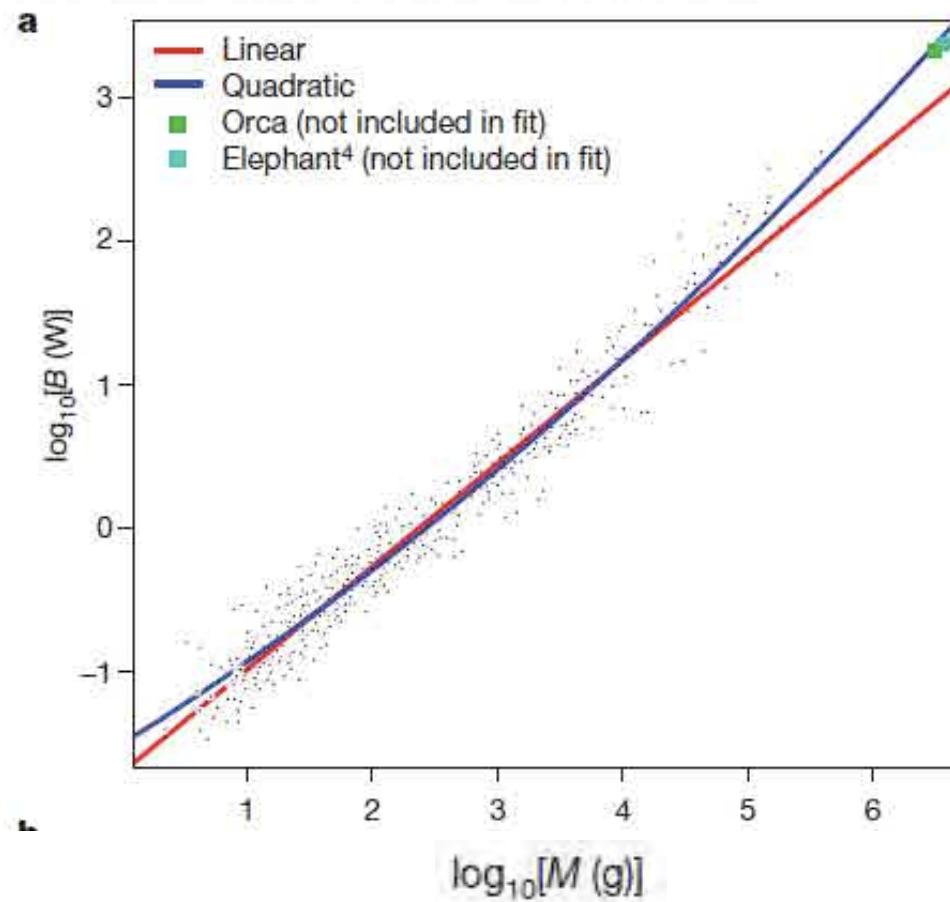
from McNab (2008)



LETTERS

Curvature in metabolic scaling

Tom Kolokotrones¹, Van Savage², Eric J. Deeds¹ & Walter Fontana¹





Why the curvature?

Oikos 121: 102–115, 2012

doi: 10.1111/j.1600-0706.2011.19505.x

© 2011 The Authors. Oikos © 2012 Nordic Society Oikos

Subject Editor: Dustin Marshall. Accepted 4 April 2011

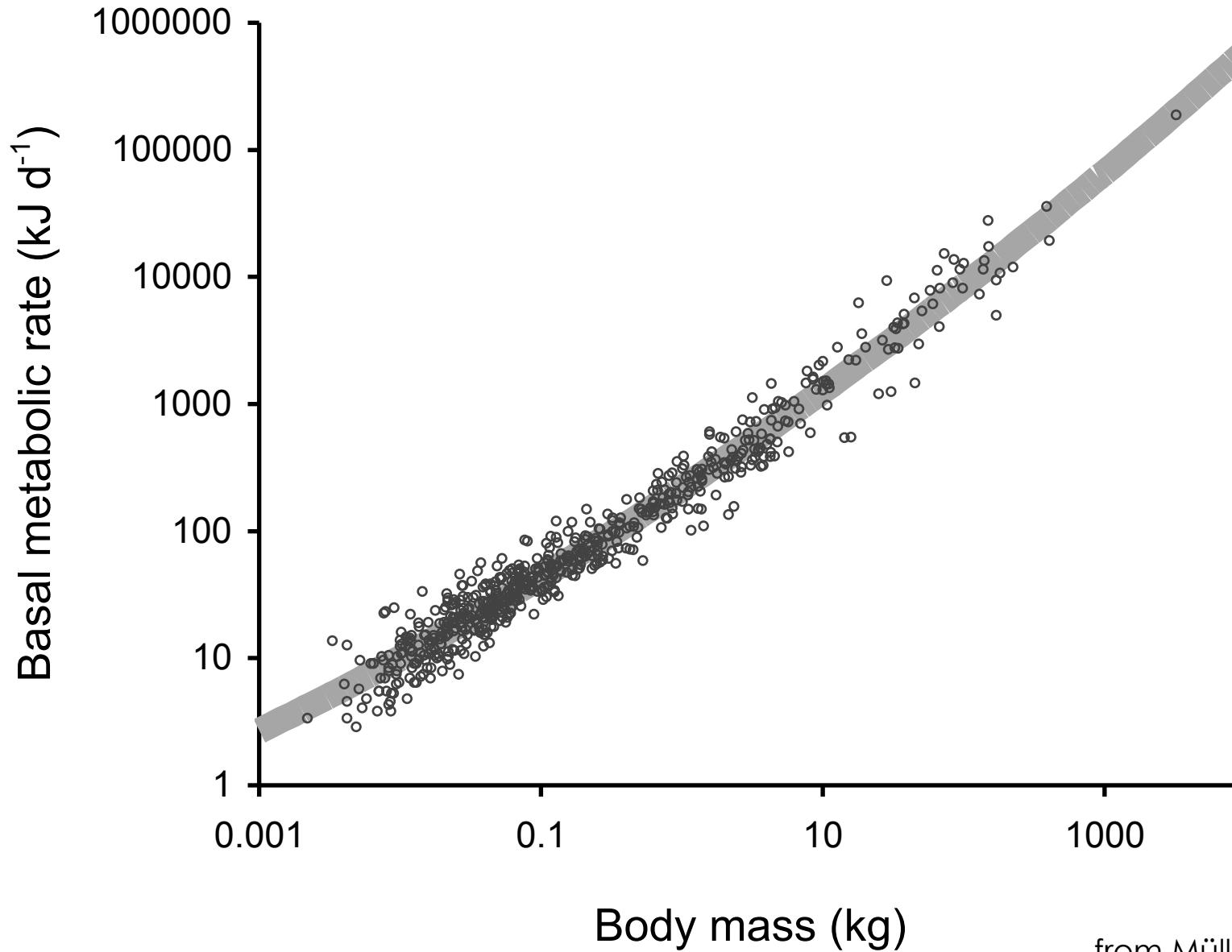
Dichotomy of eutherian reproduction and metabolism

Dennis W. H. Müller, Daryl Codron, Jan Werner, Julia Fritz, Jürgen Hummel, Eva Maria Griebeler and Marcus Clauss

D. W. H. Müller, D. Codron and M. Clauss (mclauss@vetclinics.uZH.ch), Clinic for Zoo Animals, Exotic Pets and Wildlife, Veterinary Faculty, Univ. of Zurich, Winterthurerstr. 260, CH-8057 Zurich, Switzerland. – J. Werner and E. Maria Griebeler, Inst. of Zoology, Dept. of Ecology, Johannes Gutenberg-Universität Mainz, DE-55099 Mainz, Germany. – J. Fritz, Chair of Animal Nutrition and Dietetics, Dept. of Veterinary Sciences, Schönleusenerstraße 8, DE-85764 Oberschleißheim, Germany. – J. Hummel, Inst. of Animal Science, Univ. of Bonn, Endenicher Allee 15, DE-53115 Bonn, Germany.



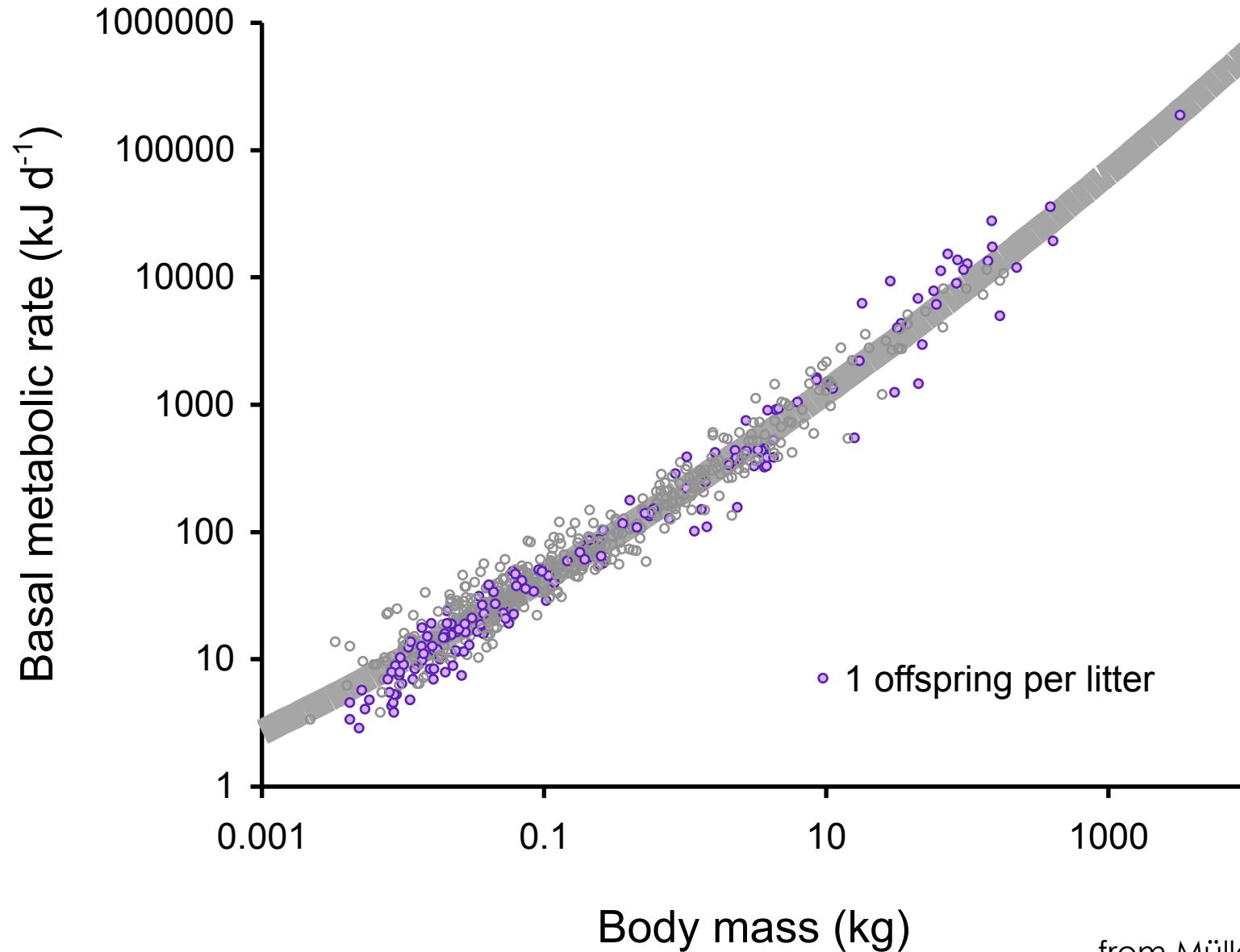
Mode of reproduction?



from Müller et al. (2012)



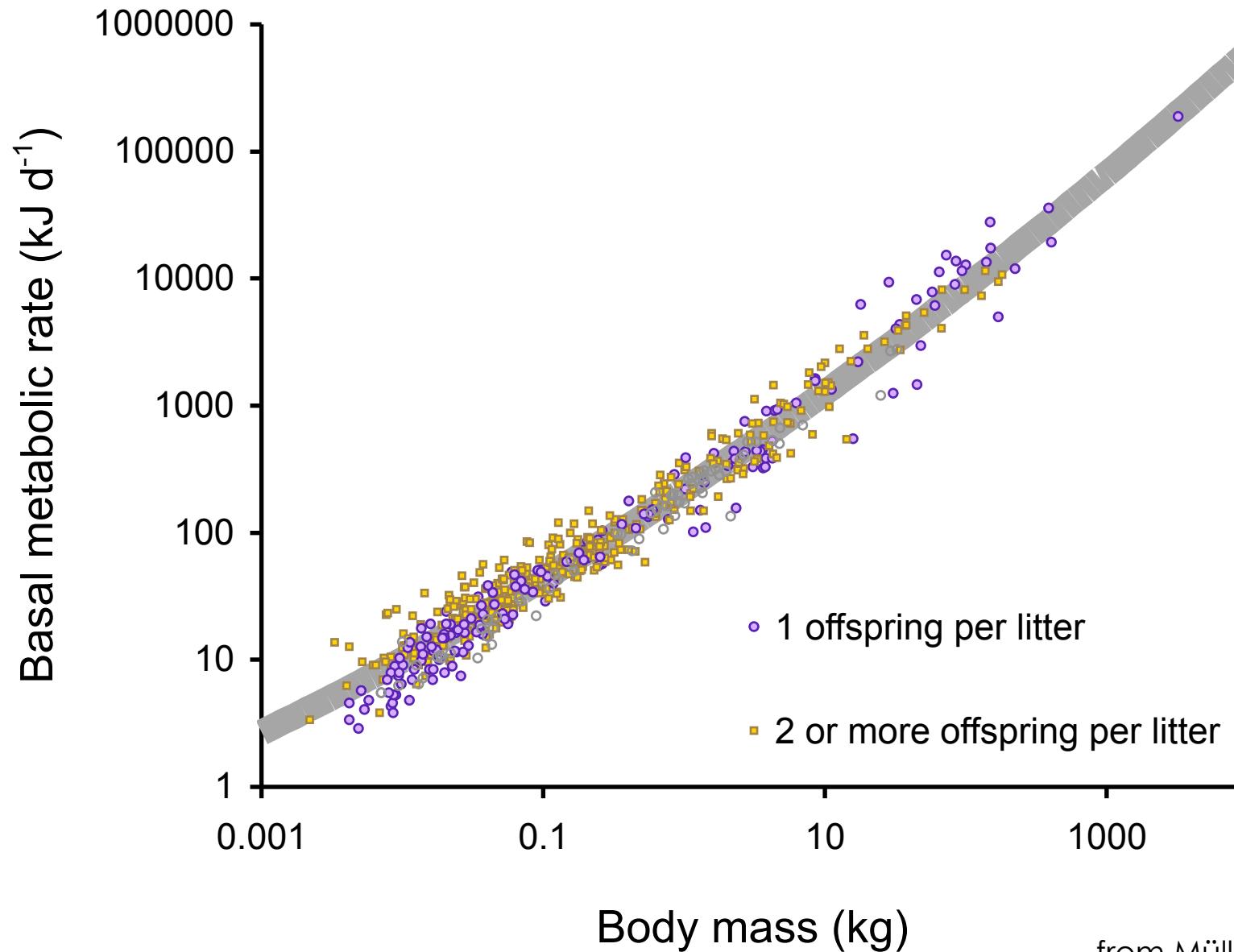
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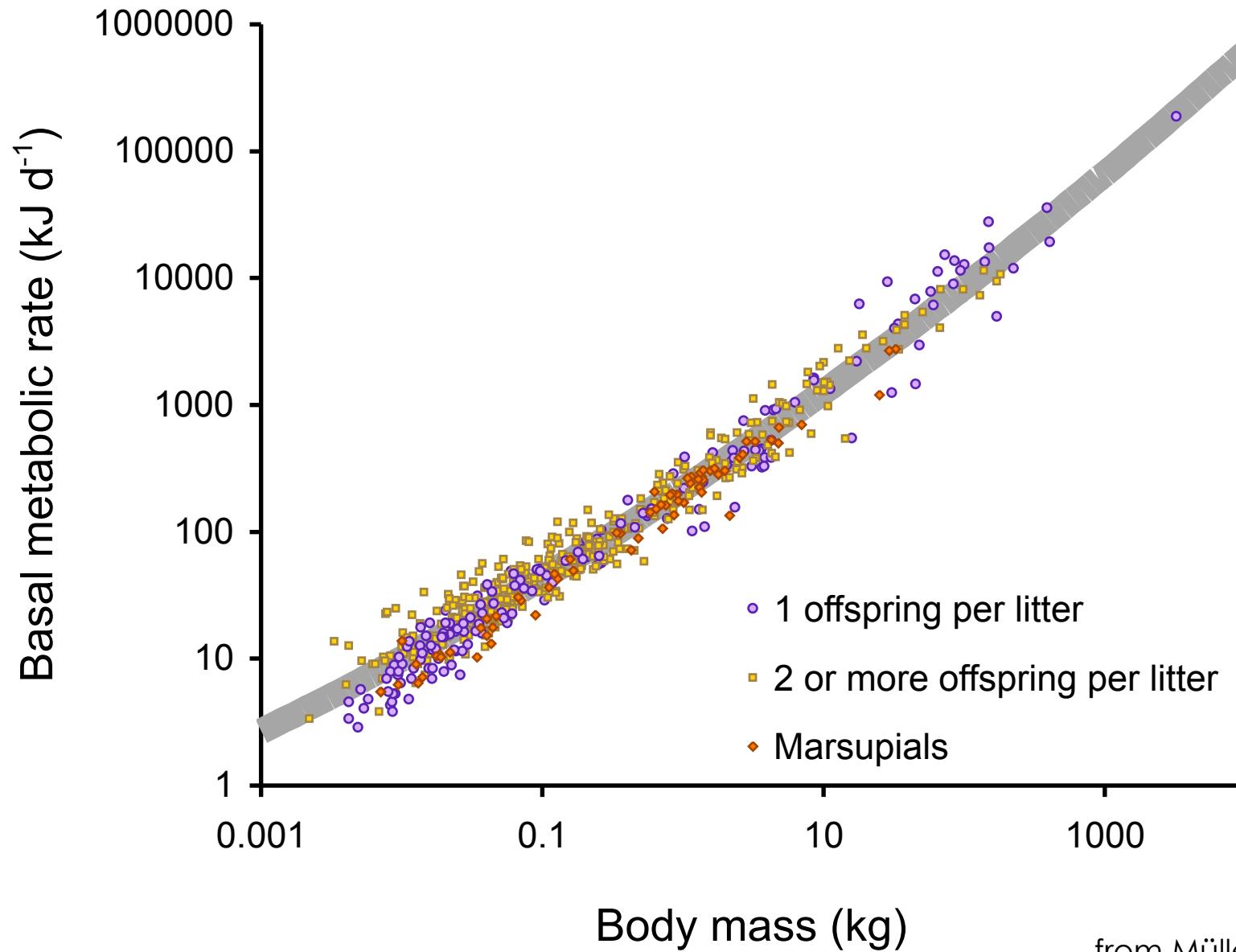
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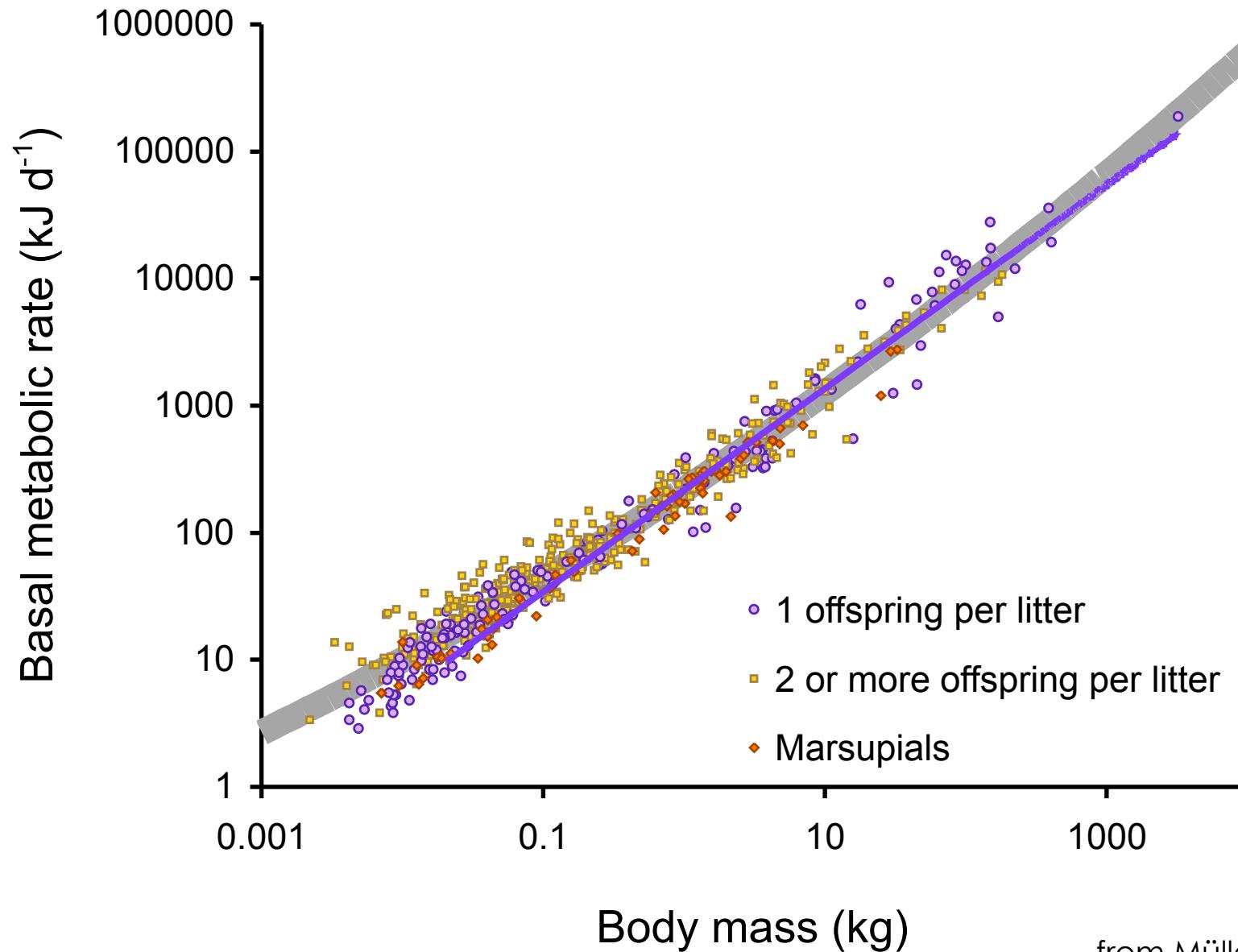
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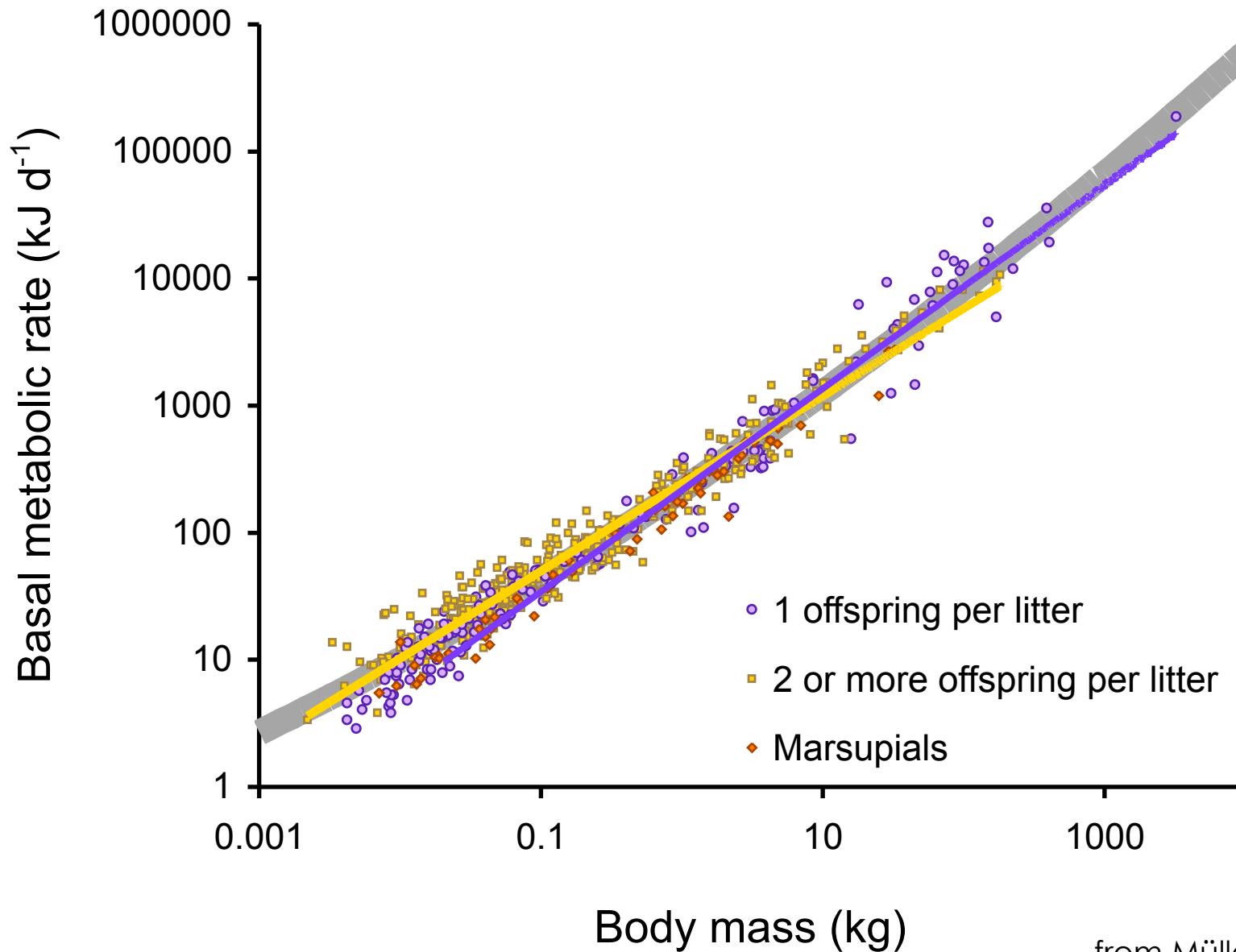
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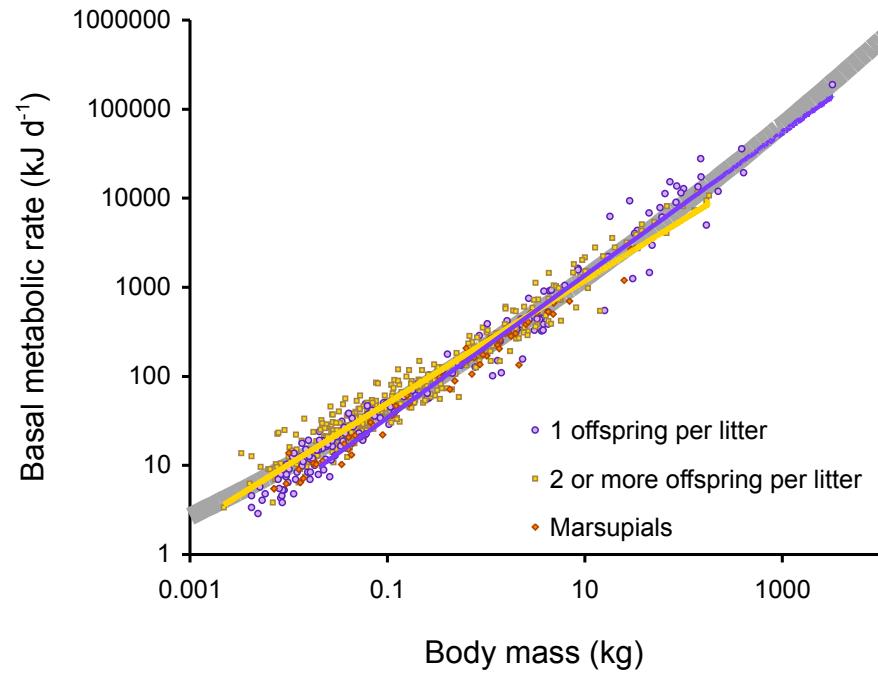
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from Müller et al. (2012)



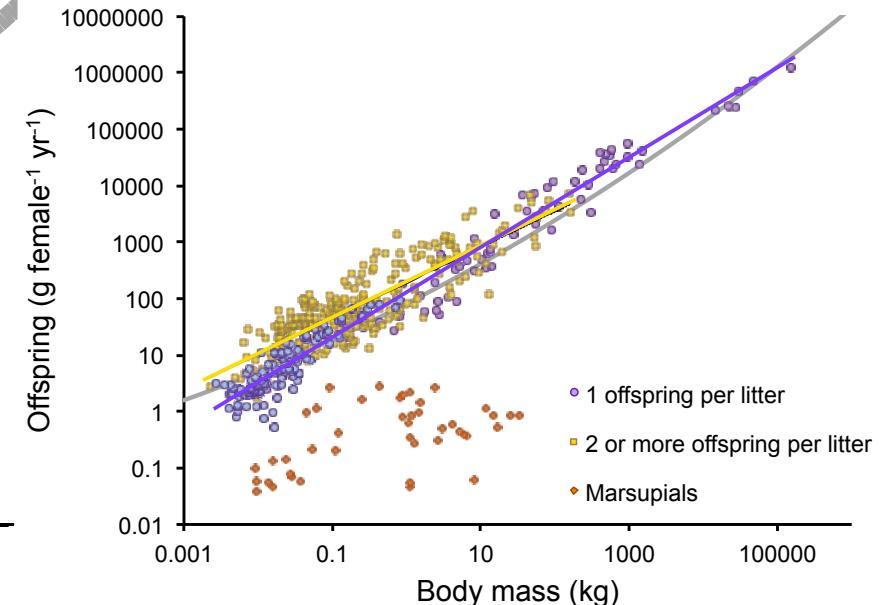
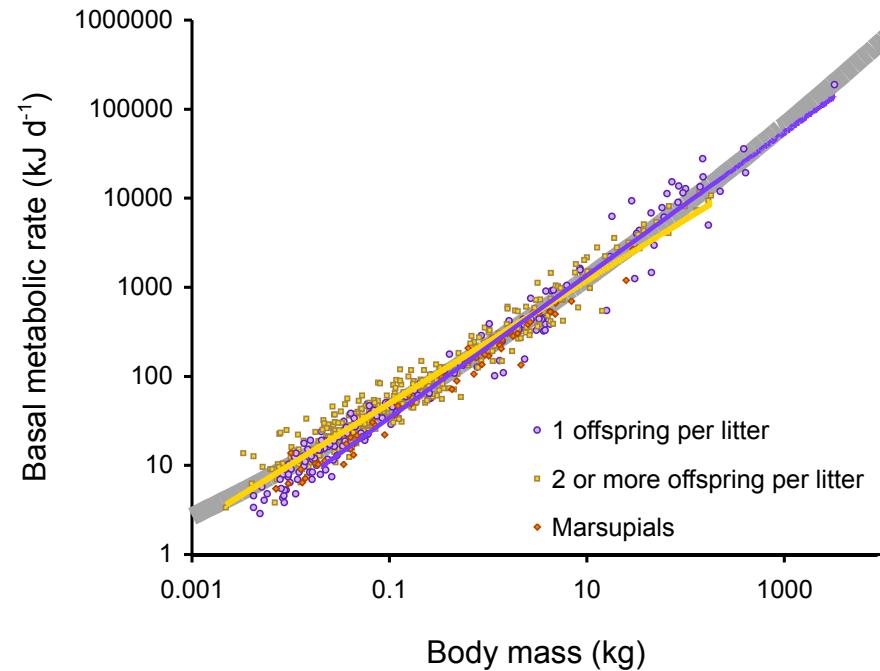
Mode of reproduction?



from Müller et al. (2012)



Mode of reproduction?



from Müller et al. (2012)



‘Jarman-Bell-principle’

Larger herbivores have a digestive advantage
because of allometric principles



Using allometries

Differences in allometric relationships ***within animal groups*** can explain species diversification and niche differentiation along a body mass gradient.



Using allometries

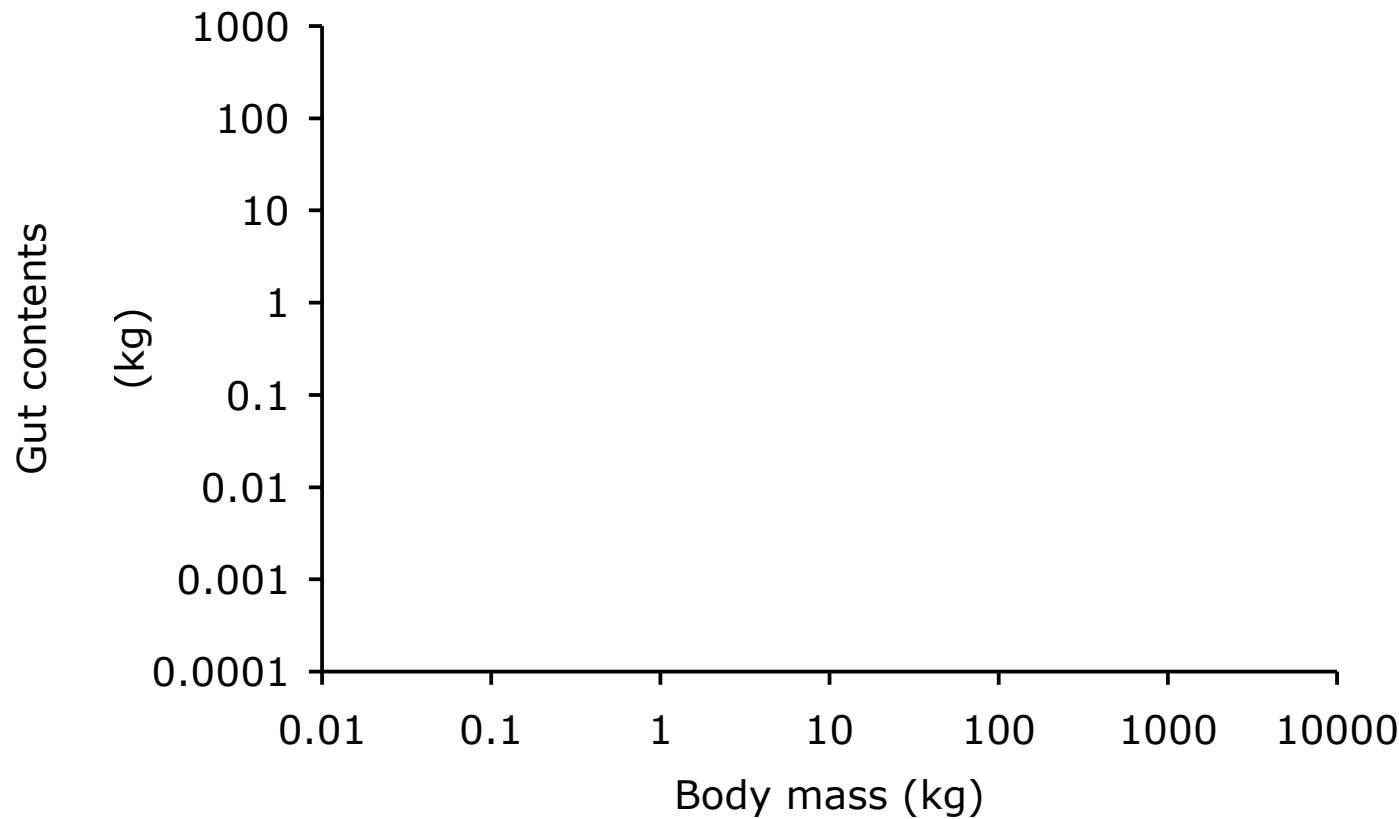
Differences in allometric relationships ***within animal groups*** can explain species diversification and niche differentiation along a body mass gradient.

One of the most prominent examples of such an argument: the '**Jarman-Bell principle**'

1. Larger herbivores eat lower quality food
2. They can do so because they have a digestive advantage due to their large body size (because of allometric principles)



General allometric considerations

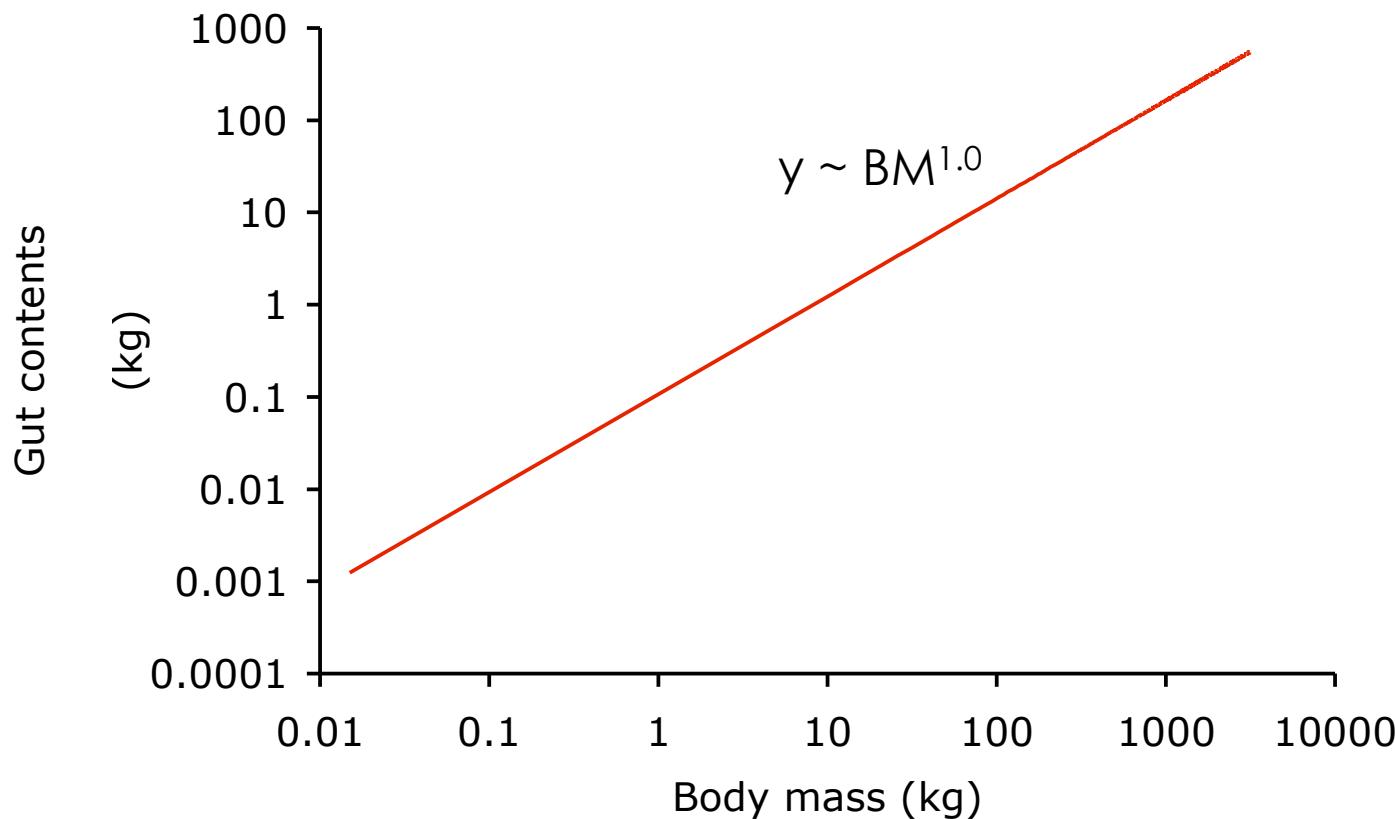


from Parra (1978), Demment & Van Soest (1985), Illius & Gordon (1992); McNab (2002)



General allometric considerations

Gut capacity (measured as gut contents) scales linearly with body mass.

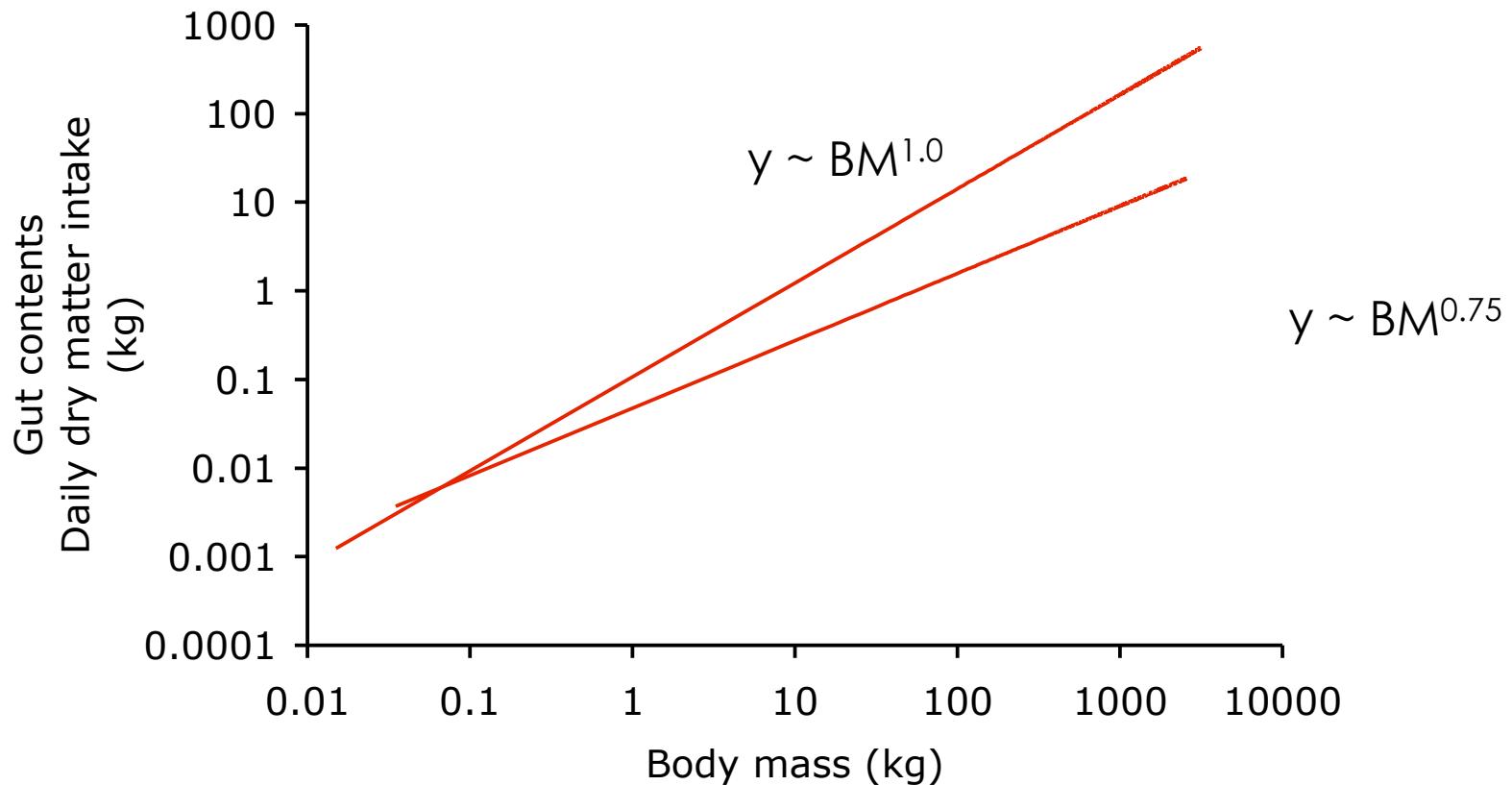


from Parra (1978), Demment & Van Soest (1985), Illius & Gordon (1992); McNab (2002)



General allometric considerations

Food intake (relating to energy requirements) scales to metabolic body mass (body mass^{0.75})

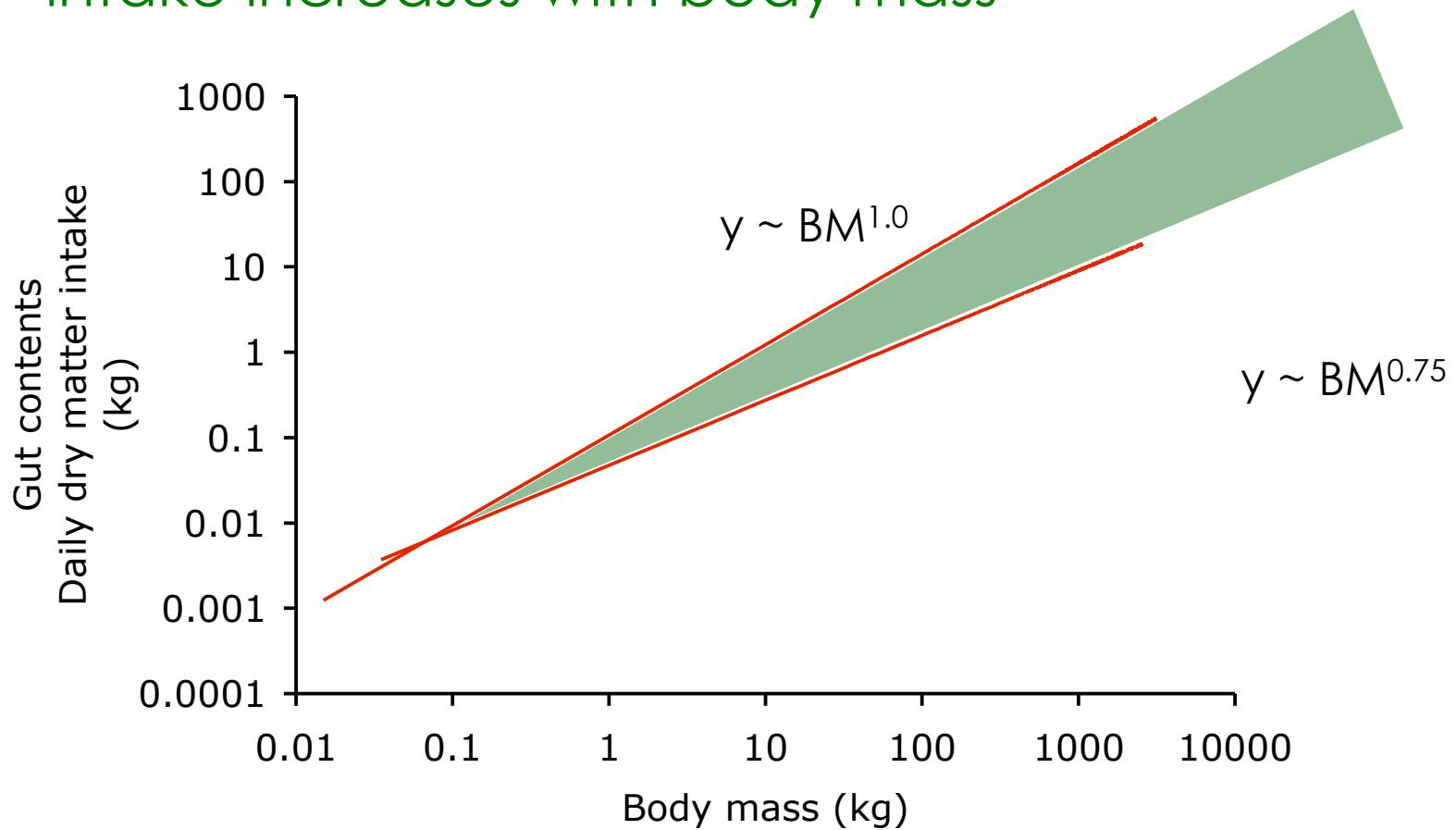


from Parra (1978), Demment & Van Soest (1985), Illius & Gordon (1992); McNab (2002)



General allometric considerations

The difference between gut capacity and food intake increases with body mass



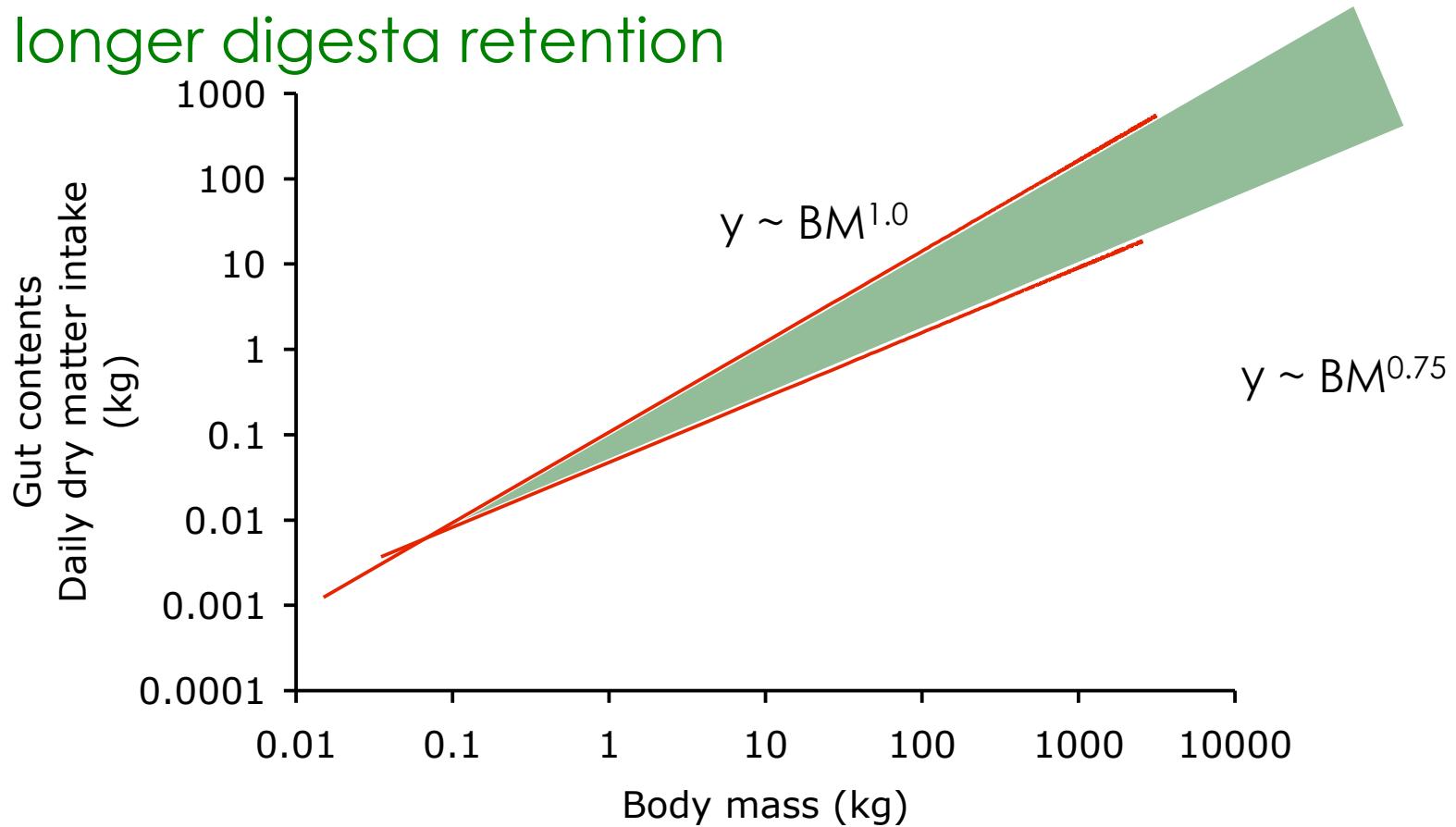
from Parra (1978), Demment & Van Soest (1985), Illius & Gordon (1992); McNab (2002)



General allometric considerations

Therefore more gut capacity per unit food intake
with increasing body mass is available

=> longer digesta retention

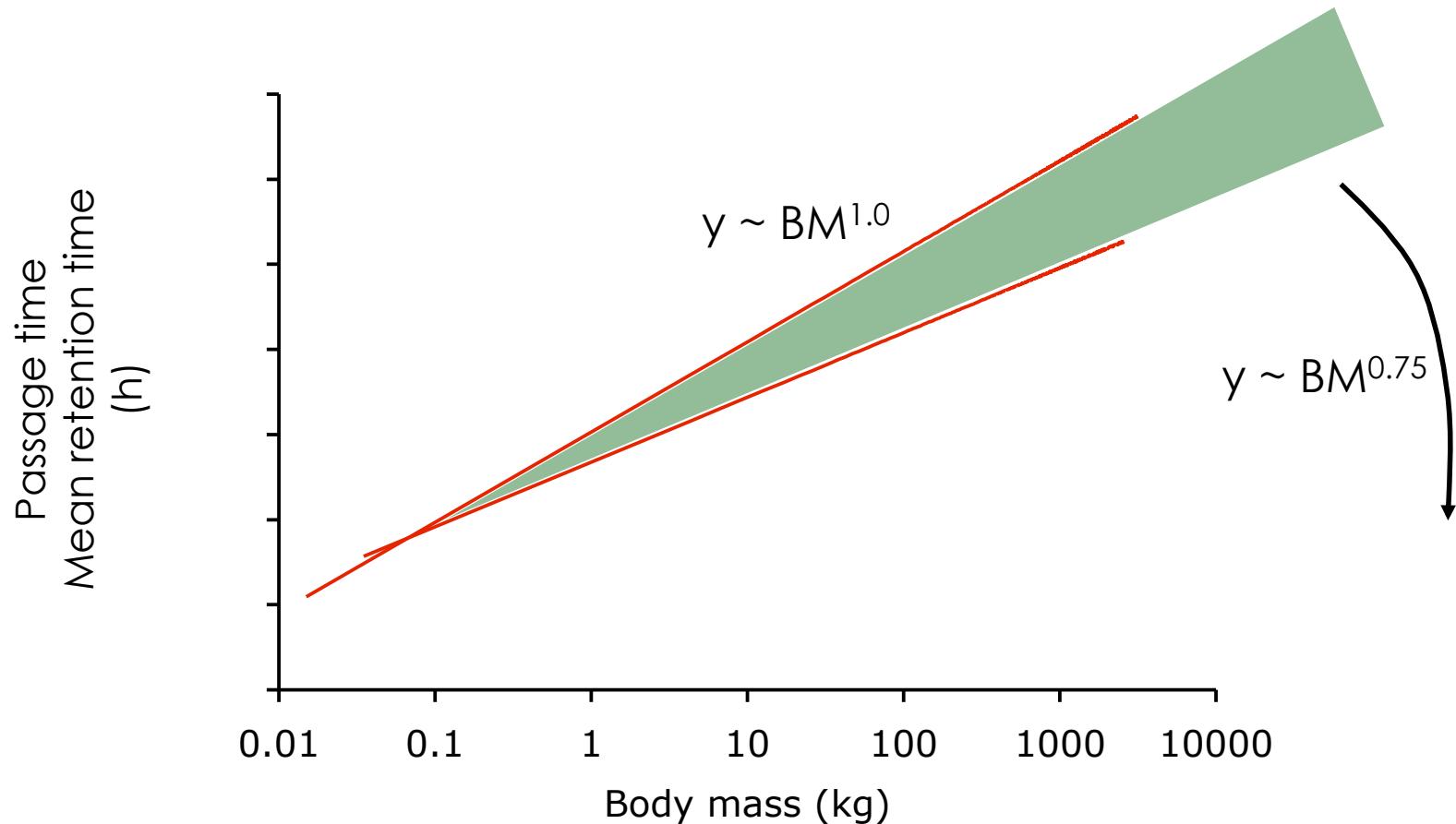


from Parra (1978), Demment & Van Soest (1985), Illius & Gordon (1992); McNab (2002)



General allometric considerations

Digesta retention scales to body mass ...

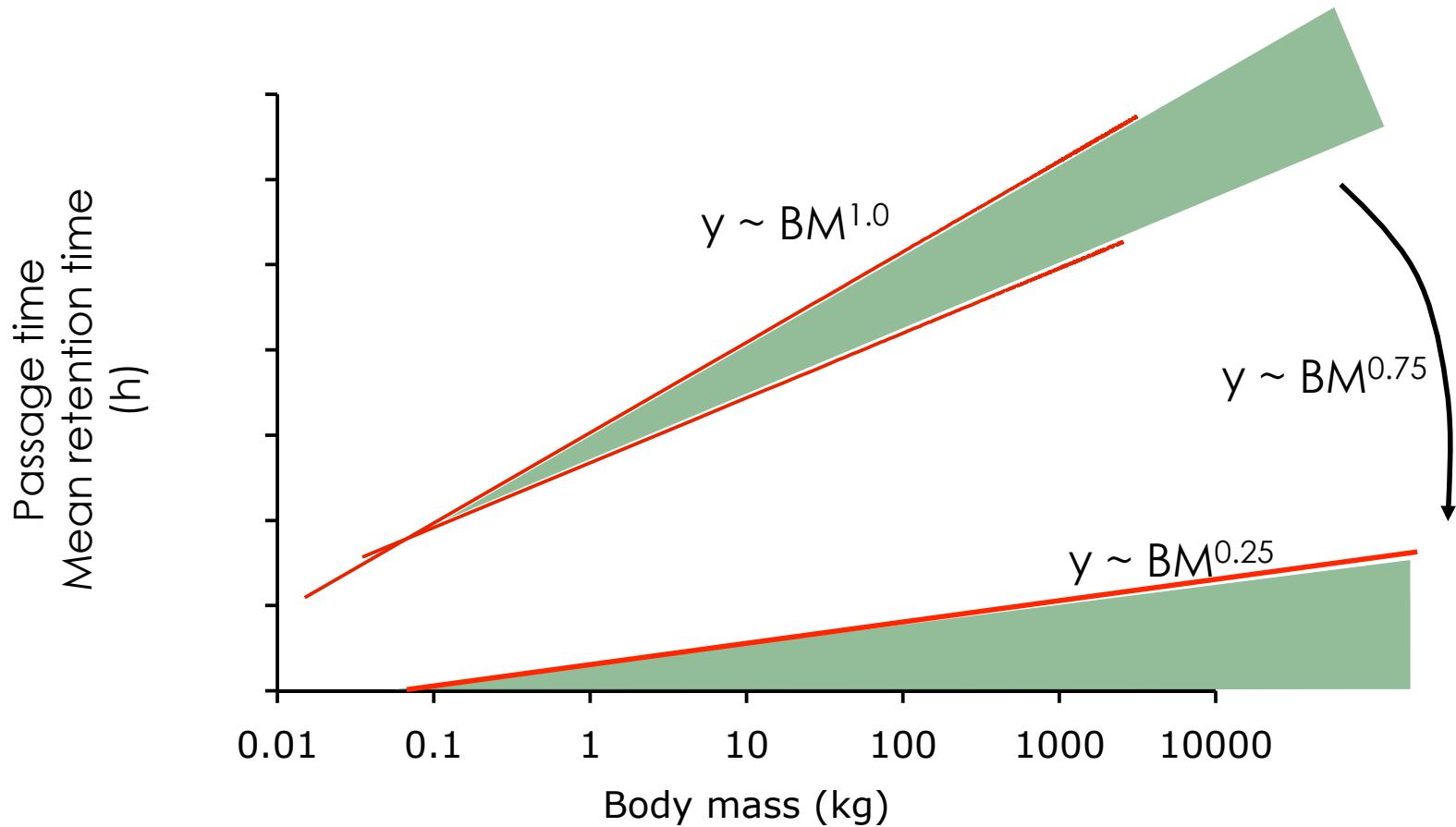


from Parra (1978), Demment & Van Soest (1985), Illius & Gordon (1992); McNab (2002) -



General allometric considerations

... to the power of 0.25

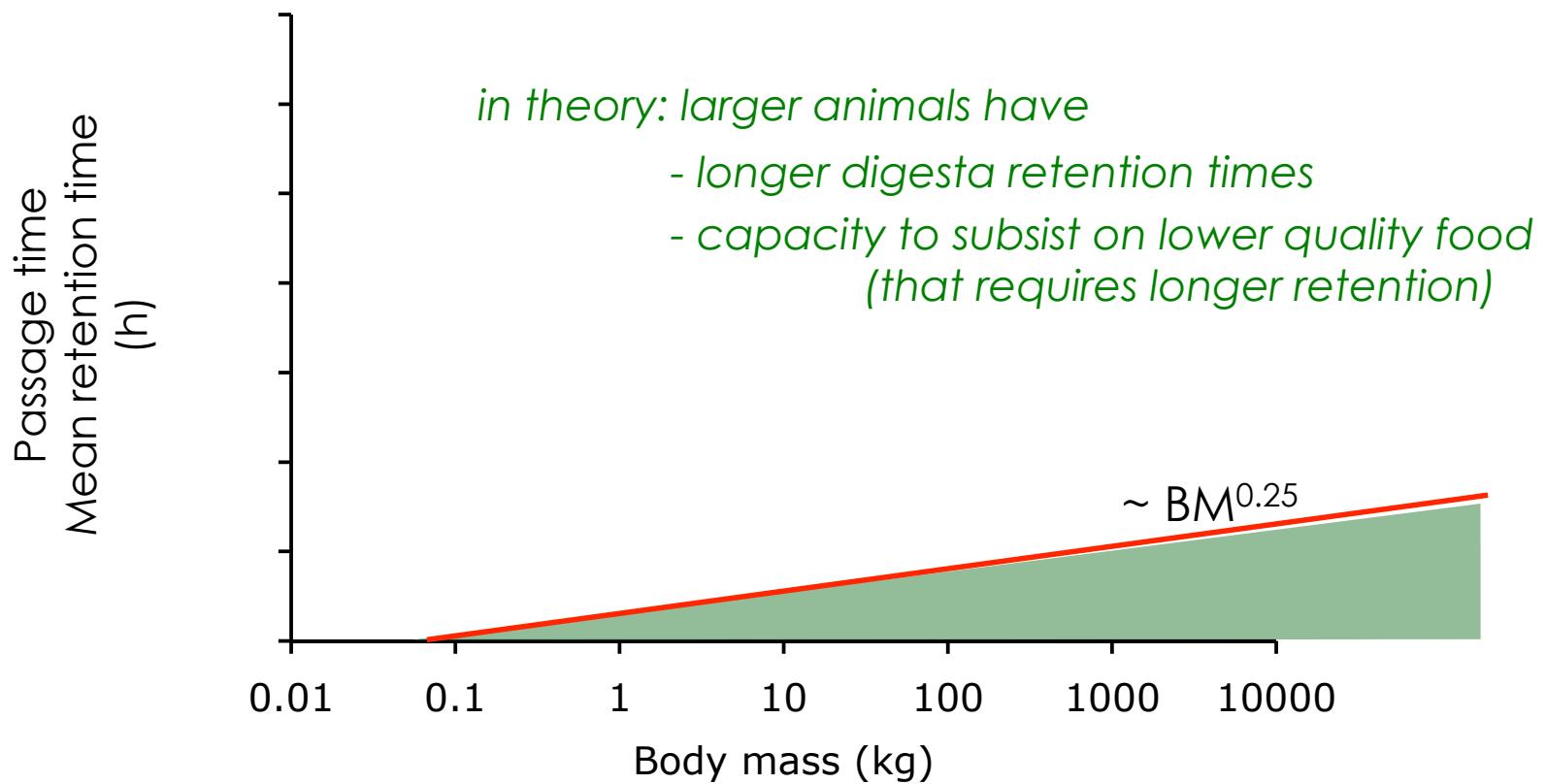


from Parra (1978), Demment & Van Soest (1985), Illius & Gordon (1992); McNab (2002)



General allometric considerations

“Therefore, larger herbivores can achieve higher digestive efficiencies”



from Parra (1978), Demment & Van Soest (1985), Illius & Gordon (1992); McNab (2002)



The ‘Jarman-Bell Principle’
is used widely to infer (herbivore)
niche differentiation along a body
size gradient
(incl. e.g. sexual segregation in dimorphic species)





Mammal Rev. 2005, Volume 35, No. 2, 174–187. Printed in Great Britain.

The digestive performance of mammalian herbivores: why big may not be that much better

MARCUS CLAUSS* and JÜRGEN HUMMEL*†



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Available online at www.sciencedirect.com



Comparative Biochemistry and Physiology, Part A 148 (2007) 249–265

CBP

www.elsevier.com/locate/cbpa

Review

A case of non-scaling in mammalian physiology? Body size, digestive capacity, food intake, and ingesta passage in mammalian herbivores[☆]

Marcus Clauss^{a,*}, Angela Schwarm^b, Sylvia Ortmann^b, W. Jürgen Streich^b, Jürgen Hummel^c



Contents lists available at ScienceDirect

Comparative Biochemistry and Physiology, Part A

journal homepage: www.elsevier.com/locate/cbpa



Is there an influence of body mass on digesta mean retention time in herbivores? A comparative study on ungulates

Patrick Steuer ^{a,*}, Karl-Heinz Südekum ^a, Dennis W.H. Müller ^b, Ragna Franz ^b, Jacques Kaandorp ^c,
Marcus Clauss ^b, Jürgen Hummel ^a



Contents lists available at SciVerse ScienceDirect

Comparative Biochemistry and Physiology, Part A

journal homepage: www.elsevier.com/locate/cbpa



Fibre digestibility in large herbivores as related to digestion type and body mass – An in vitro approach

Patrick Steuer ^{a,*}, Karl-Heinz Südekum ^a, Dennis W.H. Müller ^{b,d}, Jacques Kaandorp ^c,
Marcus Clauss ^b, Jürgen Hummel ^{a,e}



Contents lists available at ScienceDirect

Comparative Biochemistry and Physiology, Part A

journal homepage: www.elsevier.com/locate/cbpa



Faecal particle size: Digestive physiology meets herbivore diversity

Marcus Clauss ^a, Patrick Steuer ^b, Kerstin Erlinghagen-Lückerath ^b, Jacques Kaandorp ^c, Julia Fritz ^a,
Karl-Heinz Südekum ^{b,*}, Jürgen Hummel ^{b,d}





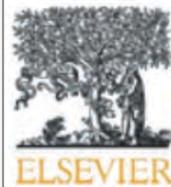
Functional Ecology 2014, 28, 1127–1134

doi: 10.1111/1365-2435.12275

Does body mass convey a digestive advantage for large herbivores?

Patrick Steuer¹, Karl-Heinz Südekum¹, Thomas Tütken^{2,†}, Dennis W. H. Müller^{3,4}, Jacques Kaandorp⁵, Martin Bucher⁶, Marcus Clauss³ and Jürgen Hummel^{*,1,7}

Comparative Biochemistry and Physiology, Part A 164 (2013) 129–140



Contents lists available at SciVerse ScienceDirect

Comparative Biochemistry and Physiology, Part A

journal homepage: www.elsevier.com/locate/cbpa



Assessing the Jarman–Bell Principle: Scaling of intake, digestibility, retention time and gut fill with body mass in mammalian herbivores

Dennis W.H. Müller ^{a,b}, Daryl Codron ^{a,c}, Carlo Meloro ^d, Adam Munn ^e, Angela Schwarm ^f, Jürgen Hummel ^{g,h}, Marcus Clauss ^{a,*}

OPEN ACCESS Freely available online

PLOS ONE

Review

Herbivory and Body Size: Allometries of Diet Quality and Gastrointestinal Physiology, and Implications for Herbivore Ecology and Dinosaur Gigantism

Marcus Clauss^{1*}, Patrick Steuer², Dennis W. H. Müller³, Daryl Codron^{1,4}, Jürgen Hummel^{2,5}





Checking the validity of a concept

1. Check if empirical data matches the hypothesis
2. Check the mathematical validity
3. Check conceptual background

(vary sequence to suit your preference or intellectual capacity)



Checking the validity of a concept



- 1. Check if empirical data matches the hypothesis**
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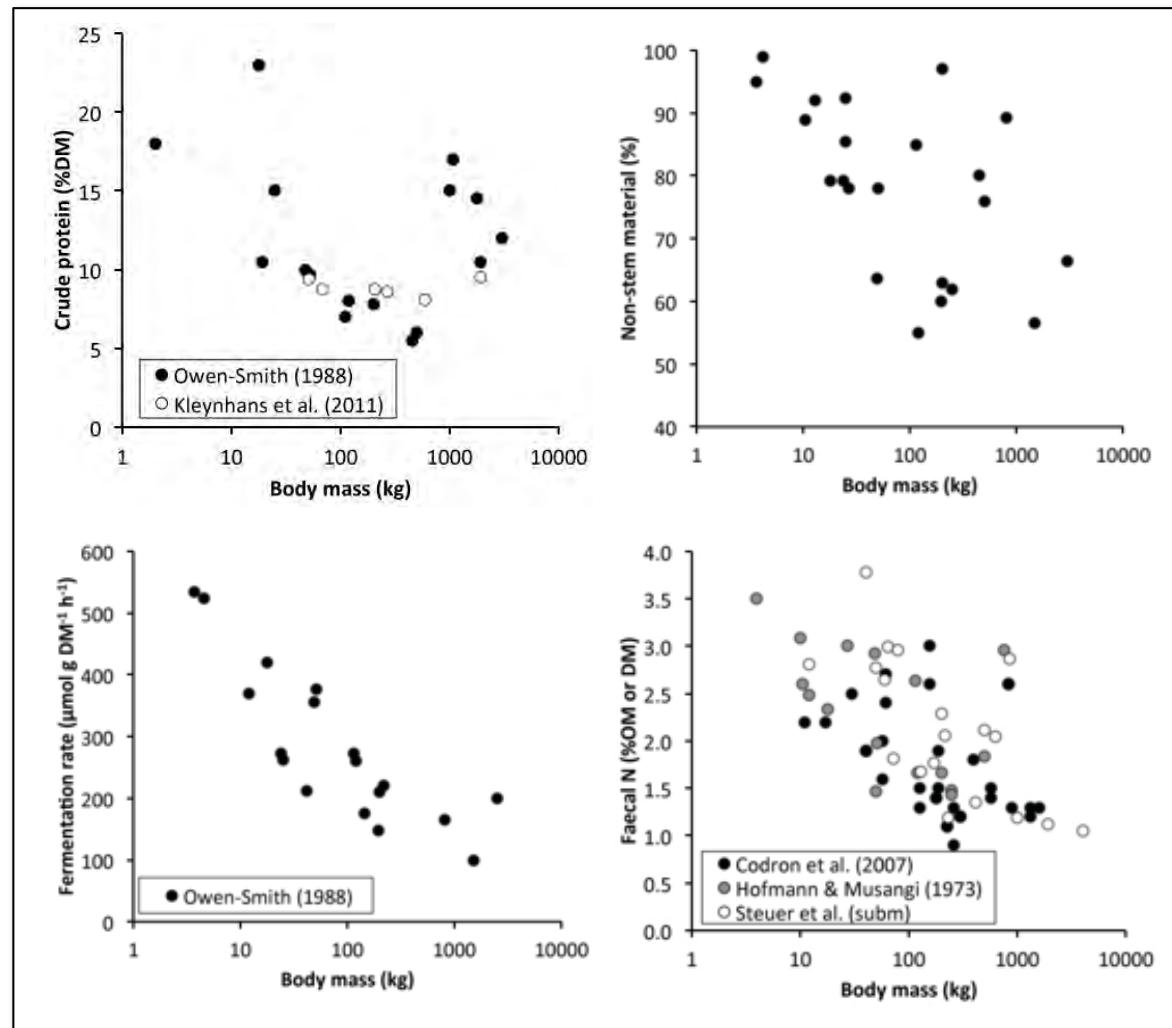
(vary sequence to suit your preference or intellectual capacity)



Diet quality



Larger herbivores eat lower-quality diets



from Clauss et al. (2013)



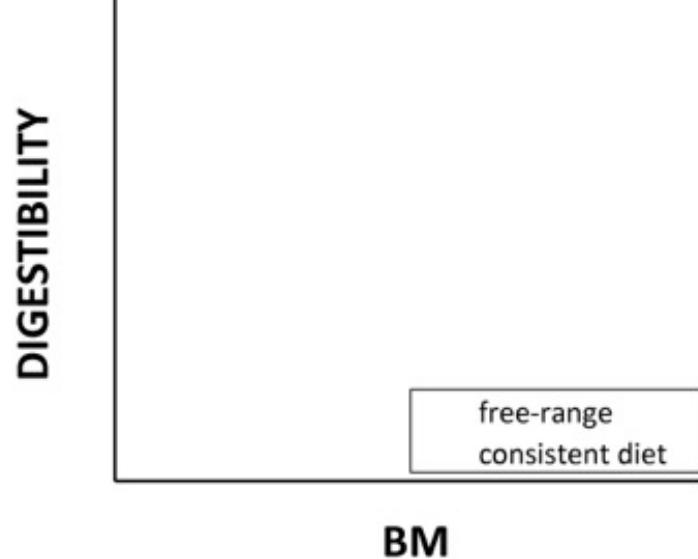
Digestive efficiency



*Do larger herbivores ingest
lower-quality diets,
and are they physiologically
equipped for a
'better' digestion of such diets?*



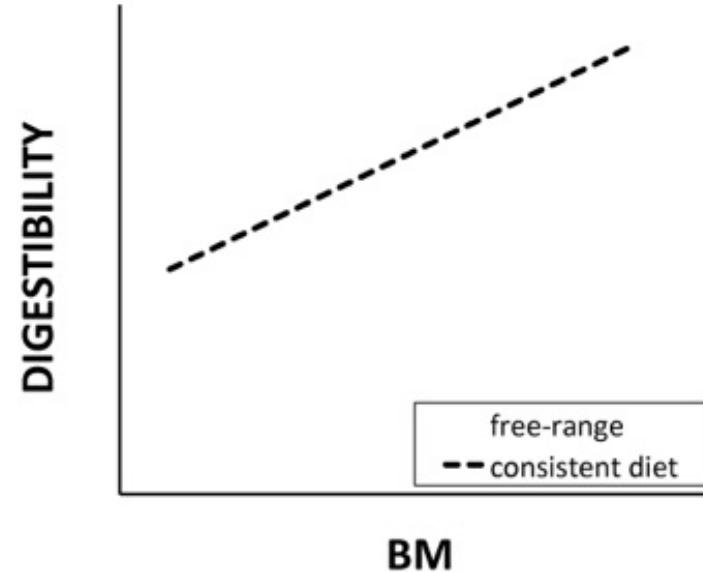
Hypothesis building



from Steuer et al. (2014)



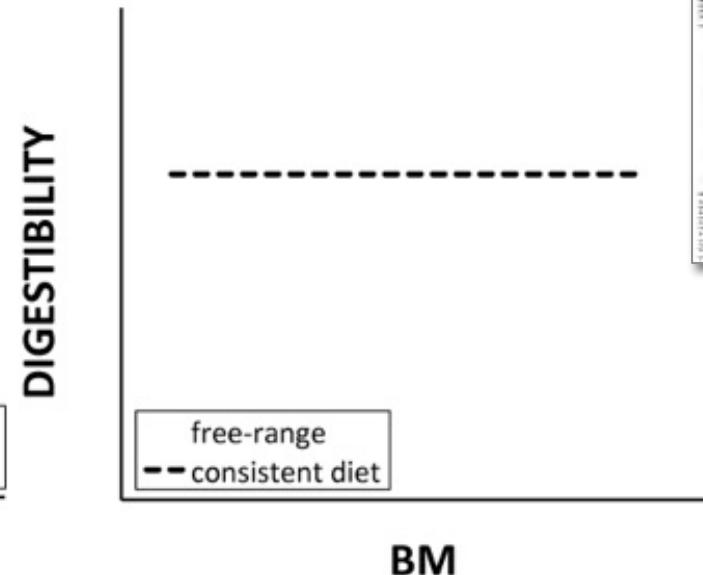
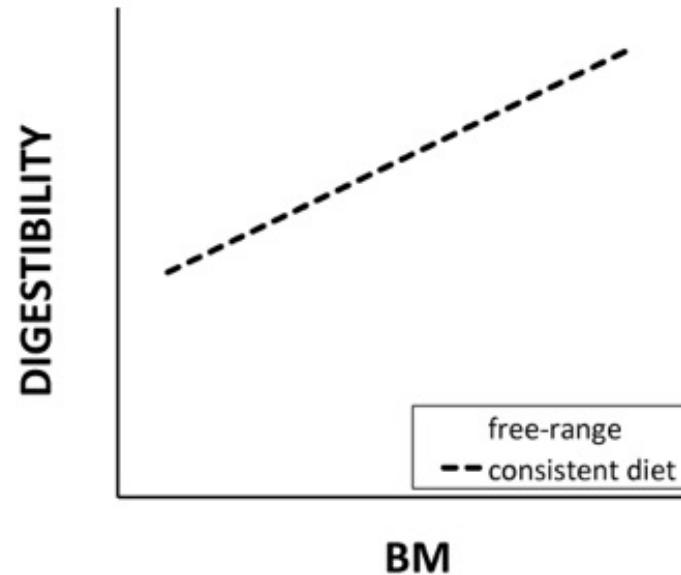
Larger size endows higher digestive efficiency ...



from Steuer et al. (2014)



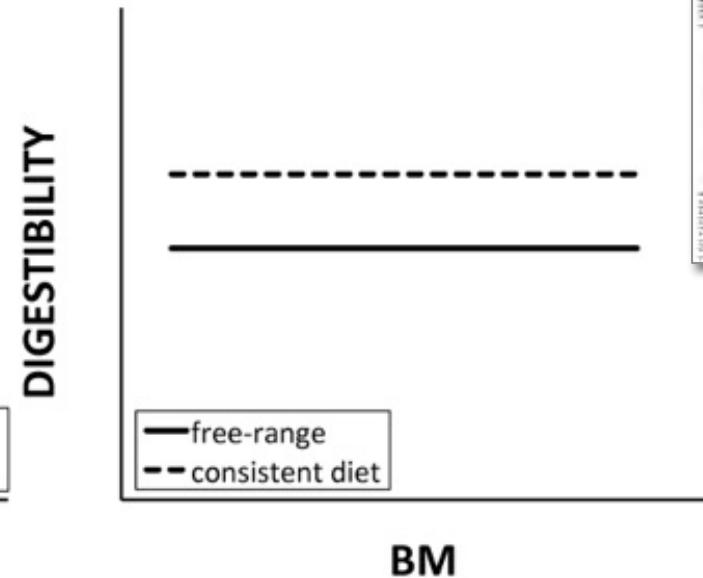
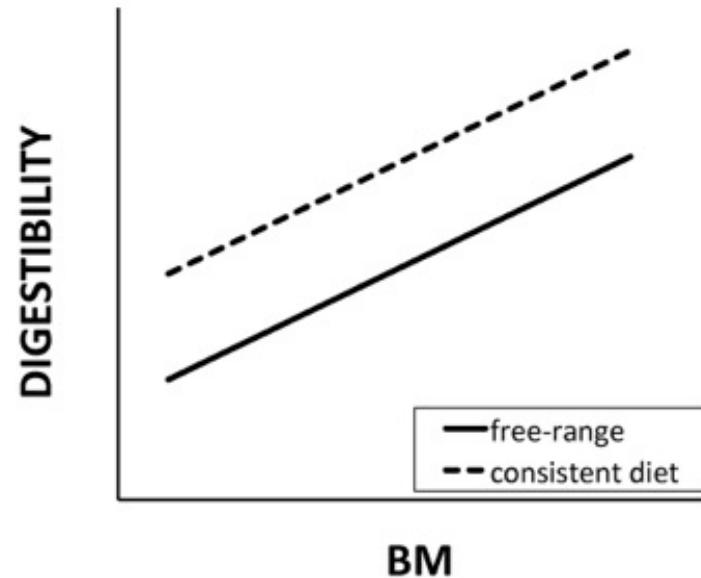
... or body size has no effect on digestibility



from Steuer et al. (2014)



Body size does not affect diet selection ...

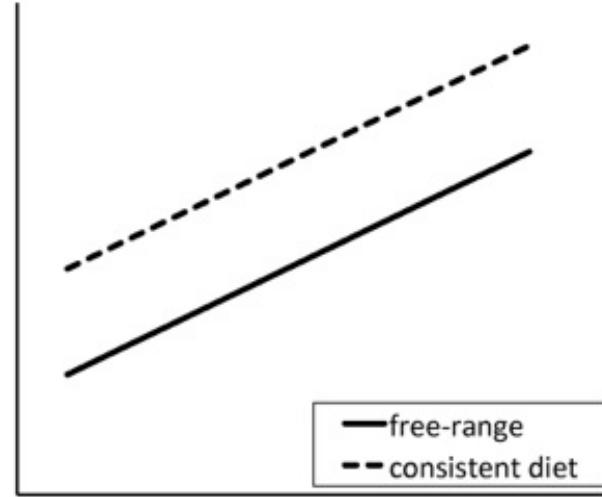


from Steuer et al. (2014)



... or larger animals eat lower quality diets

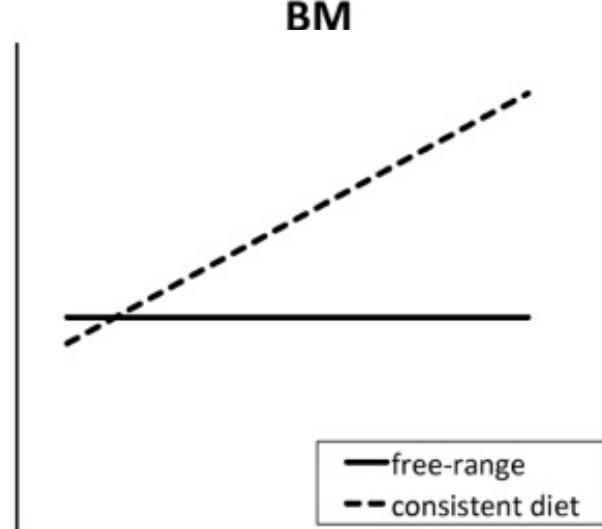
DIGESTIBILITY



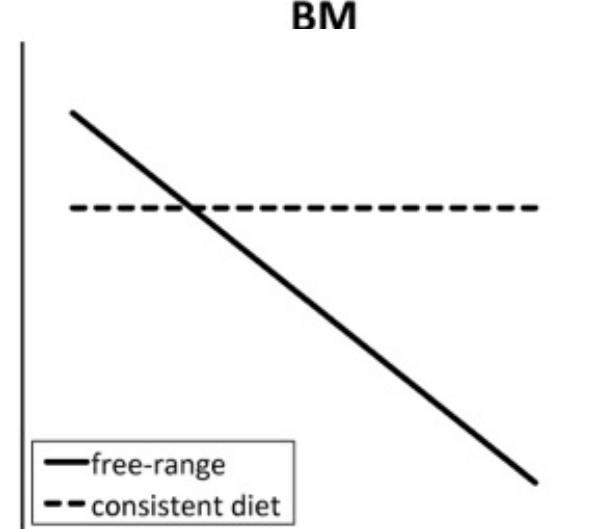
DIGESTIBILITY



DIGESTIBILITY



DIGESTIBILITY

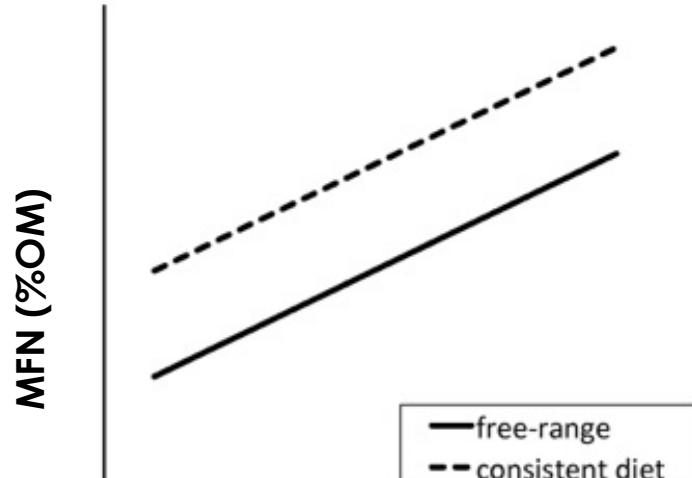


BM

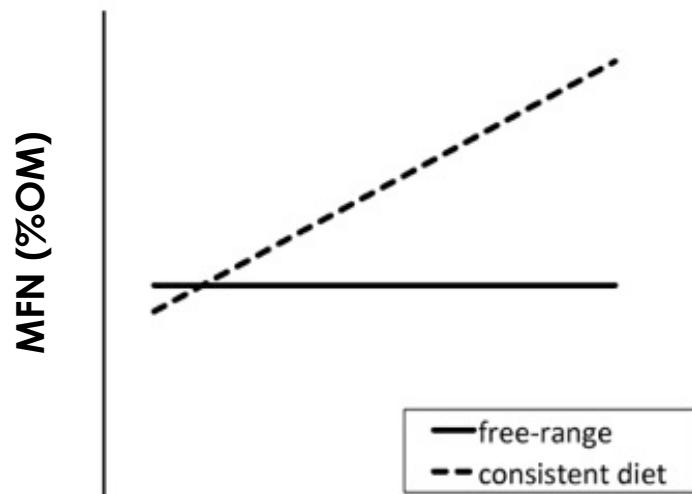
from Steuer et al. (2014)



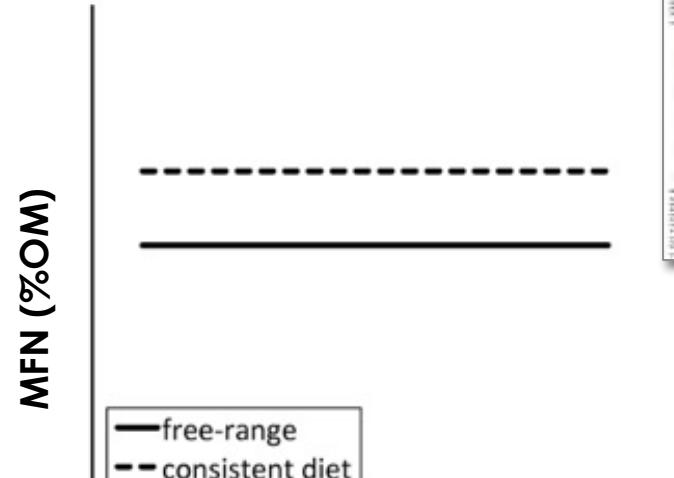
Measuring digestibility ...



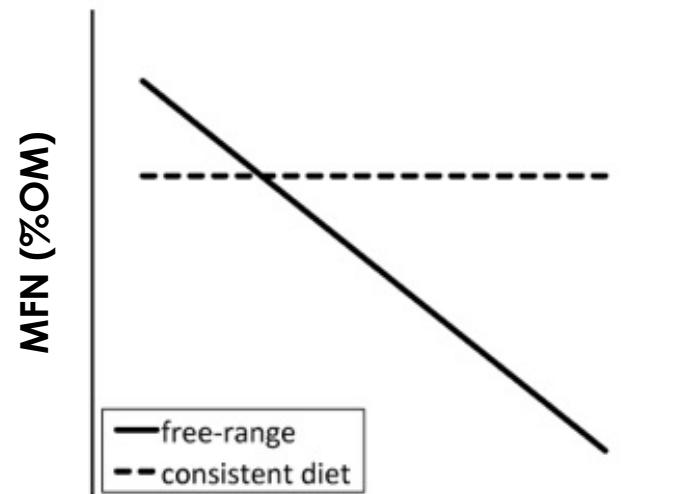
BM



BM



BM



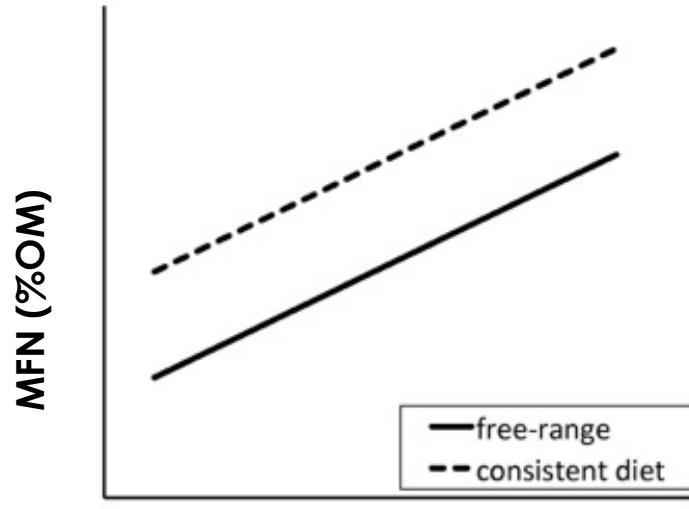
BM

from Steuer et al. (2014)

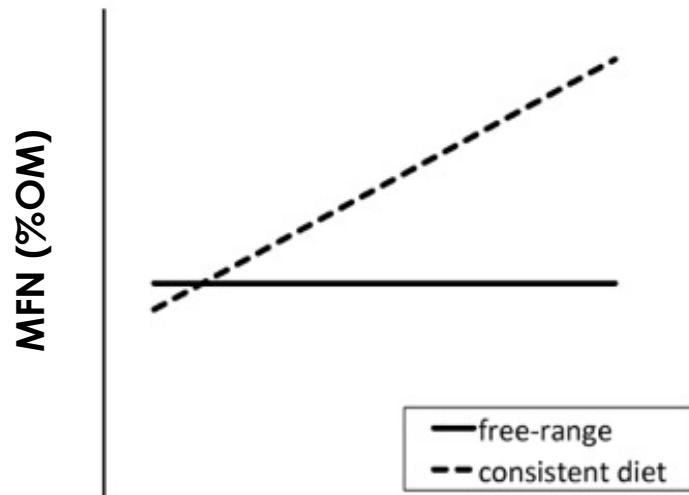




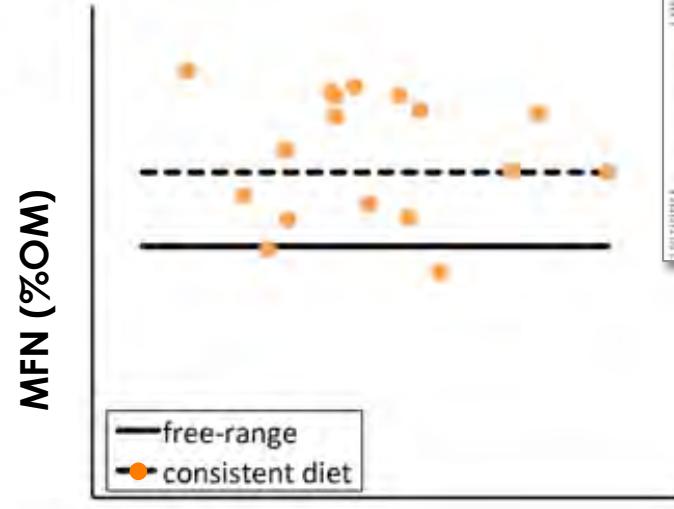
... in zoo animals on a consistent diet



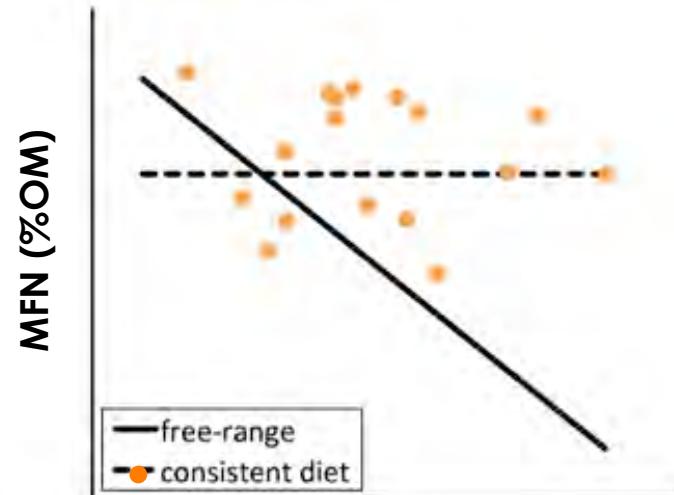
BM



BM



BM



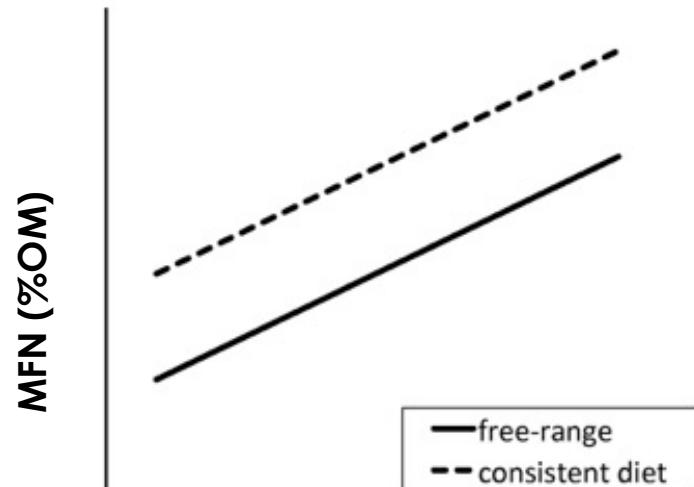
BM

from Steuer et al. (2014)

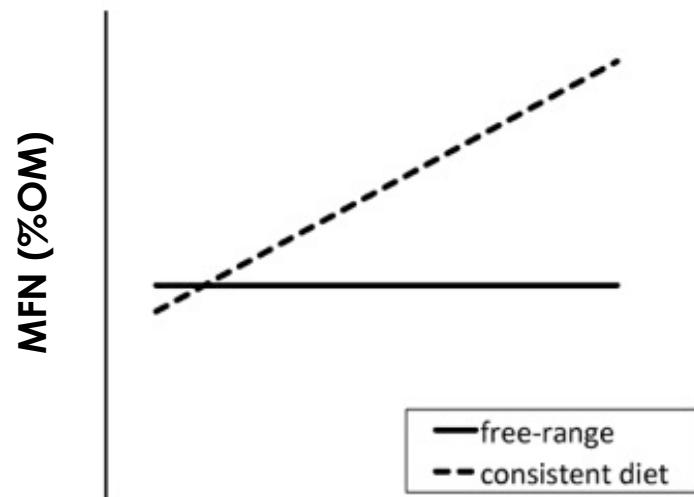




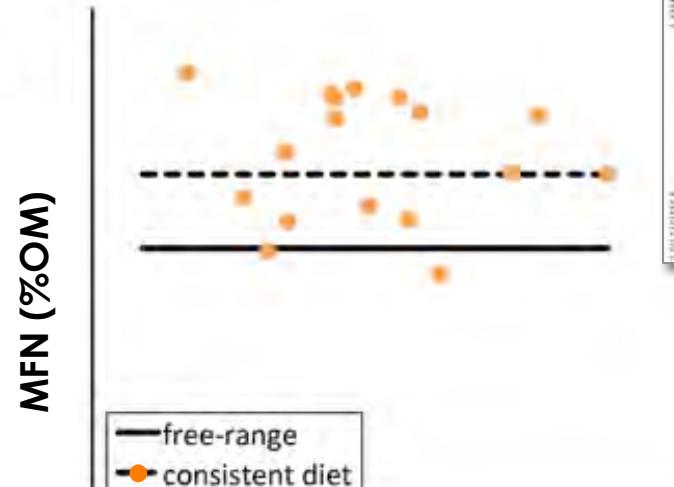
... in free-ranging animals



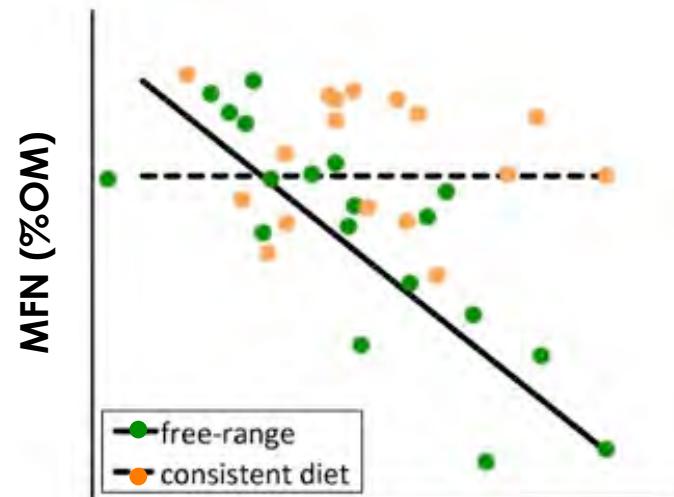
BM



BM



BM



BM

from Steuer et al. (2014)



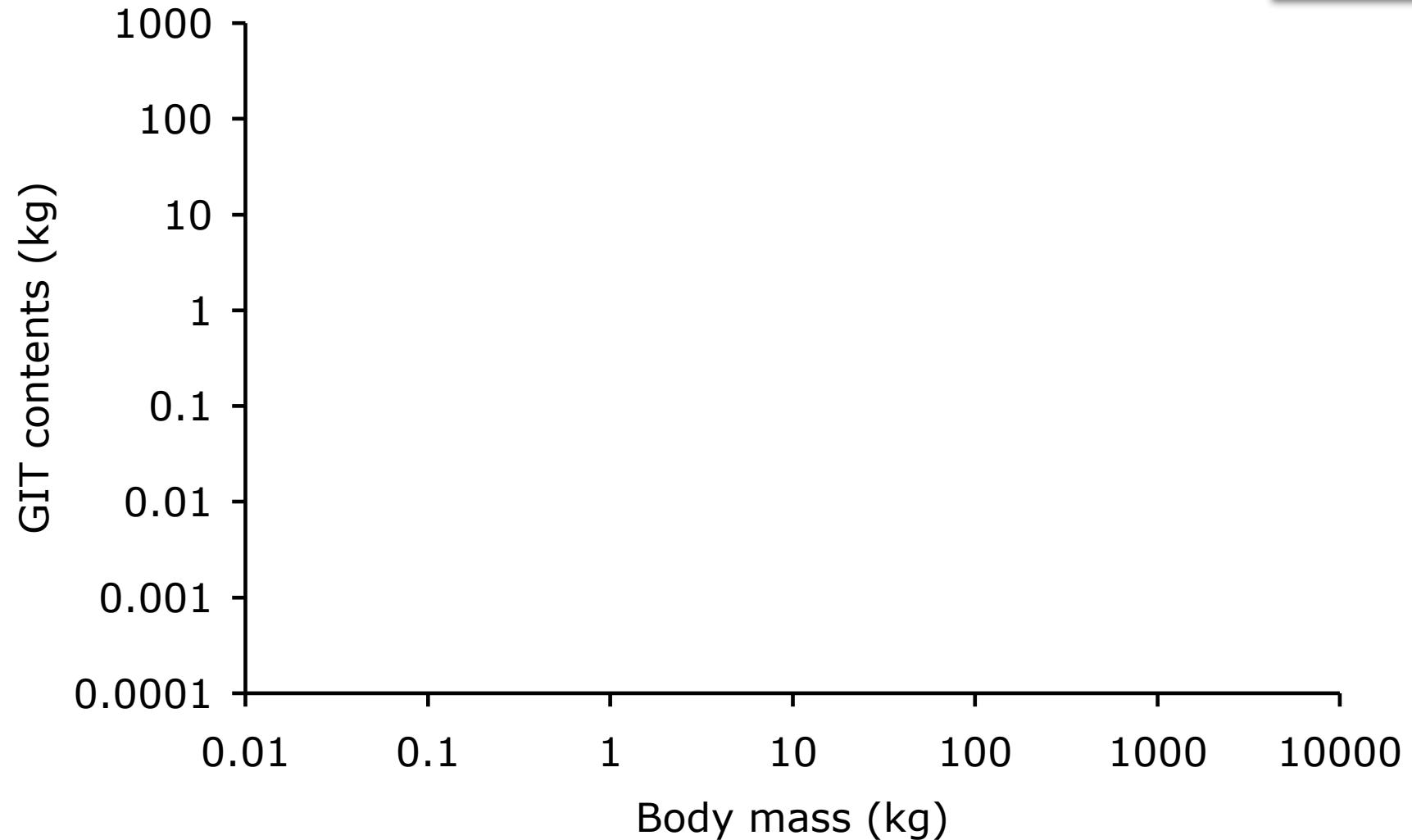


Gut capacity



Wet gut content mass

(measured by slaughtering)

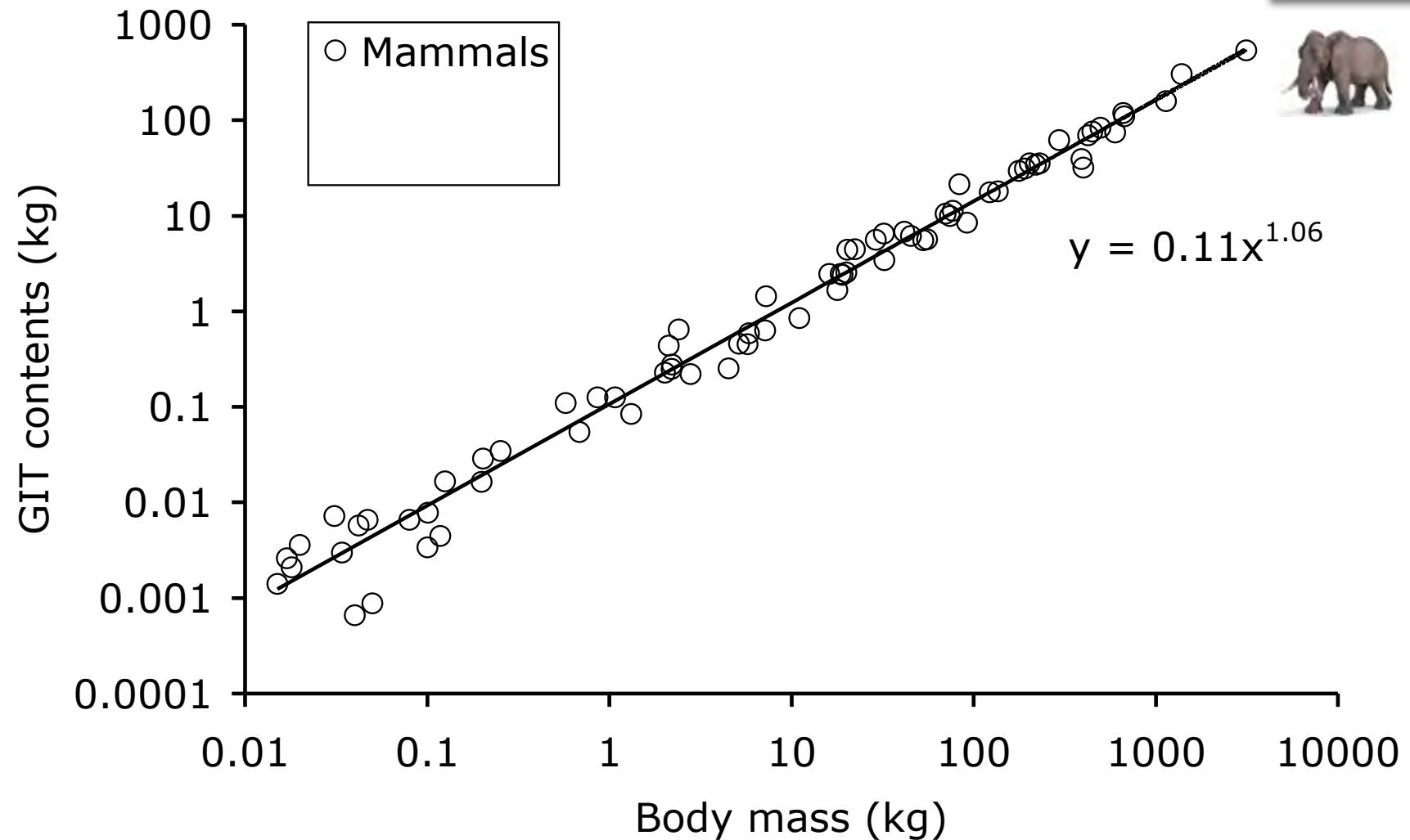


mammal data collection Clauss et al. (2007), reptile from Franz et al. (2009), bird from Fritz et al. (2012)



Wet gut content mass

(measured by slaughtering)

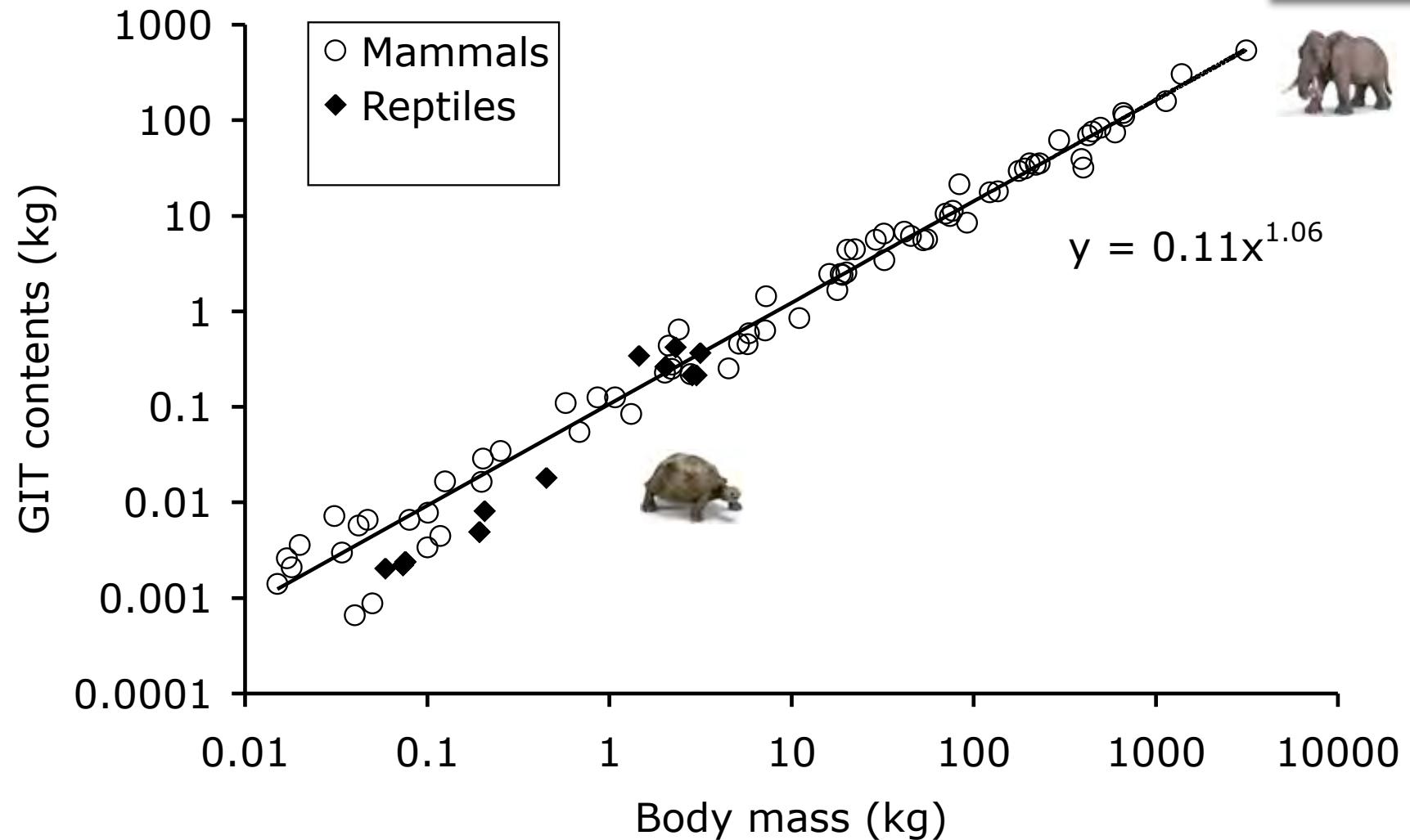


mammal data collection Clauss et al. (2007), reptile from Franz et al. (2009), bird from Fritz et al. (2012)



Wet gut content mass

(measured by slaughtering)

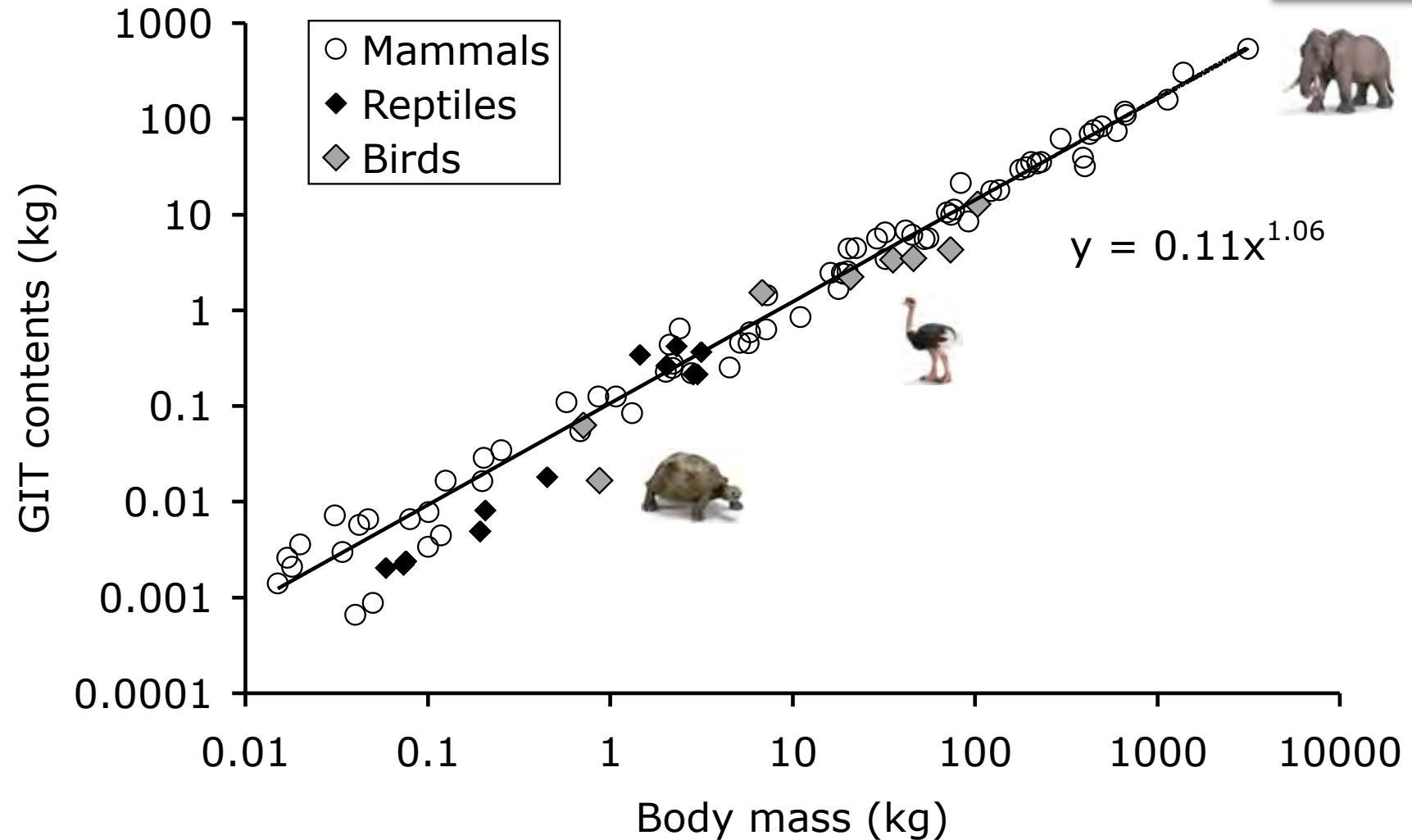


mammal data collection Clauss et al. (2007), reptile from Franz et al. (2009), bird from Fritz et al. (2012)



Wet gut content mass

(measured by slaughtering)



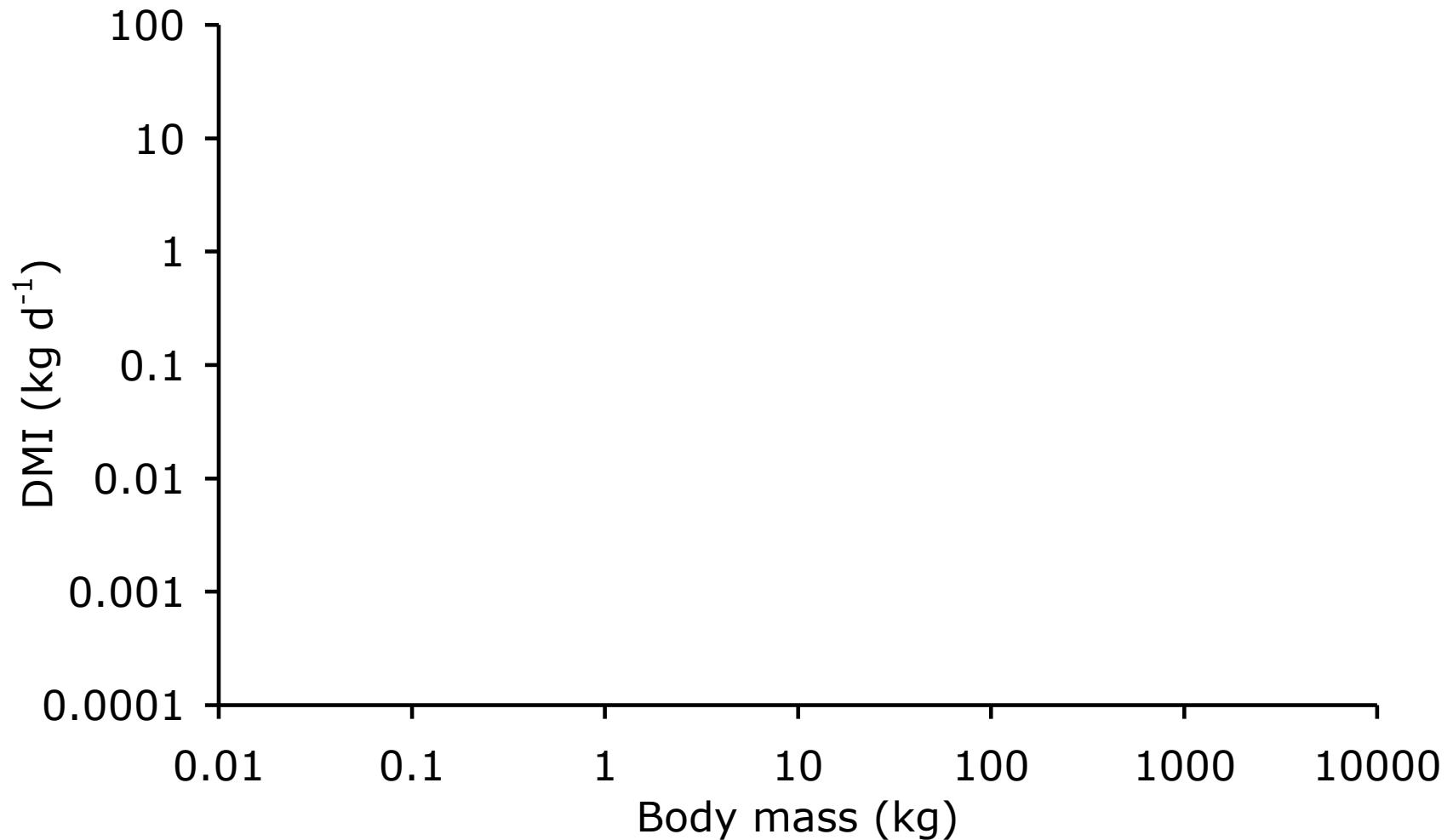
mammal data collection Clauss et al. (2007), reptile from Franz et al. (2009), bird from Fritz et al. (2012)



Food intake



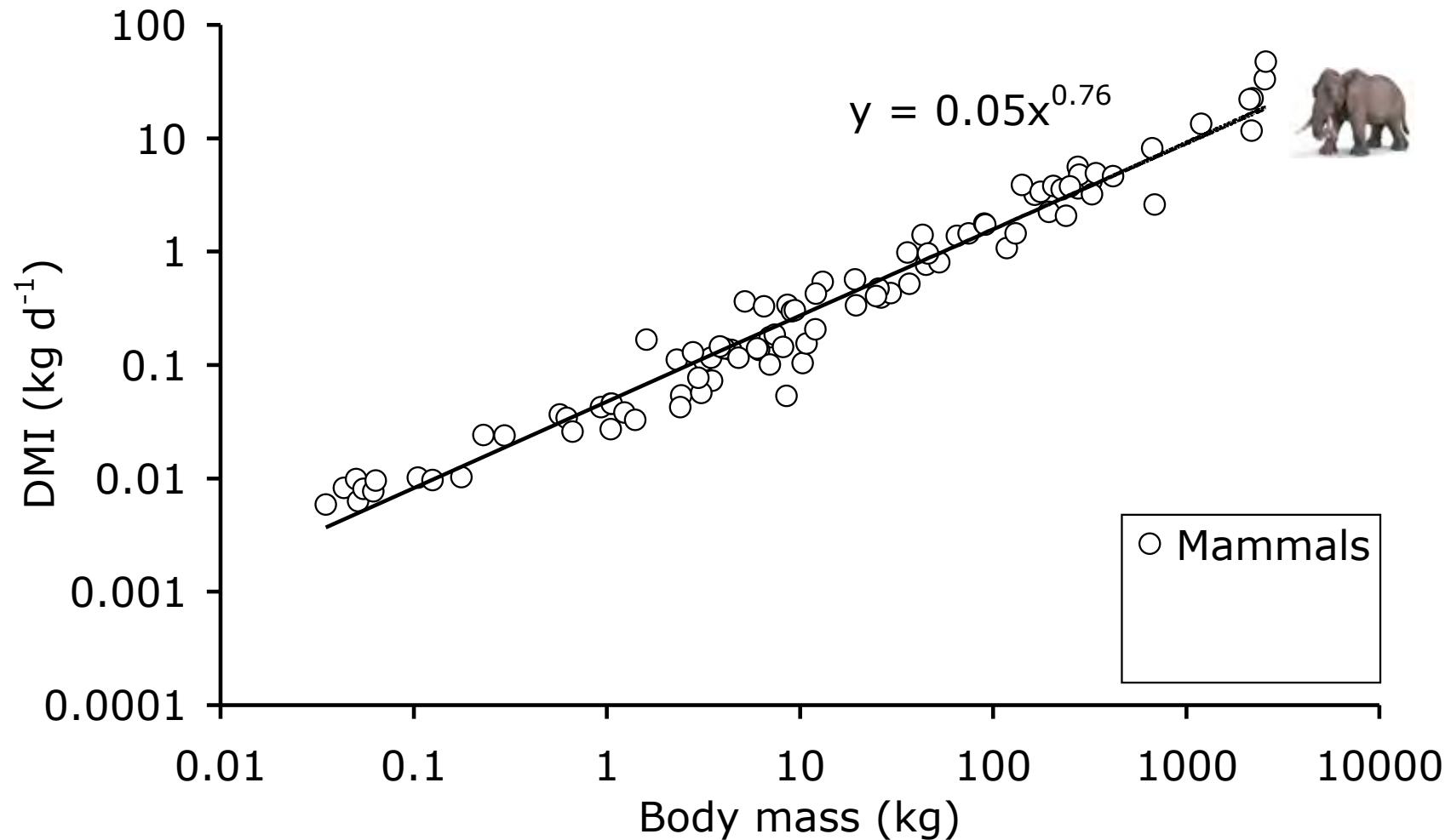
Food intake



mammal data collection Clauss et al. (2007), reptile from Franz et al. (2009), bird from Fritz et al. (2012)



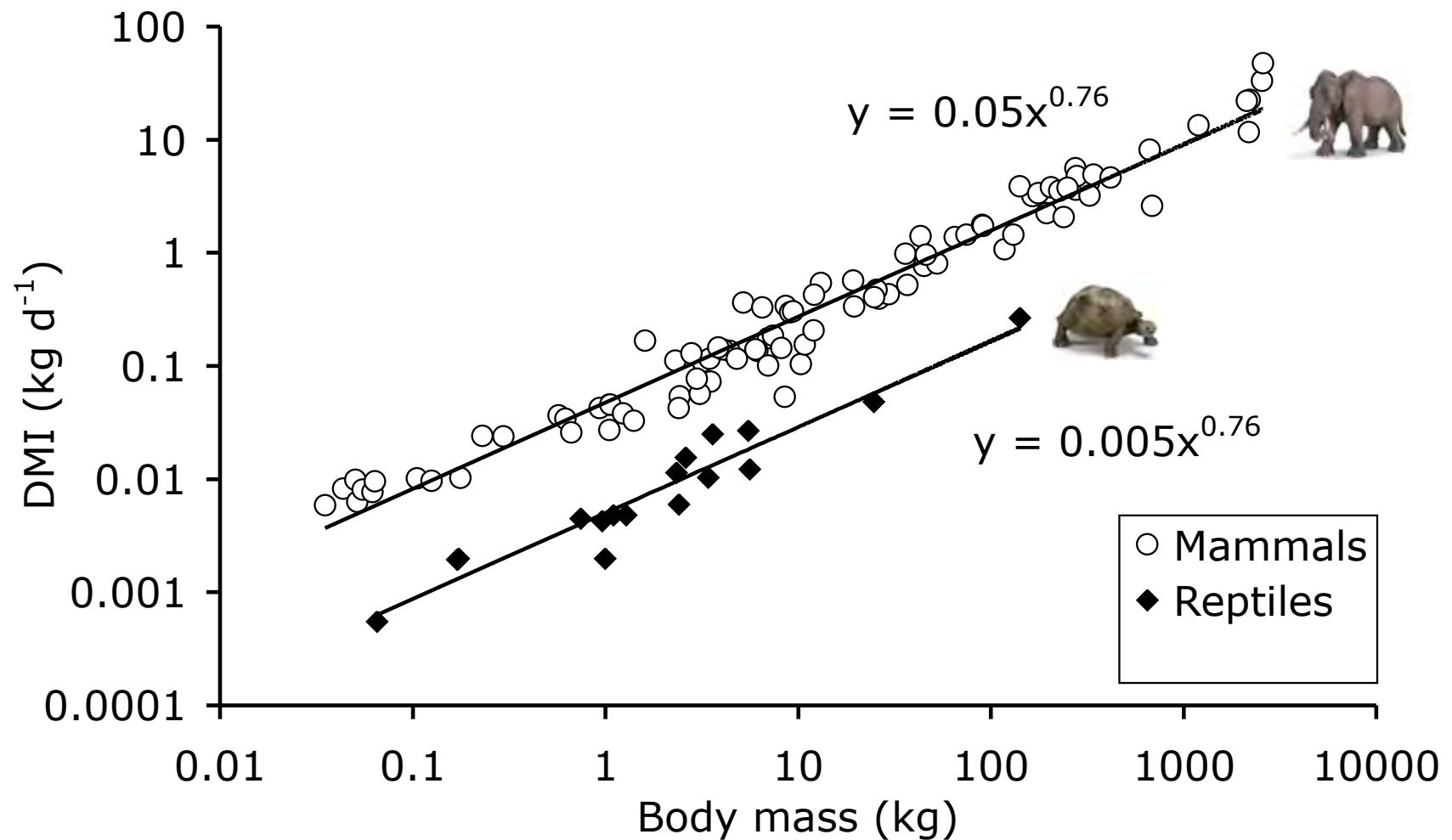
Food intake



mammal data collection Clauss et al. (2007), reptile from Franz et al. (2009), bird from Fritz et al. (2012)



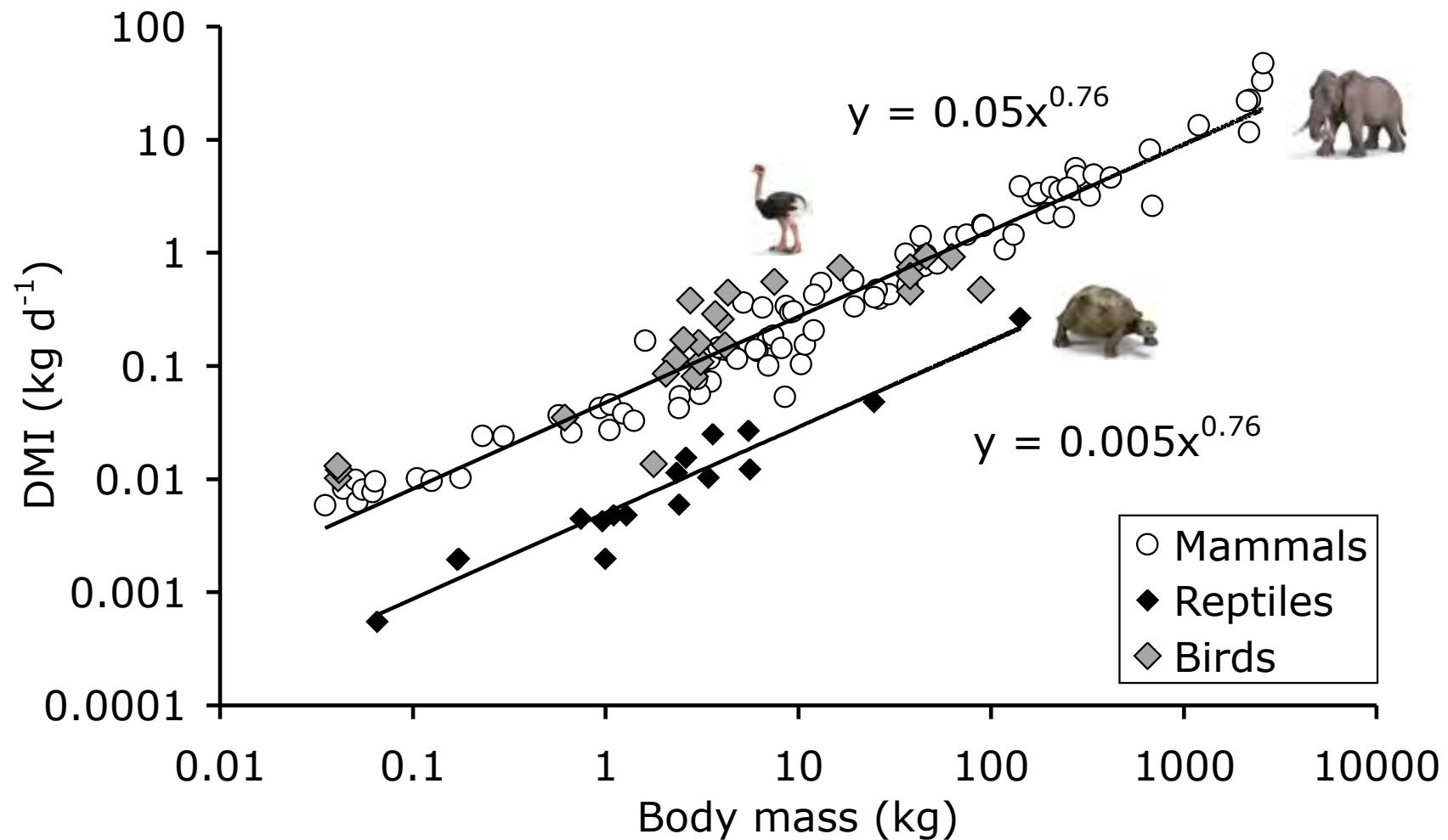
Food intake



mammal data collection Clauss et al. (2007), reptile from Franz et al. (2009), bird from Fritz et al. (2012)



Food intake



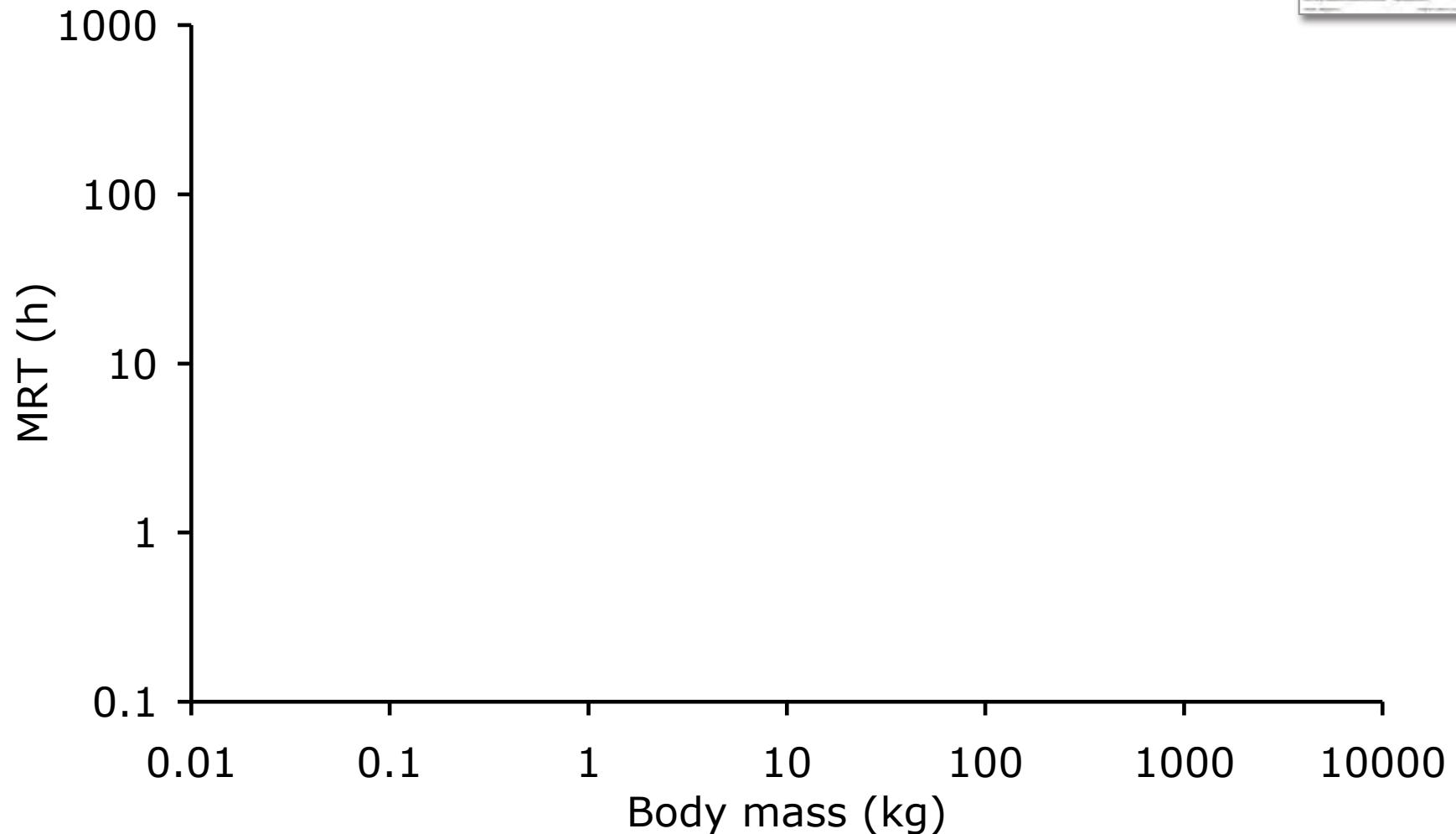
mammal data collection Clauss et al. (2007), reptile from Franz et al. (2009), bird from Fritz et al. (2012)



Digesta retention



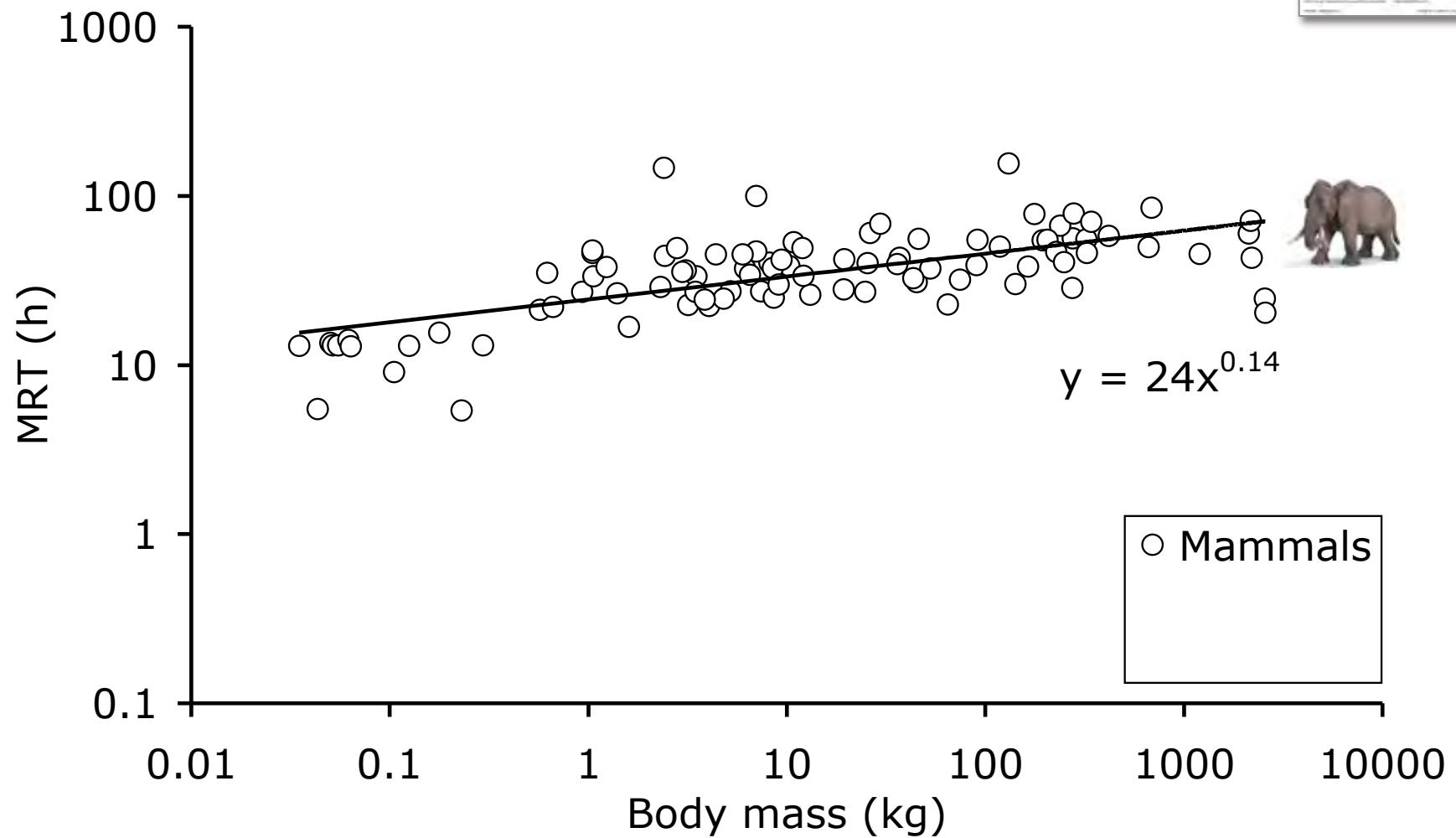
Mean retention time



mammal data collection Clauss et al. (2007), reptile from Franz et al. (2009), bird from Fritz et al. (2012)



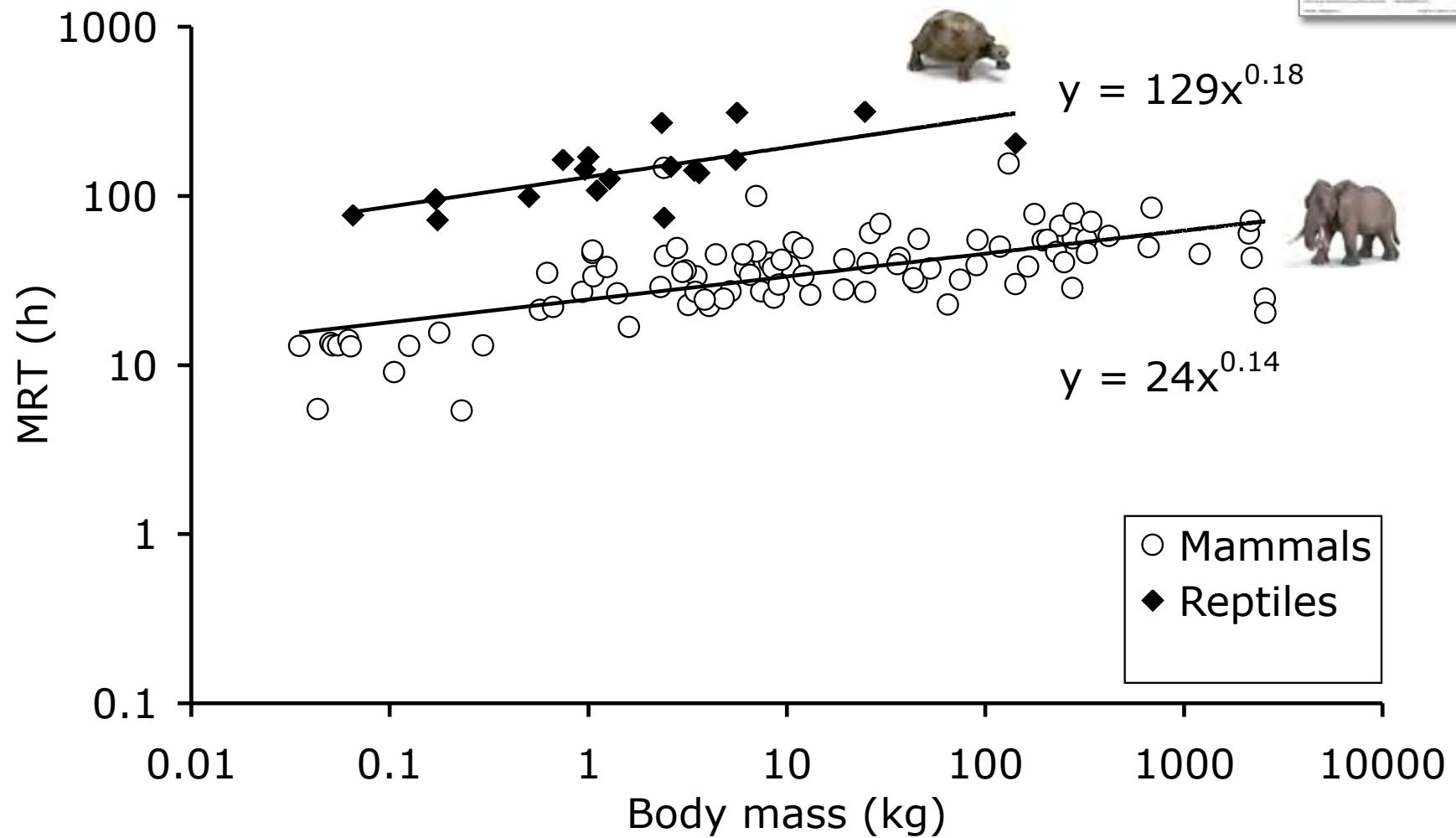
Mean retention time



mammal data collection Clauss et al. (2007), reptile from Franz et al. (2009), bird from Fritz et al. (2012)



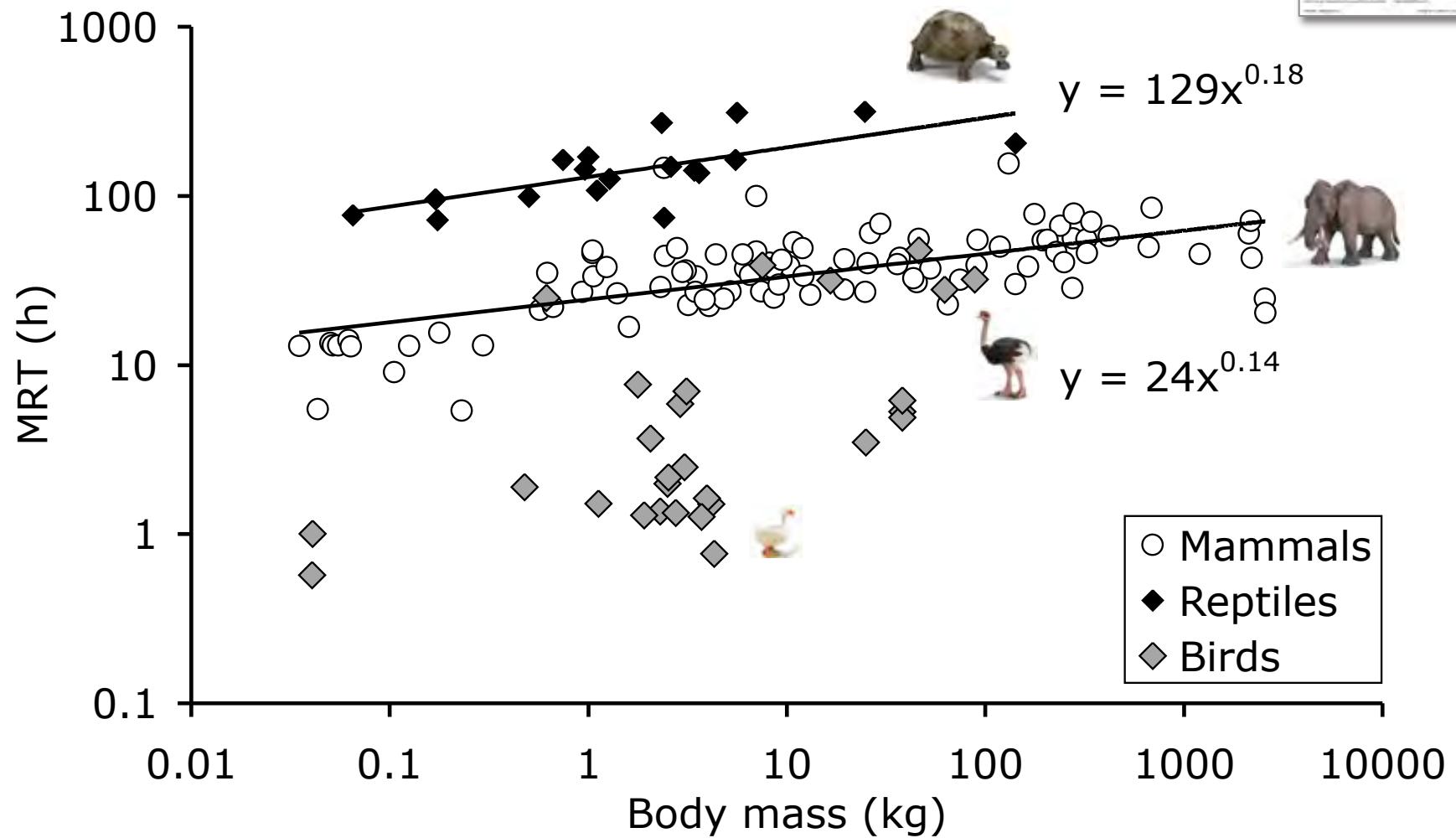
Mean retention time



mammal data collection Clauss et al. (2007), reptile from Franz et al. (2009), bird from Fritz et al. (2012)



Mean retention time



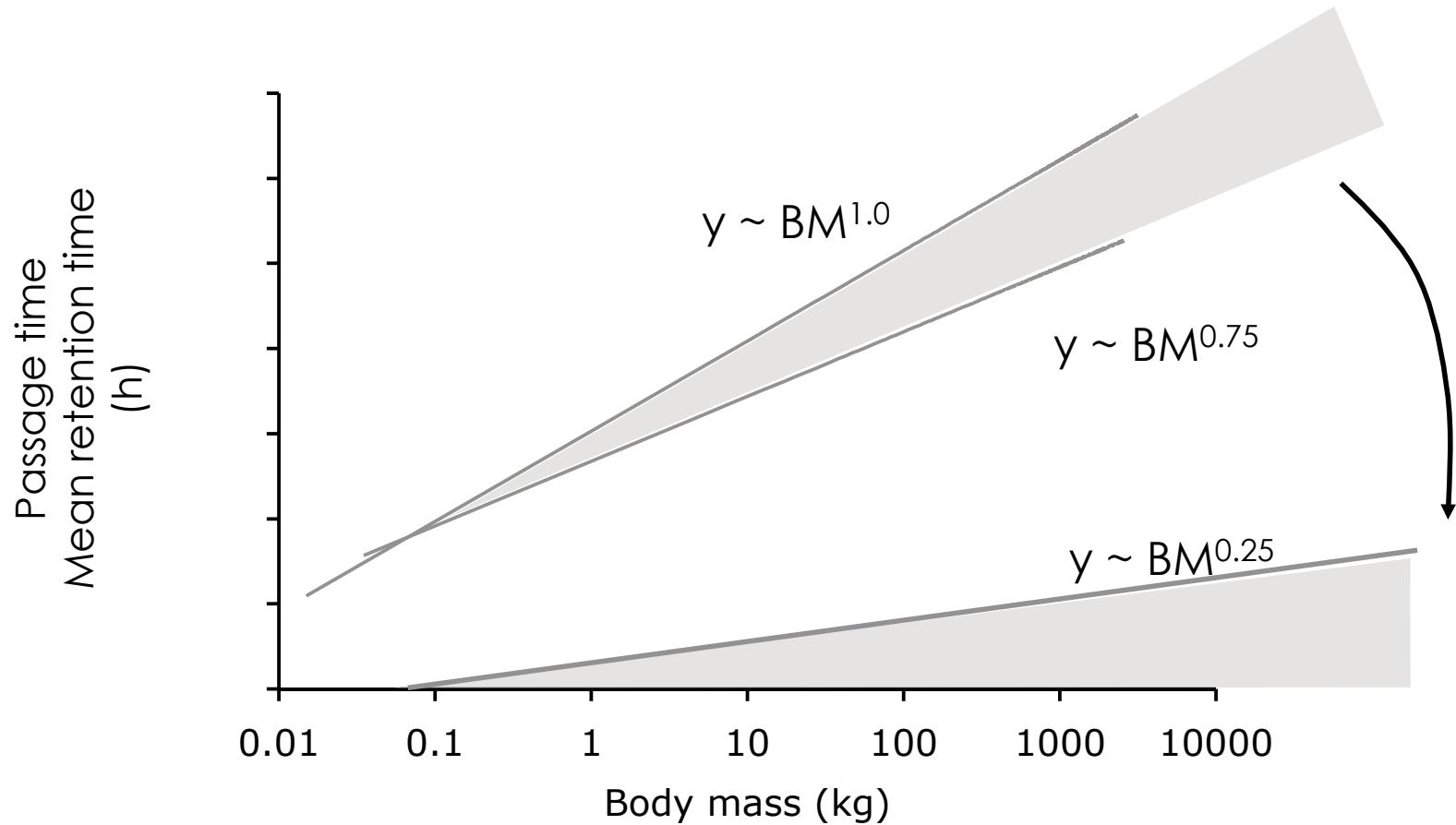
mammal data collection Clauss et al. (2007), reptile from Franz et al. (2009), bird from Fritz et al. (2012)



So what now?



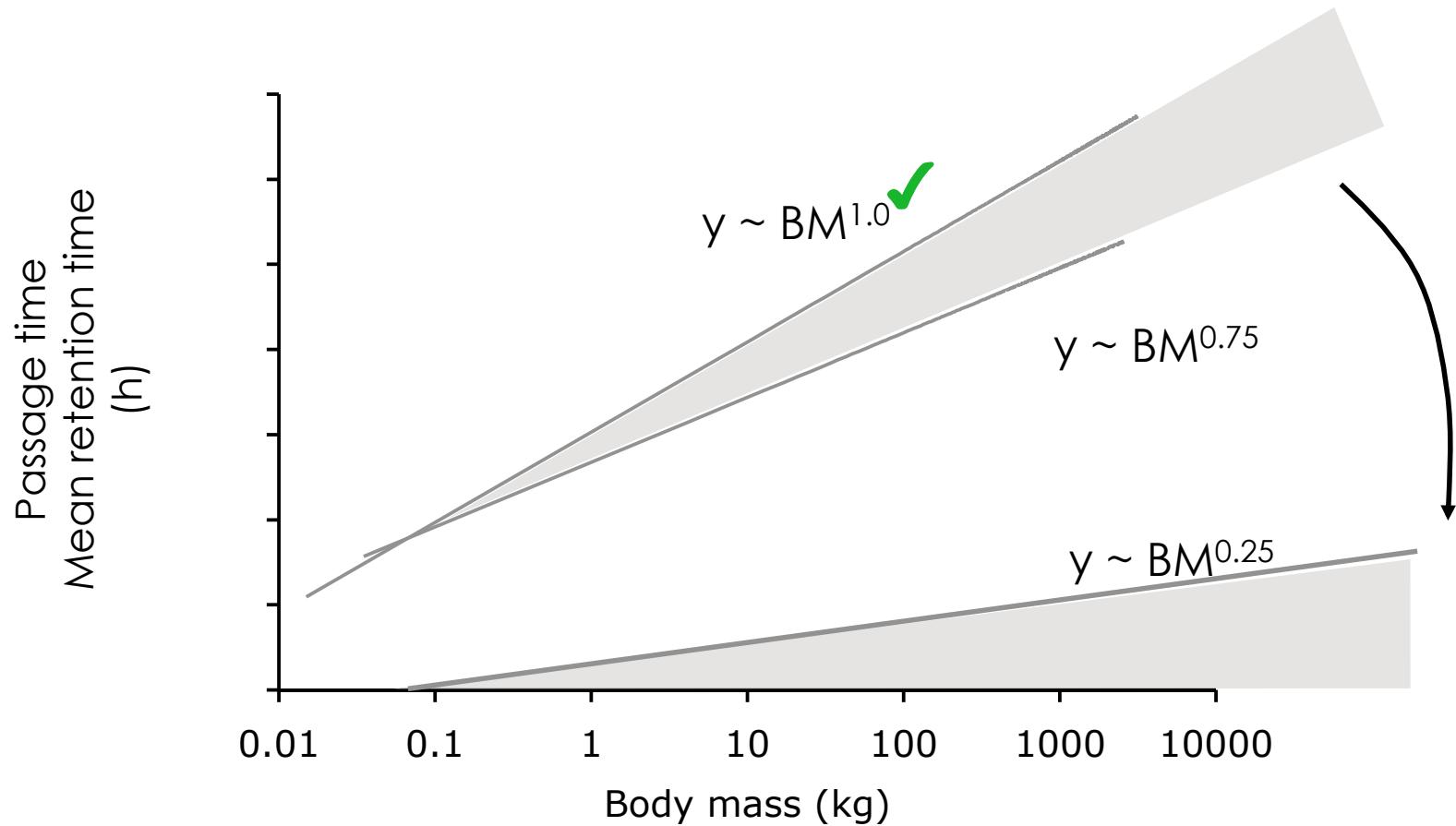
General allometric considerations



from Parra (1978), Demment & Van Soest (1985), Illius & Gordon (1992); McNab (2002)



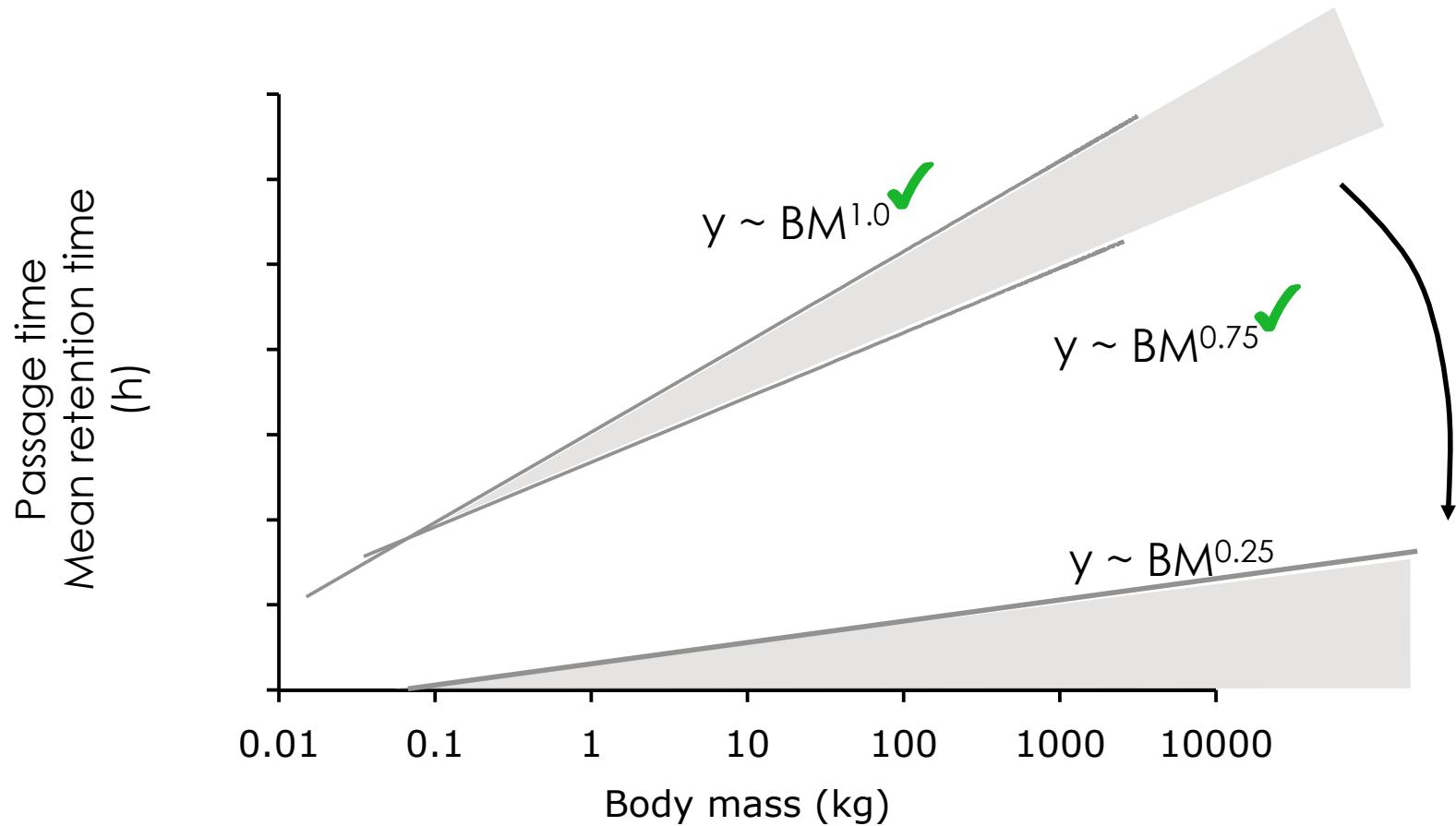
General allometric considerations



from Parra (1978), Demment & Van Soest (1985), Illius & Gordon (1992); McNab (2002)



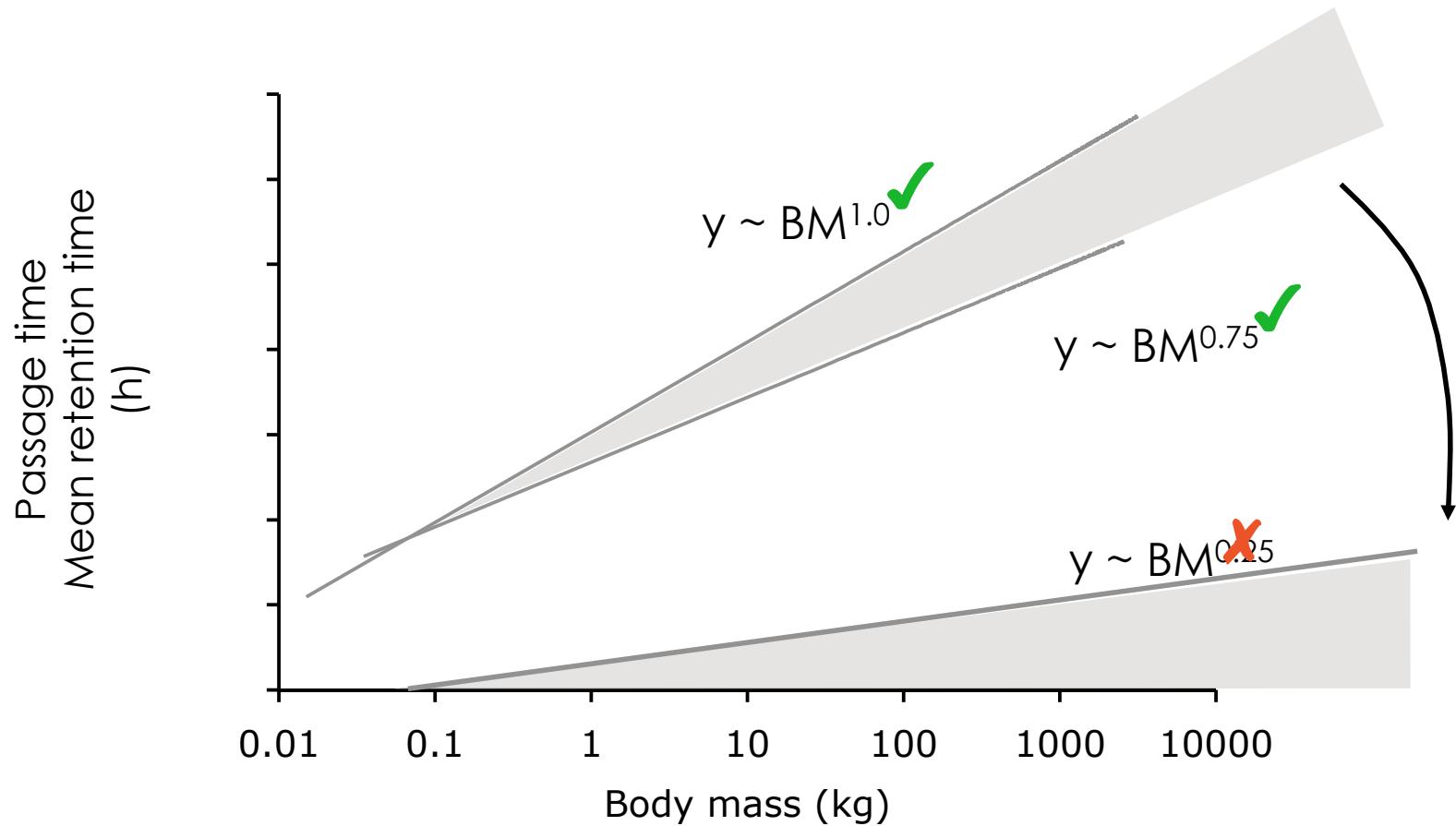
General allometric considerations



from Parra (1978), Demment & Van Soest (1985), Illius & Gordon (1992); McNab (2002)



General allometric considerations



from Parra (1978), Demment & Van Soest (1985), Illius & Gordon (1992); McNab (2002)



A serious problem

If gut capacity scales to $BM^{1.0}$, and food intake to $BM^{0.75}$, then a lack of scaling of retention time to $BM^{0.25}$ begs for an explanation!

- is this an effect of different datasets (intake/retention from feeding trials; gut contents from slaughter measurements)?
- are 1.0 and 0.75 the *really real* exponents?



Using a single dataset

Gut capacity (not as wet mass, but as dry mass) can be calculated from food intake, digesta retention time and digestibility.

Hence, a data collection can be created (sufficient data available in mammals) of studies that measured these parameters that includes a gut capacity estimate *in the same animals*.

Determination of digesta fill and passage rate from nonabsorbed particulate phase markers using the single dosing method

D. F. HOLLEMAN AND R. G. WHITE

Institute of Arctic Biology, University of Alaska—Fairbanks, Fairbanks, AK 99775-0180, U.S.A.

Received May 11, 1987

HOLLEMAN, D. F., and WHITE, R. G. 1989. Determination of digesta fill and passage rate from nonabsorbed particulate phase markers using the single dosing method. *Can. J. Zool.* **67**: 488–494.

A method is given for analyzing particulate digestive marker data in terms of digesta fill, fecal output, and digesta passage times. The method applies the Stewart–Hamilton Principle to data obtained from a single marker dosing followed by feces sampling; it assumes steady-state conditions for the digesta, but makes no assumptions concerning compartmentalization of digesta. Data analyses are presented for an experiment with sheep in which a particle phase marker, cerium-141 chloride, was used. The estimate of fecal output obtained was $1.8 \pm 2.2\%$ (mean percent difference \pm SE) greater than the actual fecal output; the *in vivo* estimate of total digesta fill was $3.3 \pm 3.4\%$ less than measured digesta fill. For comparison, the present data were also analyzed using two established compartment modeling approaches, namely a time-independent and a time-dependent two-compartment model. The only significant difference between the estimated parameters as obtained from the Stewart–Hamilton method and the compartmental models was a significantly shorter transit time as estimated by the time-dependent model.

HOLLEMAN, D. F., et WHITE, R. G. 1989. Determination of digesta fill and passage rate from nonabsorbed particulate phase markers using the single dosing method. *Can. J. Zool.* **67** : 488–494.



Using a single dataset

Measurement

Scaling (95%CI)





Using a single dataset

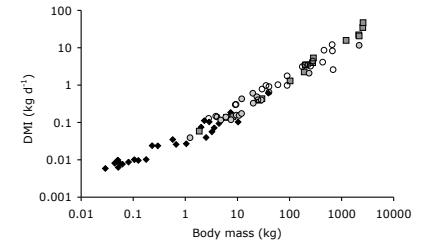


Measurement

Dry matter intake

Scaling (95%CI)

0.76 (0.73-0.79)



from Müller et al. (2013)



Using a single dataset



Measurement

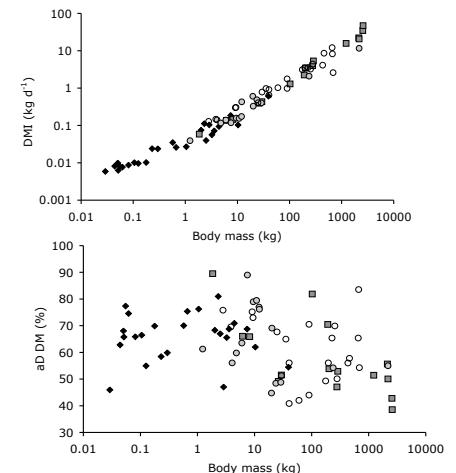
Scaling (95%CI)

Dry matter intake

0.76 (0.73-0.79)

Digestibility

-0.03 (-0.04--0.01)



from Müller et al. (2013)



Using a single dataset

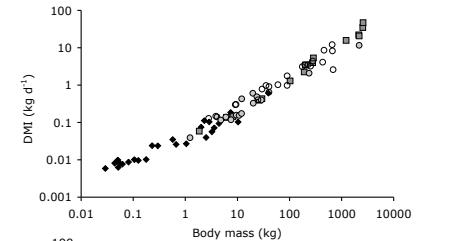


Measurement

Scaling (95%CI)

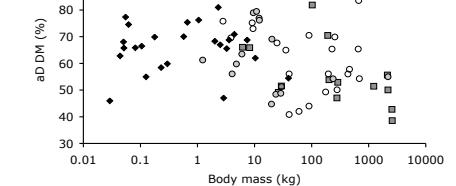
Dry matter intake

0.76 (0.73-0.79)



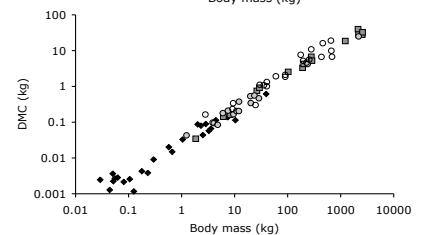
Digestibility

-0.03 (-0.04--0.01)



Dry matter gut fill

0.93 (0.90-0.96)



from Müller et al. (2013)



Using a single dataset



Measurement

Scaling (95%CI)

Dry matter intake

0.76 (0.73-0.79)

Digestibility

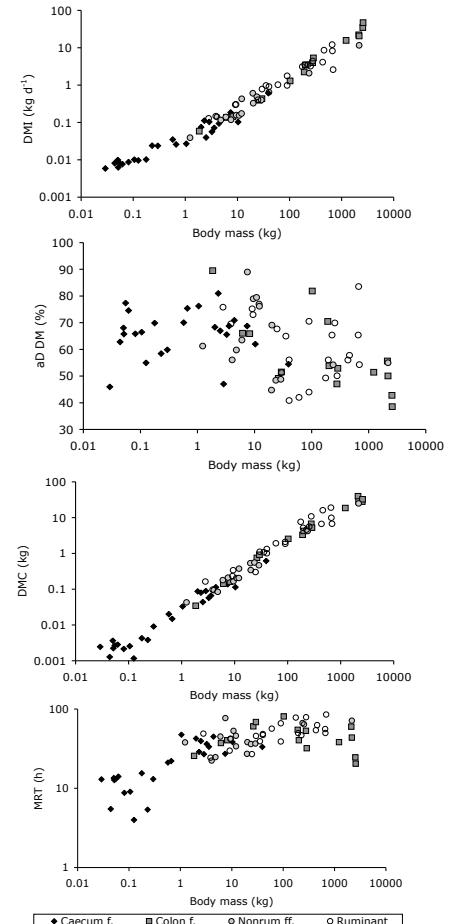
-0.03 (-0.04--0.01)

Dry matter gut fill

0.93 (0.90-0.96)

Particle retention time

0.16 (0.12-0.19)



from Müller et al. (2013)



The *really real* exponents

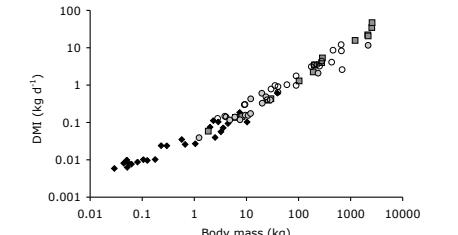


Measurement

Scaling (95%CI)

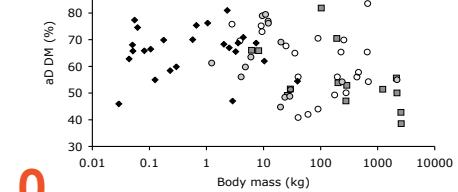
Dry matter intake

0.76 (0.73-0.79)



Digestibility

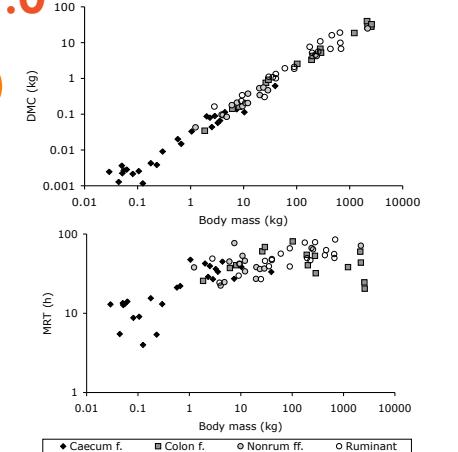
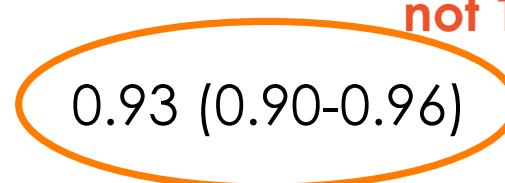
-0.03 (-0.04--0.01)



Dry matter gut fill

0.93 (0.90-0.96)

not 1.0



Particle retention time

0.16 (0.12-0.19)

from Müller et al. (2013)



The *really real* exponents

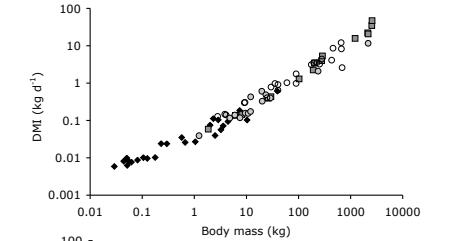


Measurement

Scaling (95%CI)

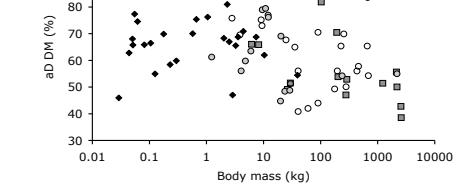
Dry matter intake

0.76 (0.73-0.79)



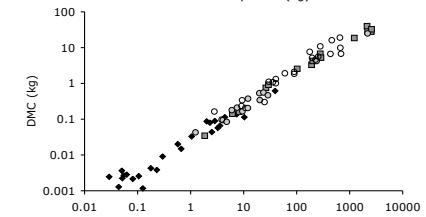
Digestibility

-0.03 (-0.04--0.01)



Dry matter gut fill

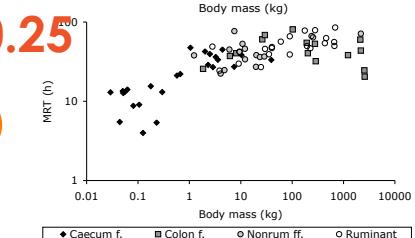
0.93 (0.90-0.96)



Particle retention time

0.16 (0.12-0.19)

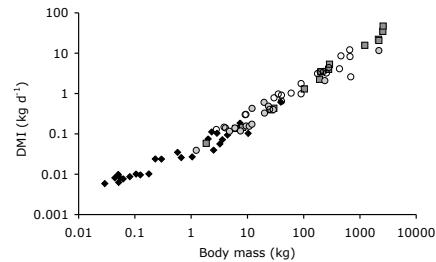
not 0.25



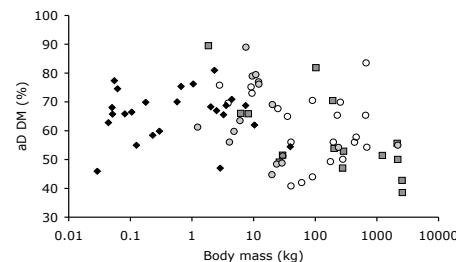
from Müller et al. (2013)



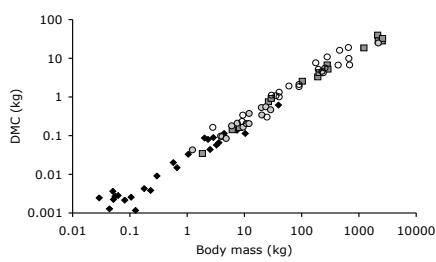
The curvature in herbivore digestive physiology



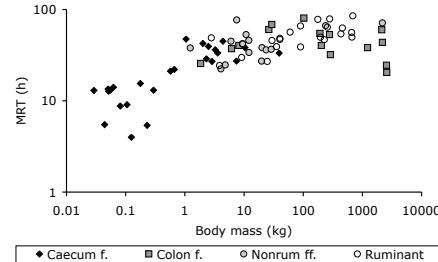
Dry matter intake



Digestibility



Dry matter gut content

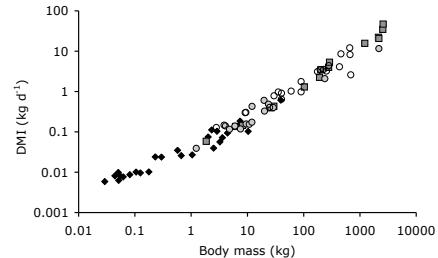


Particle retention time

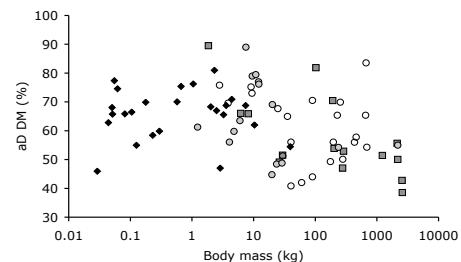
from Müller et al. (2013)



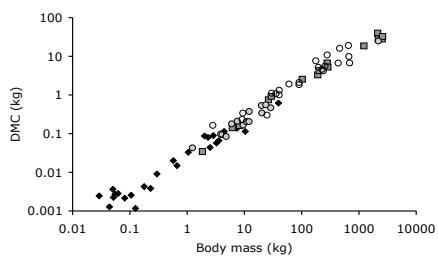
The curvature in herbivore digestive physiology - plotting residuals



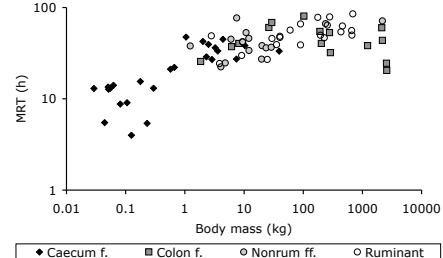
Dry matter intake



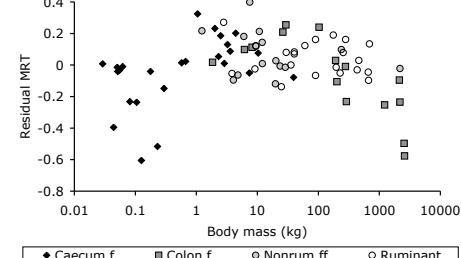
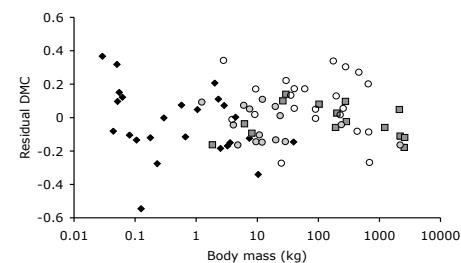
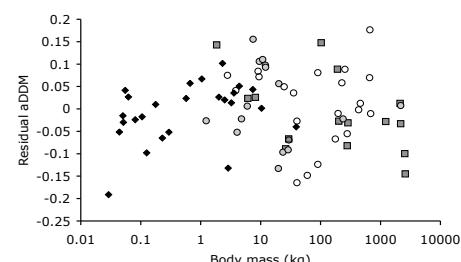
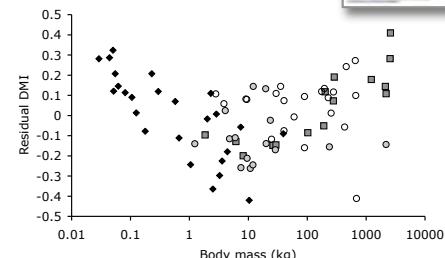
Digestibility



Dry matter gut content



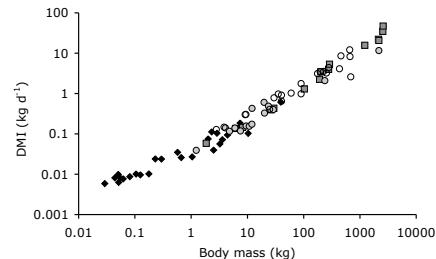
Particle retention time



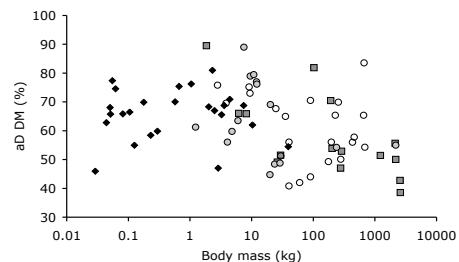
from Müller et al. (2013)



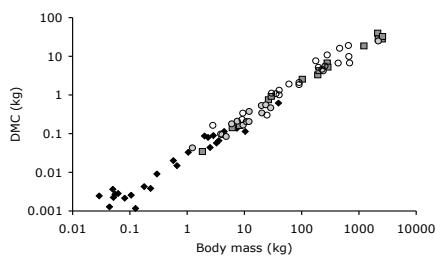
The curvature in herbivore digestive physiology - plotting residuals



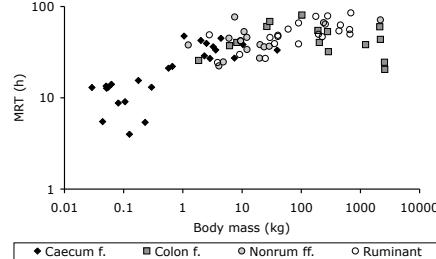
Dry matter intake



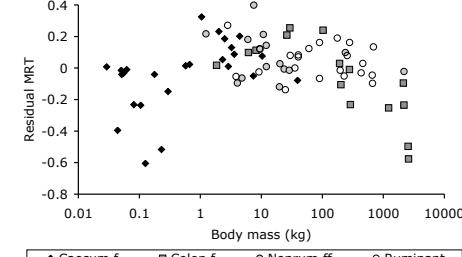
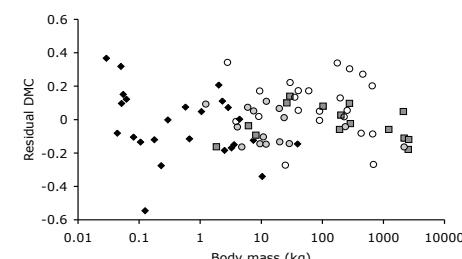
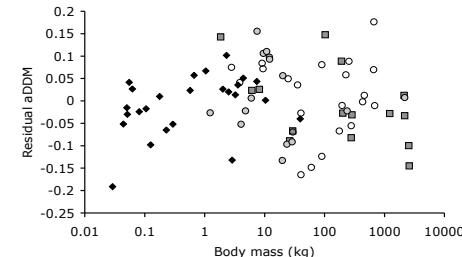
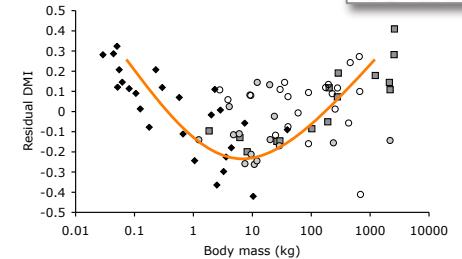
Digestibility



Dry matter gut content



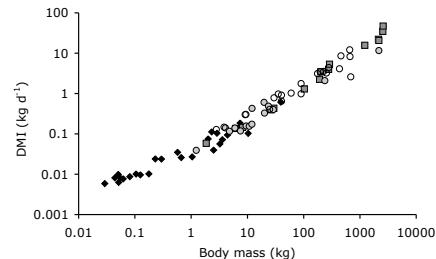
Particle retention time



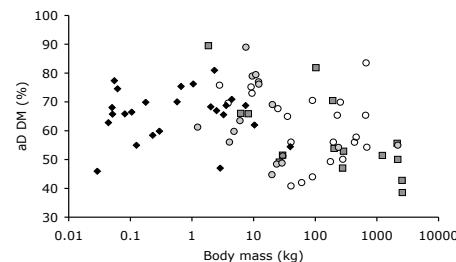
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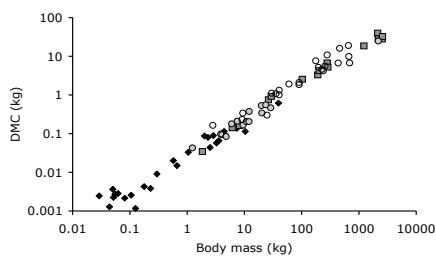
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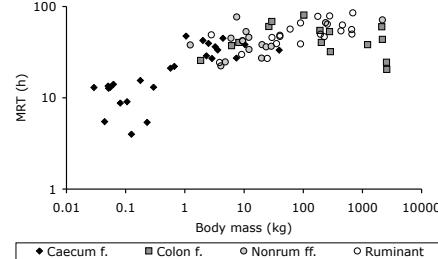
Dry matter intake



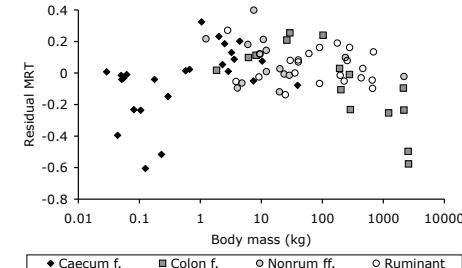
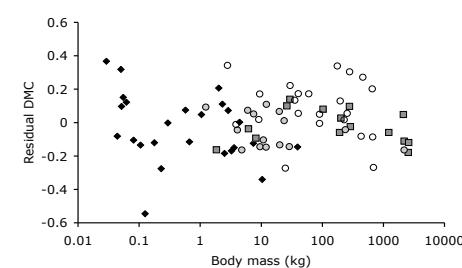
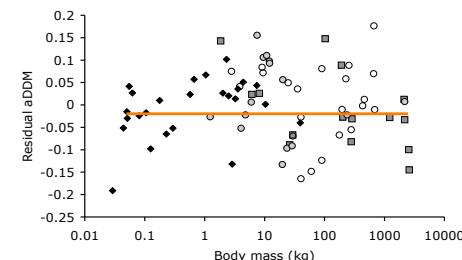
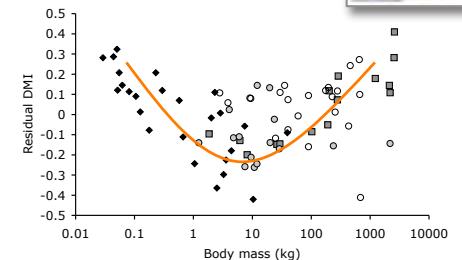
Digestibility



Dry matter gut content



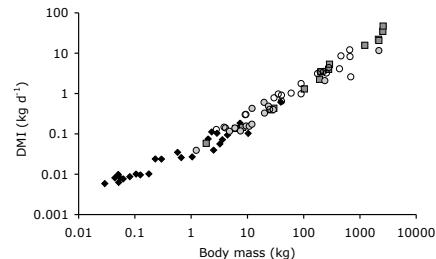
Particle retention time



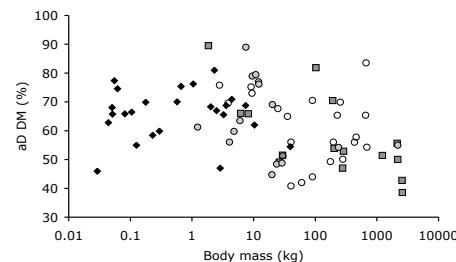
from Müller et al. (2013)



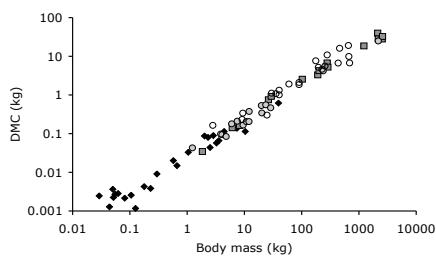
The curvature in herbivore digestive physiology - plotting residuals



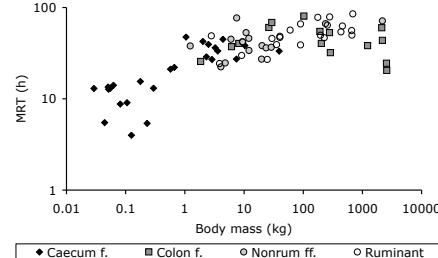
Dry matter intake



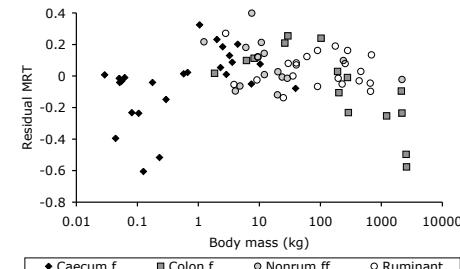
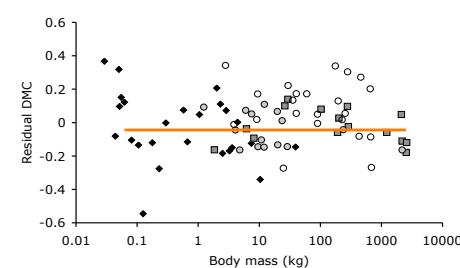
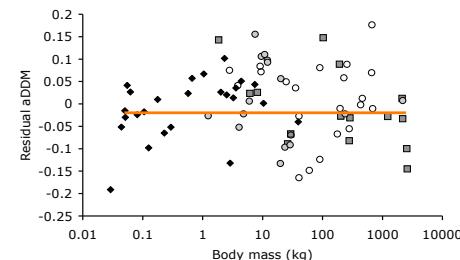
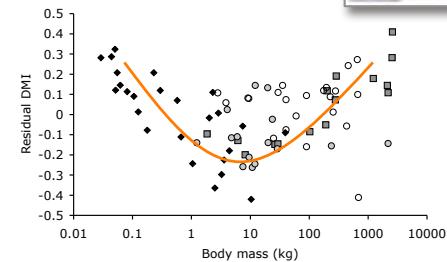
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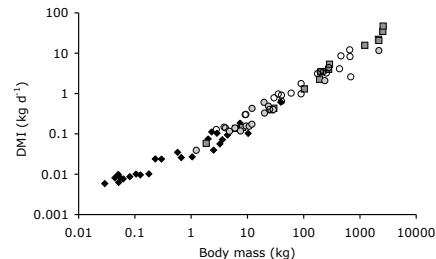
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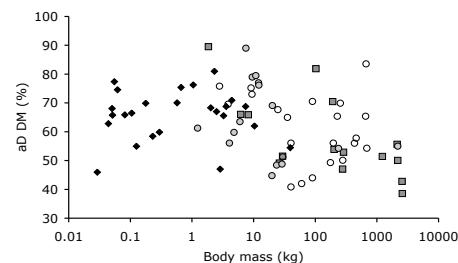
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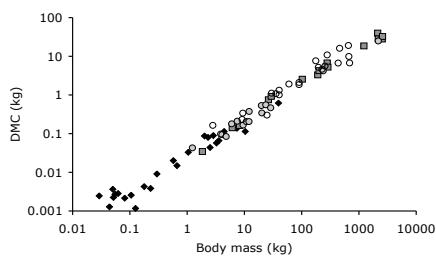
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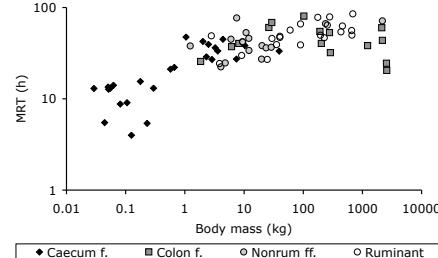
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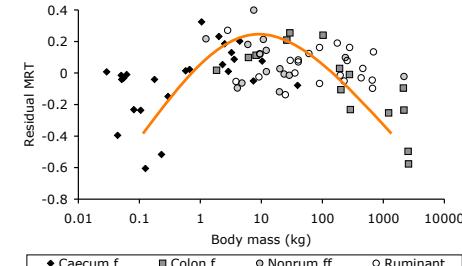
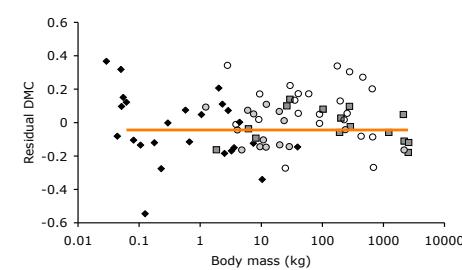
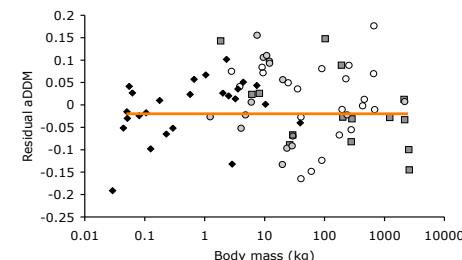
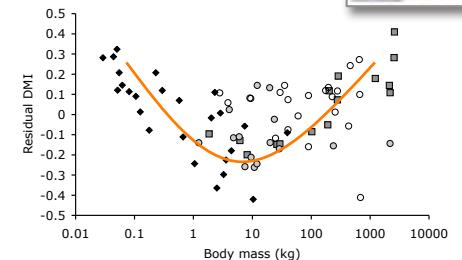
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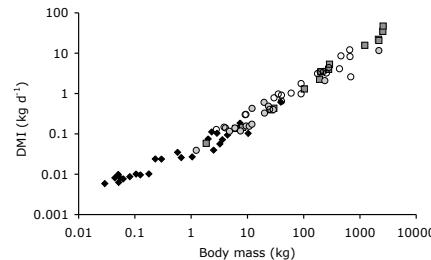
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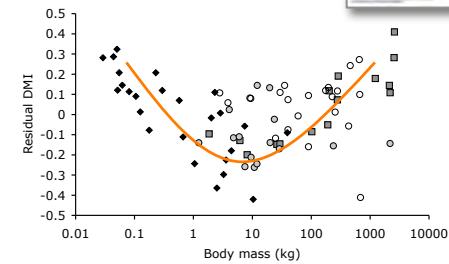
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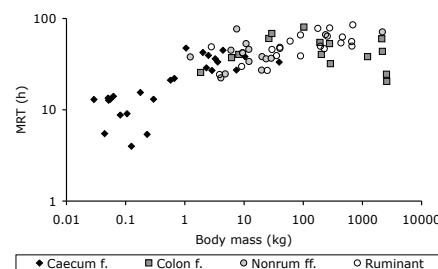
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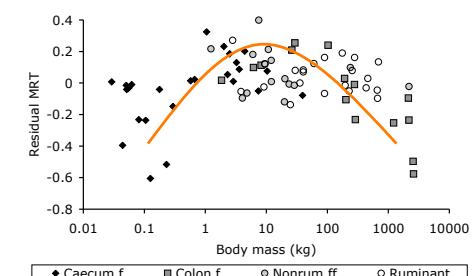
Dry matter intake



*corresponding
inverse
curvatures*



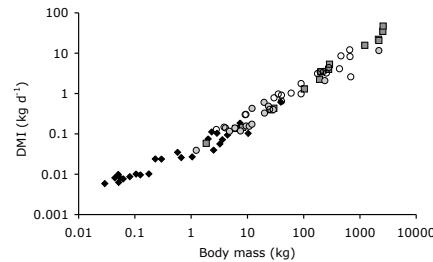
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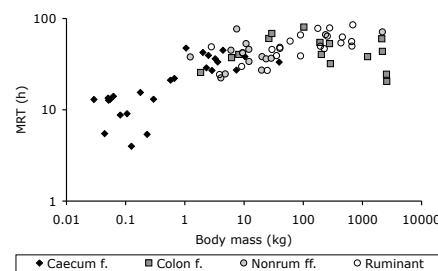
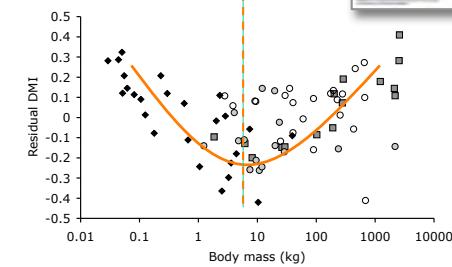
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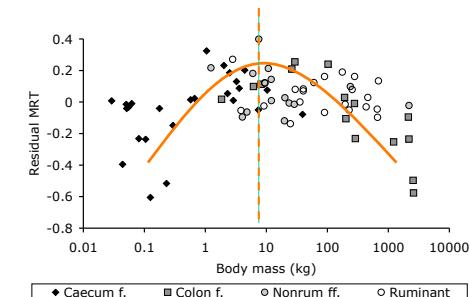
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Dry matter intake



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from Müller et al. (2013)



The *really real* exponents



Measurement

Scaling (95%CI)

> 1 Litter size = 1

Dry matter intake	0.66 (0.63-0.70)	0.86 (0.82-0.91)
Digestibility	-0.02 (-0.05--0.01)	-0.05 (-0.07--0.03)
Dry matter gut fill	0.91 (0.83-0.99)	0.94 (0.89-0.98)
Particle retention time	0.23 (0.16-0.31)	0.05 (0.01-0.09)

< 10 kg body mass > 10 kg

Dry matter intake	0.62 (0.57-0.68)	0.89 (0.82-0.96)
Digestibility	0.02 (-0.01-0.05)	-0.03 (-0.07-0.01)
Dry matter gut fill	0.91 (0.83-0.98)	0.92 (0.85-0.99)
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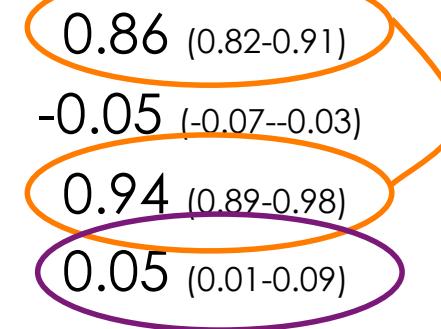


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Checking the validity of a concept

1. **Check if empirical data matches the hypothesis**
(it does not – no difference in intake and gut capacity in large species)
2. Check the mathematical validity
3. Check conceptual background

(vary sequence to suit your preference or intellectual capacity)



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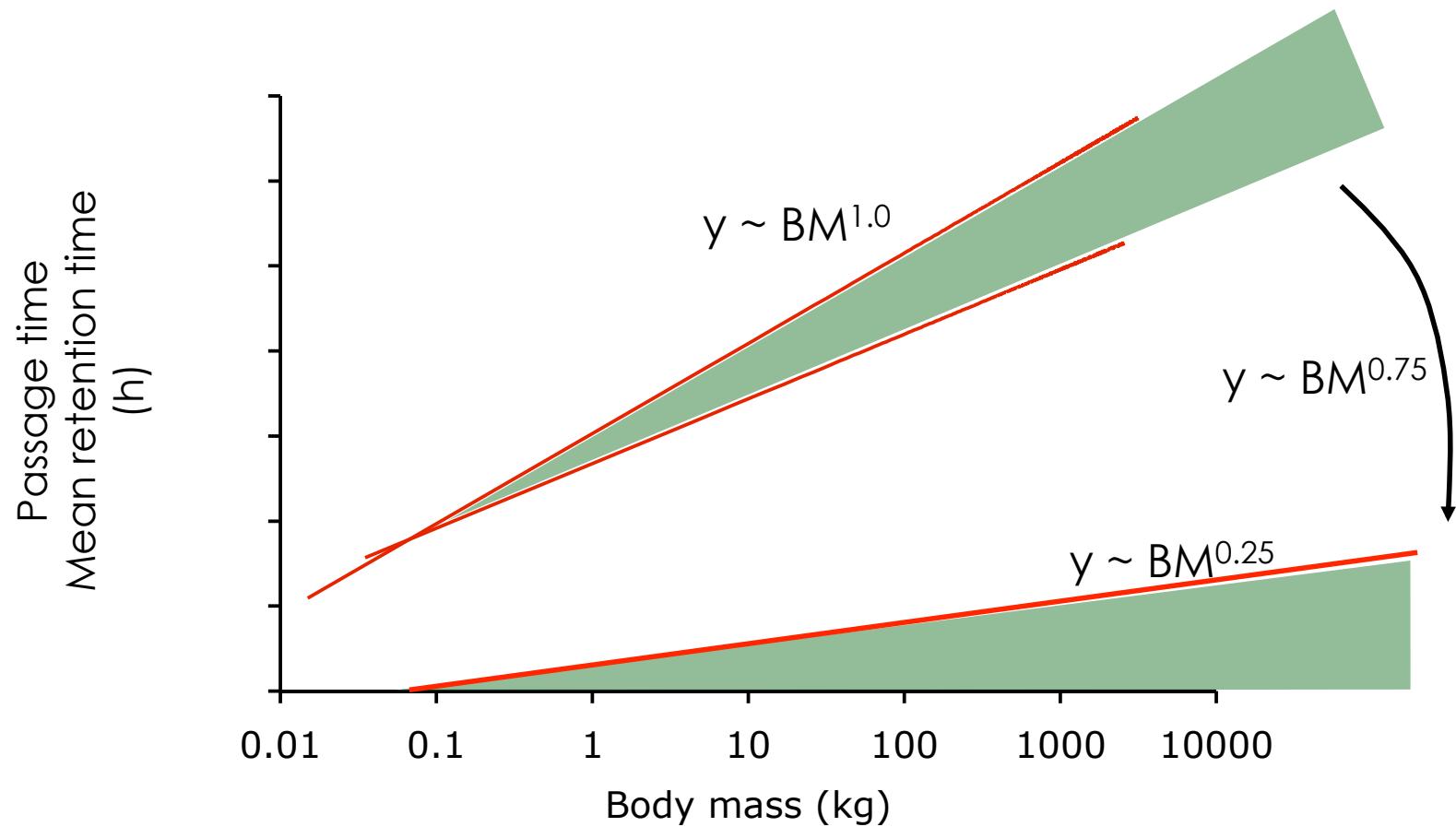
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Circular reasoning



from Parra (1978), Demment & Van Soest (1985), Illius & Gordon (1992); McNab (2002)



A logical flaw



The time digesta passes through the gut depends on



A logical flaw



The time digesta passes through the gut depends on

- the size of the gut (capacity) BM^a



A logical flaw



The time digesta passes through the gut depends on

- the size of the gut (capacity) BM^a
 - the intake rate (how much per unit time) BM^b



A logical flaw



The time digesta passes through the gut depends on

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- ... **and the digestibility** (how much material disappears without ‘pushing on’!) BM^c



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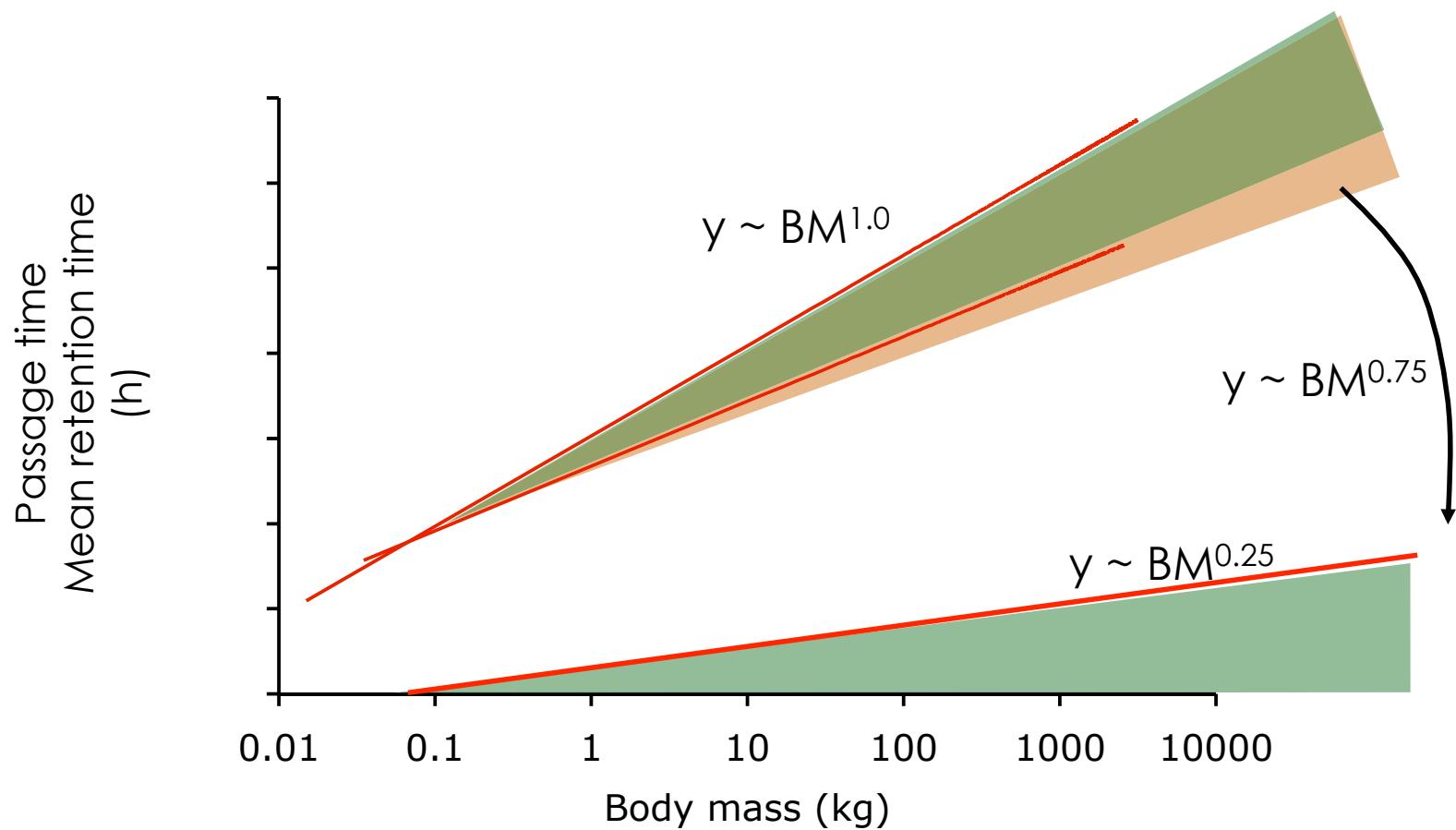
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One cannot use the thus-derived scaling of MRT to make conclusions on the scaling of digestibility!



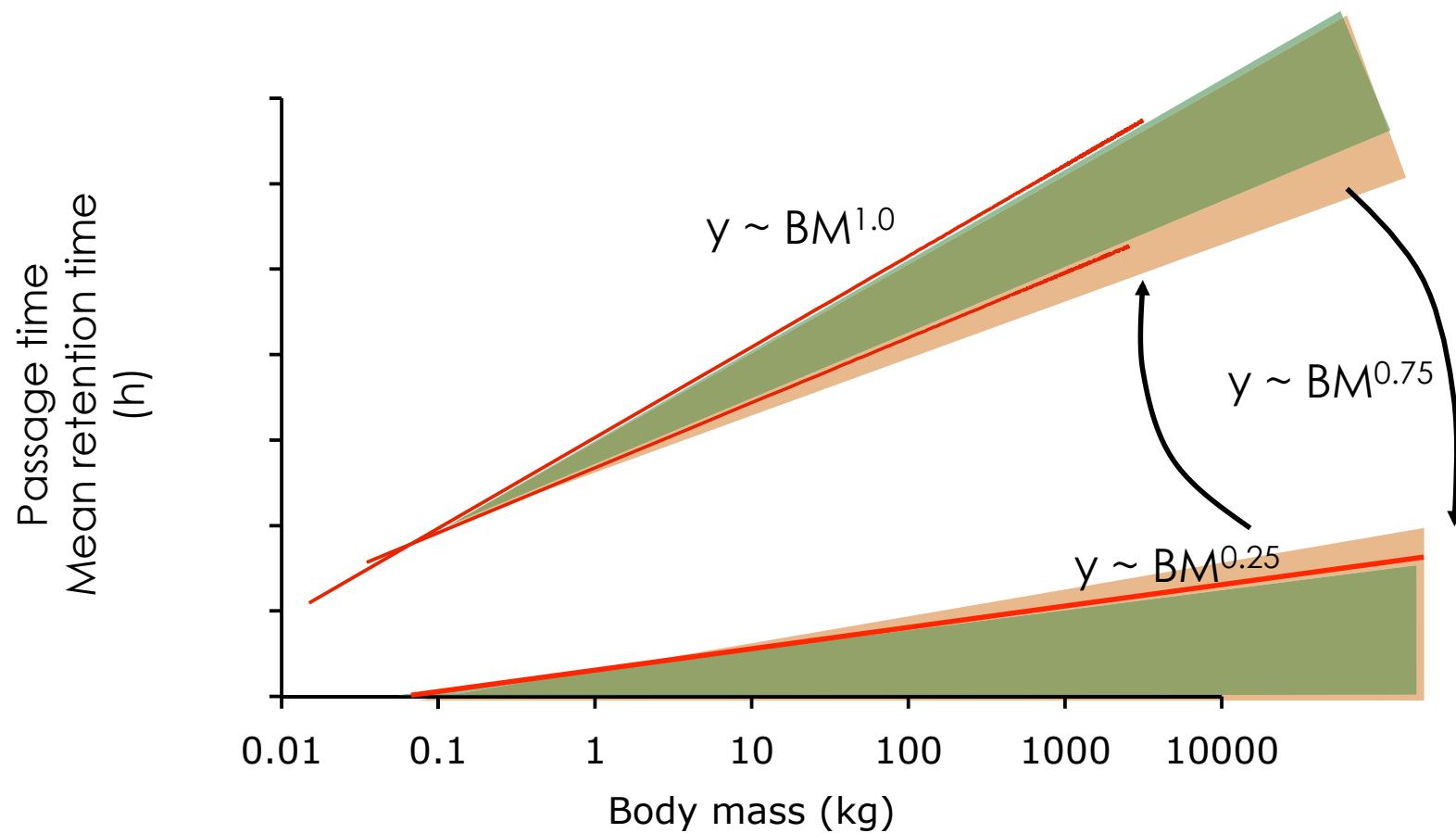
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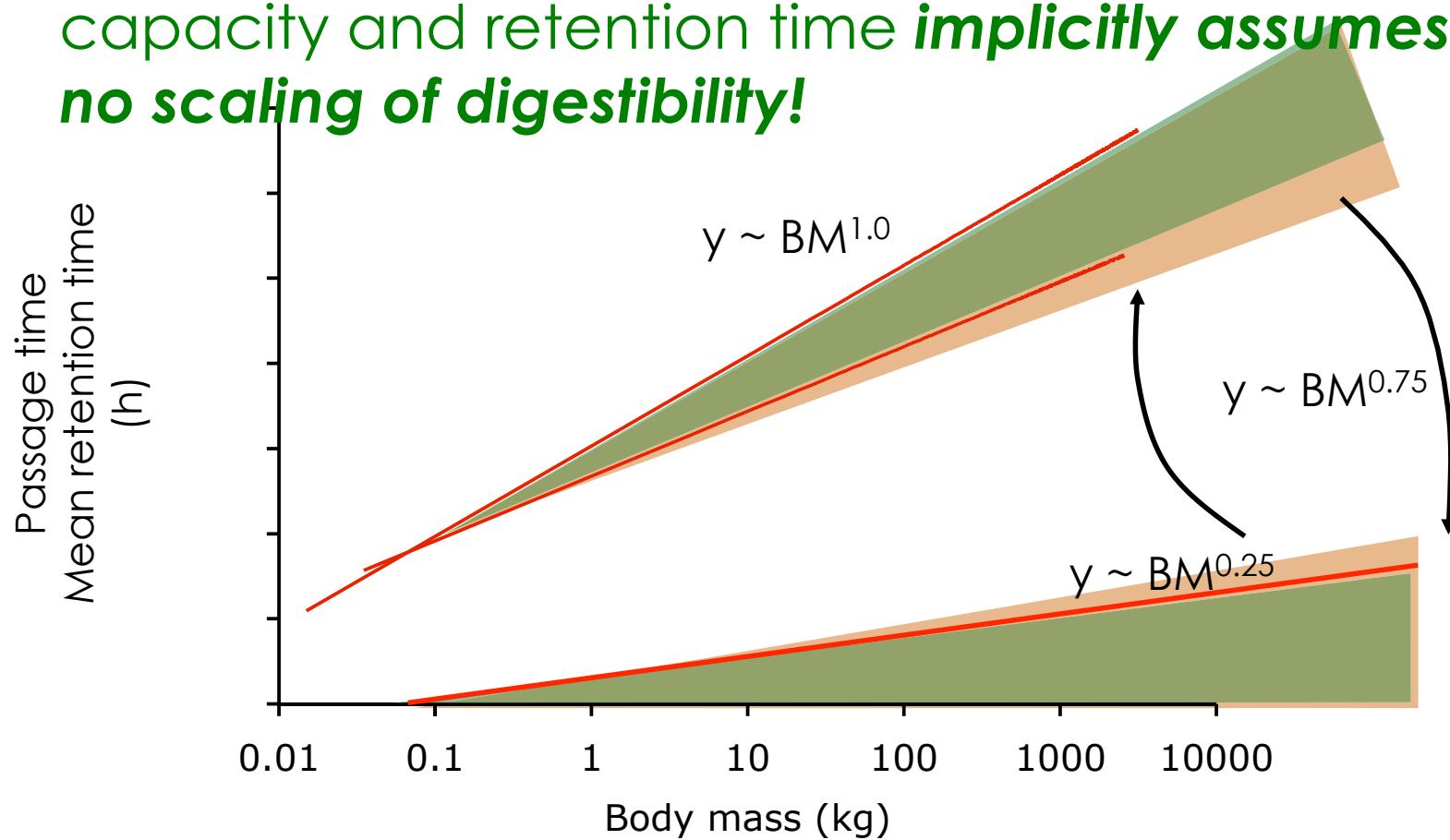
from Parra (1978), Demment & Van Soest (1985), Illius & Gordon (1992); McNab (2002)



Circular reasoning



Due to physical laws, the link between intake, capacity and retention time **implicitly assumes no scaling of digestibility!**



from Parra (1978), Demment & Van Soest (1985), Illius & Gordon (1992); McNab (2002)



Checking the validity of a concept

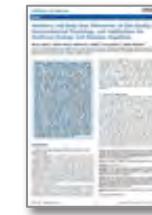
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Conceptual problems



1. One important aspect of 'decreasing diet quality' in large herbivores is a higher proportion of lignified fibre. Lignin is indigestible, no matter how long the retention time. The assumed 'advantage' would therefore only apply for herbivores where 'lower diet quality' means 'higher levels of cellulose but not lignin' – an unlikely scenario to start with.



Conceptual problems



2. What about other, potential digestive **disadvantages** linked to larger body size – such as
 - digesta particle size?
 - methane losses?



Oikos 118: 1623–1632, 2009

doi: 10.1111/j.1600-0706.2009.17807.x,

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Subject Editor: John Vucetich. Accepted 7 May 2009

Comparative chewing efficiency in mammalian herbivores

Julia Fritz, Jürgen Hummel, Ellen Kienzle, Christian Arnold, Charles Nunn and Marcus Clauss

Evolutionary Ecology Research, 2010, 12: 727–738

Methane production in relation to body mass of ruminants and equids

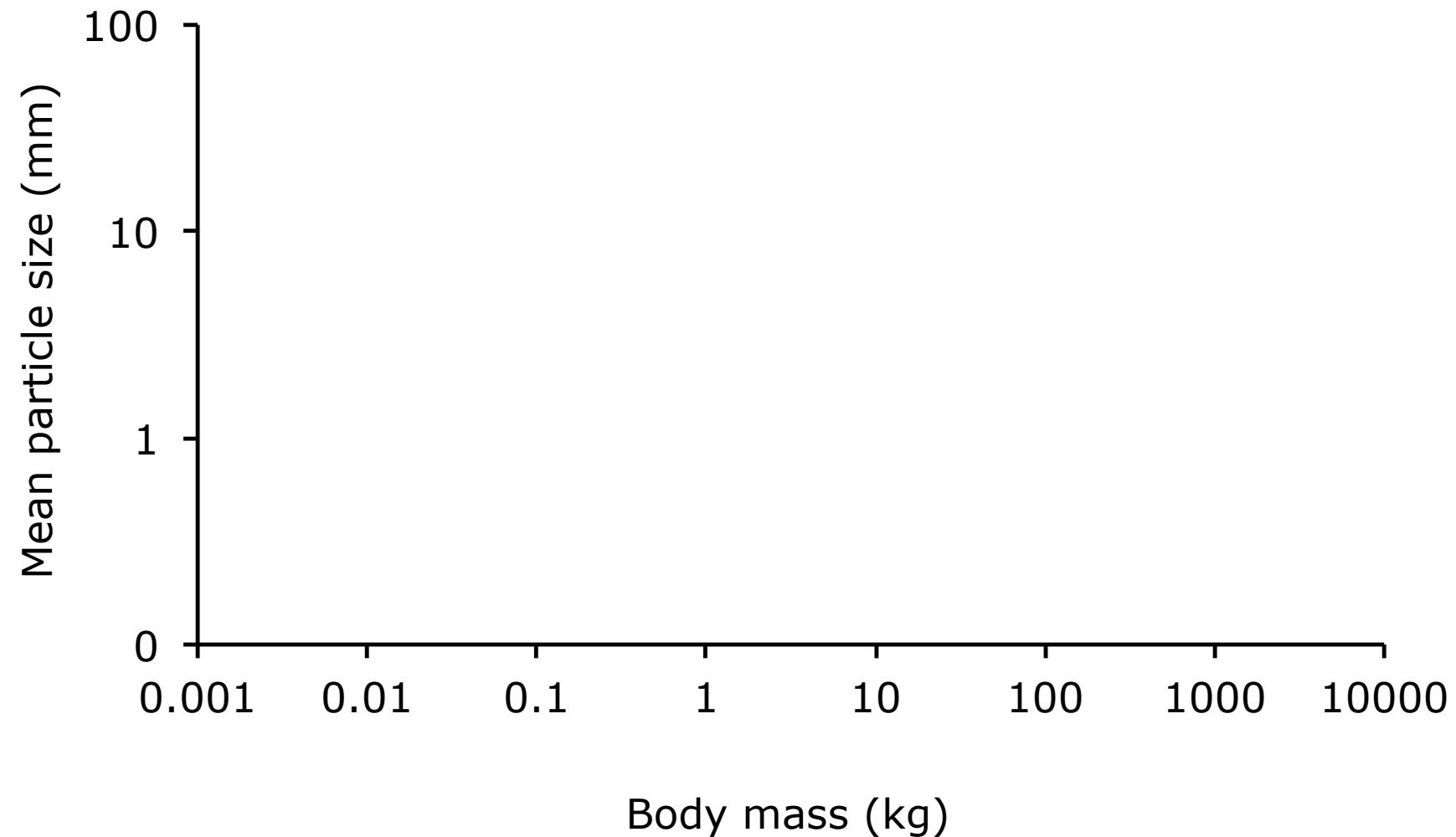
Ragna Franz¹, Carla R. Soliva², Michael Kreuzer², Patrick Steuer³,
Jürgen Hummel³ and Marcus Clauss¹



Particle size



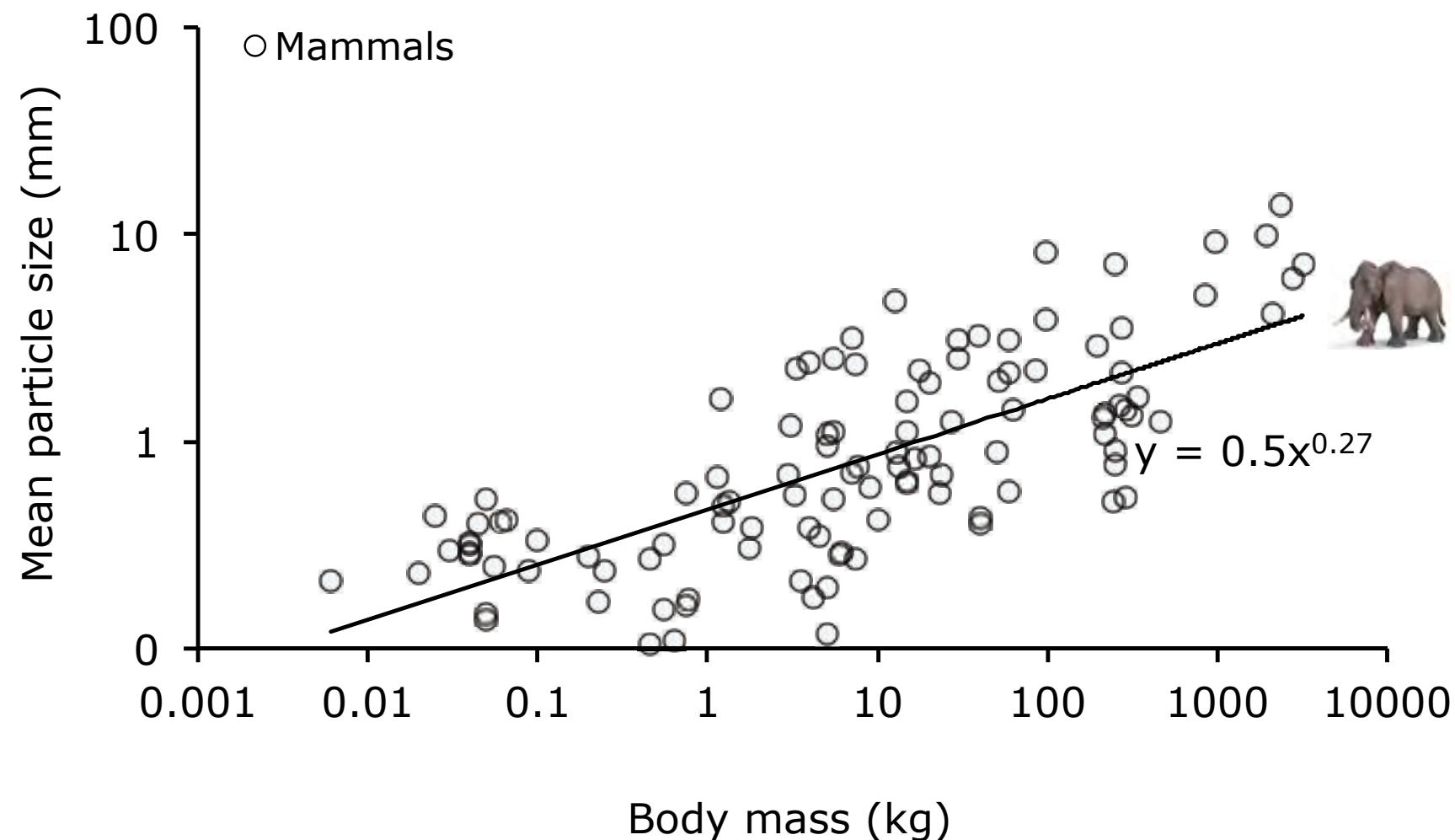
Faecal particle size allometry in herbivores



(Fritz et al. 2009, 2010, 2011)



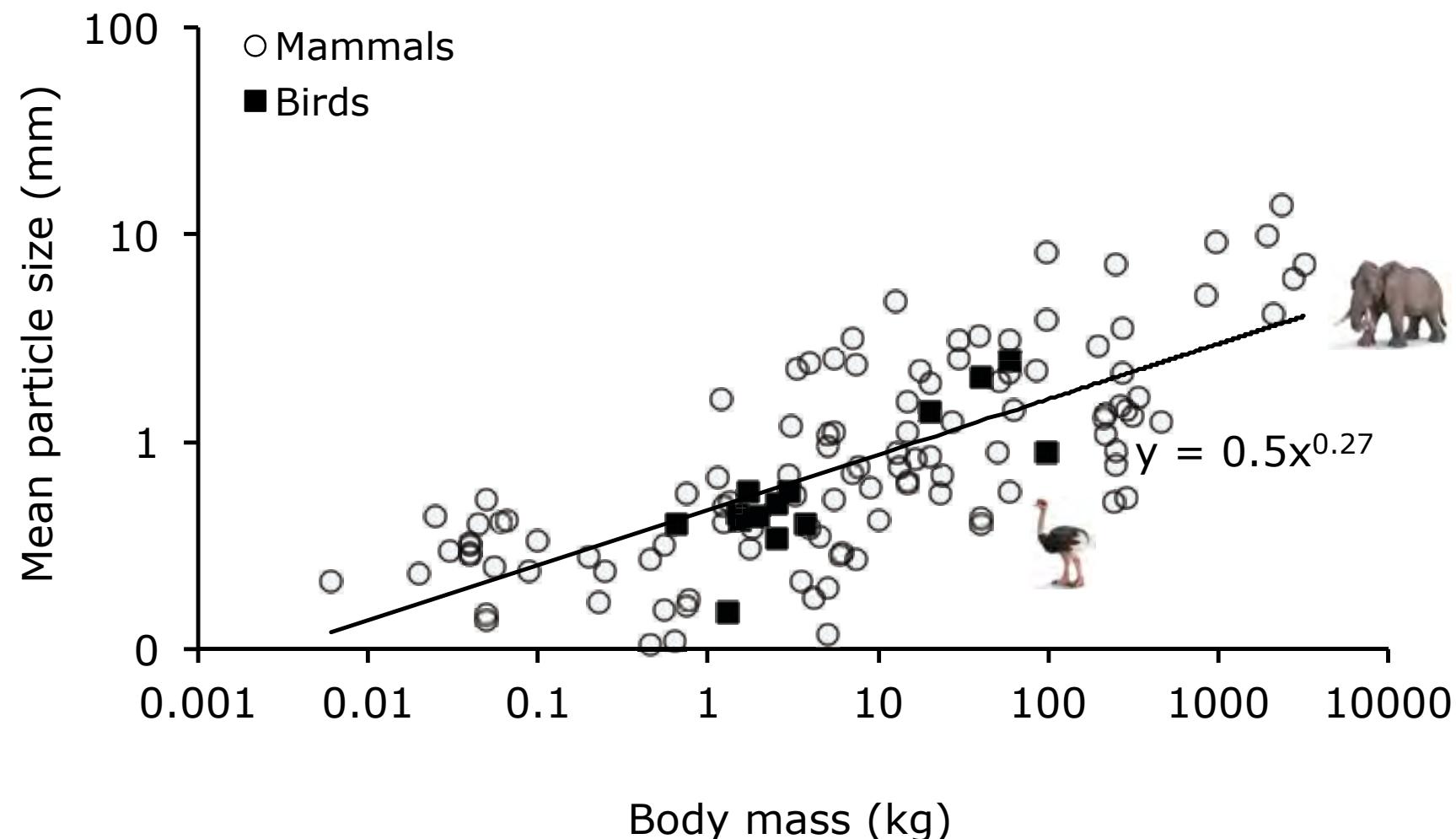
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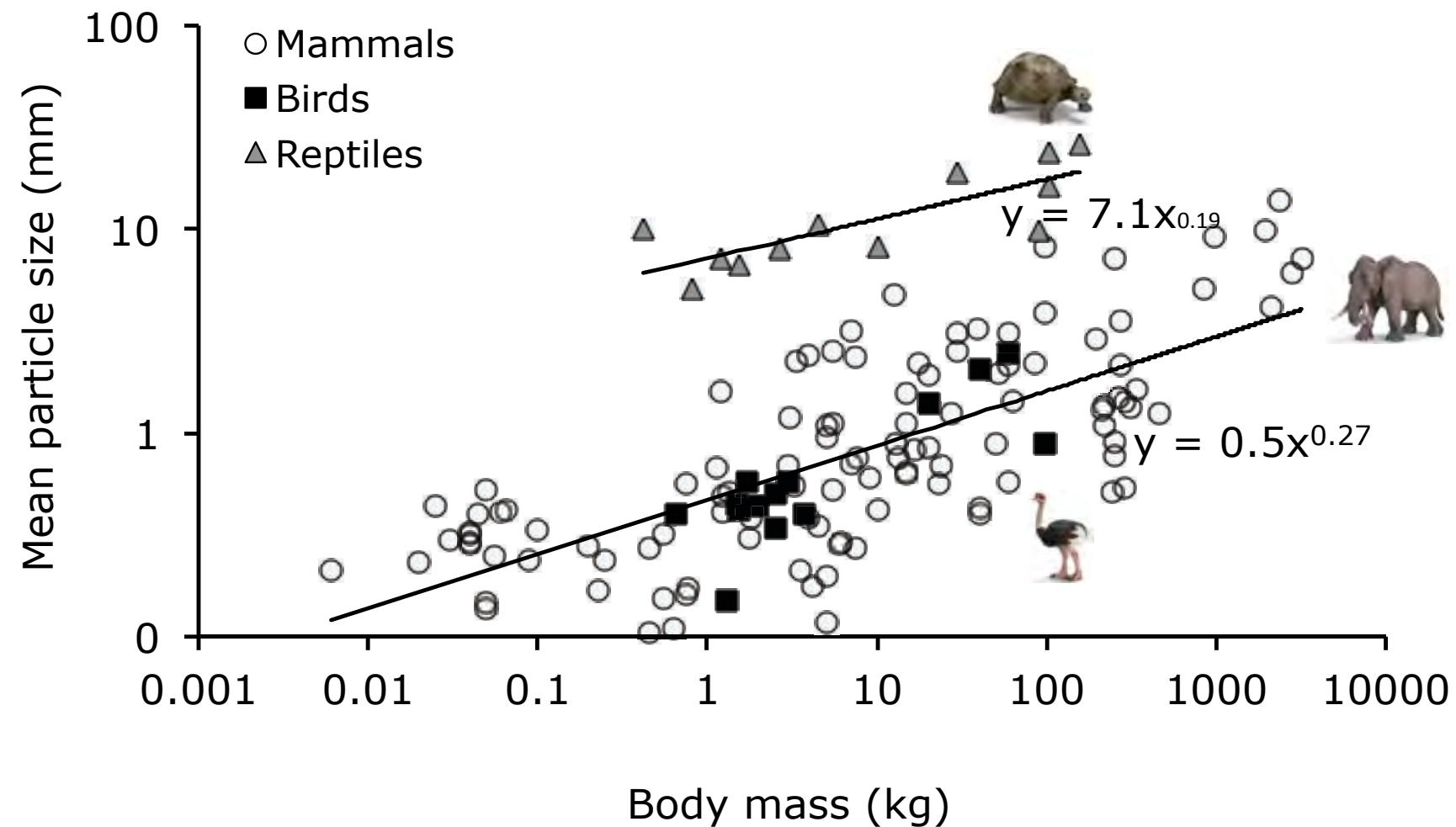
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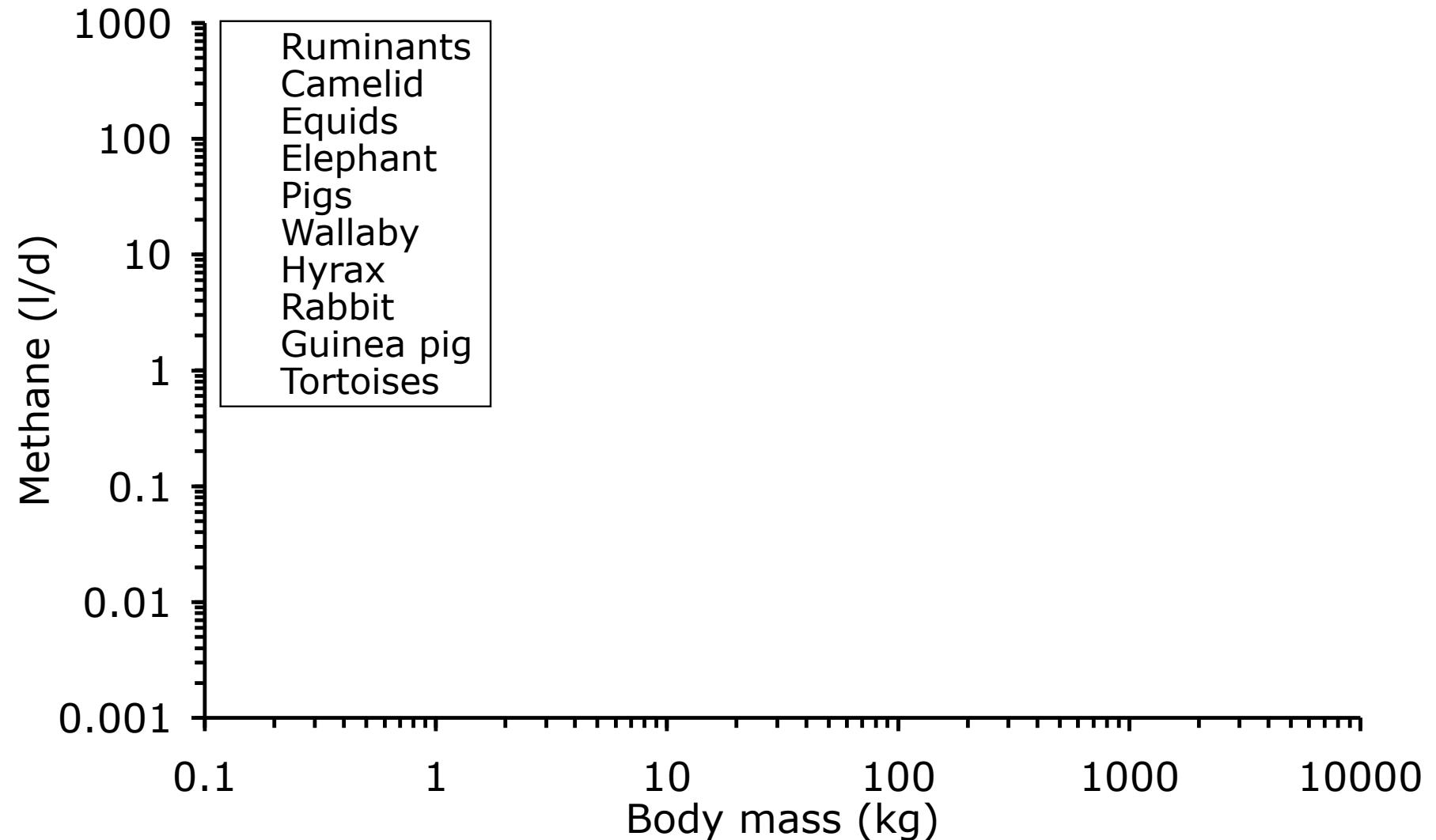
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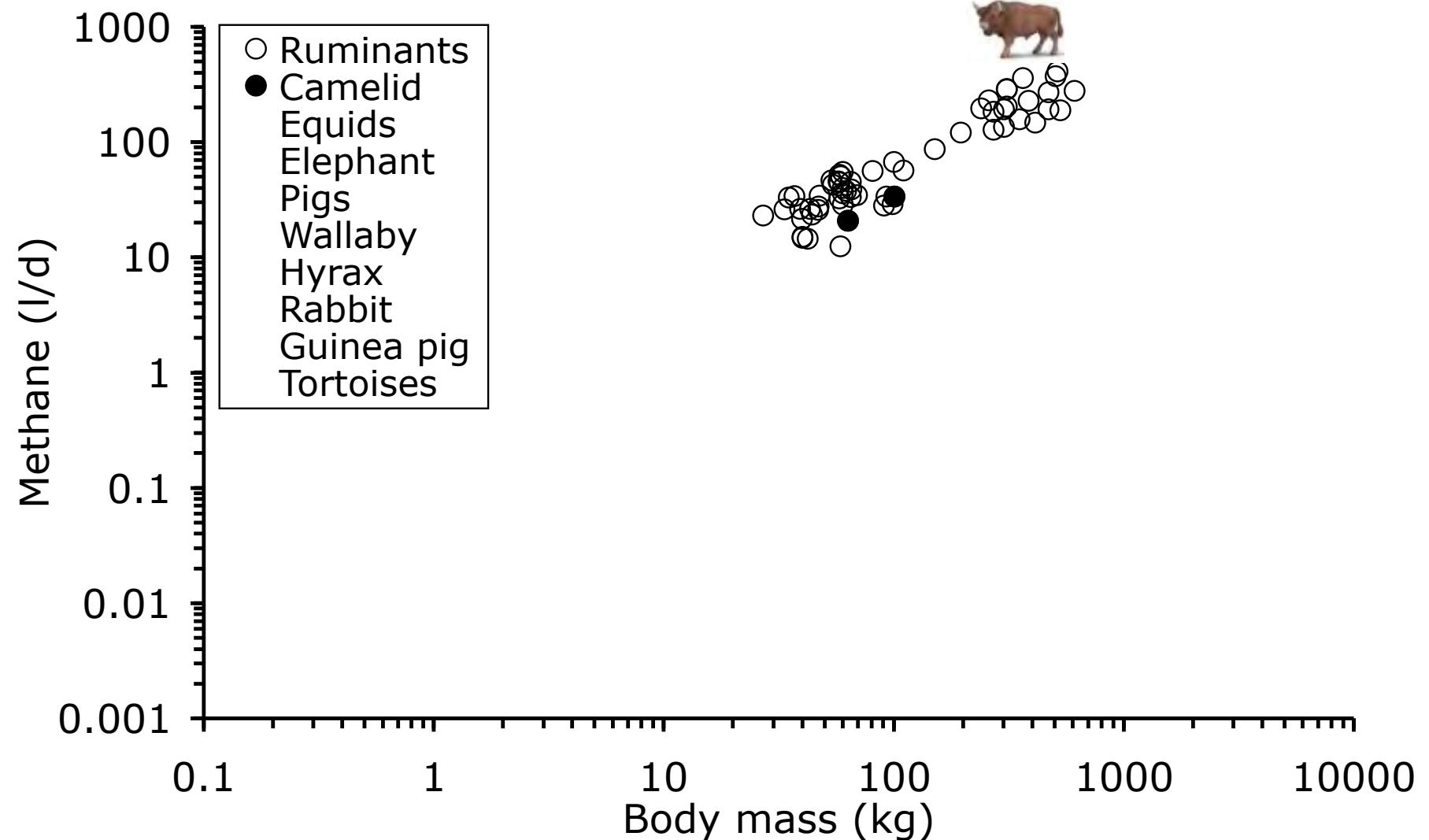
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Literature collection and own data (Franz et al. 2010, 2011ab)



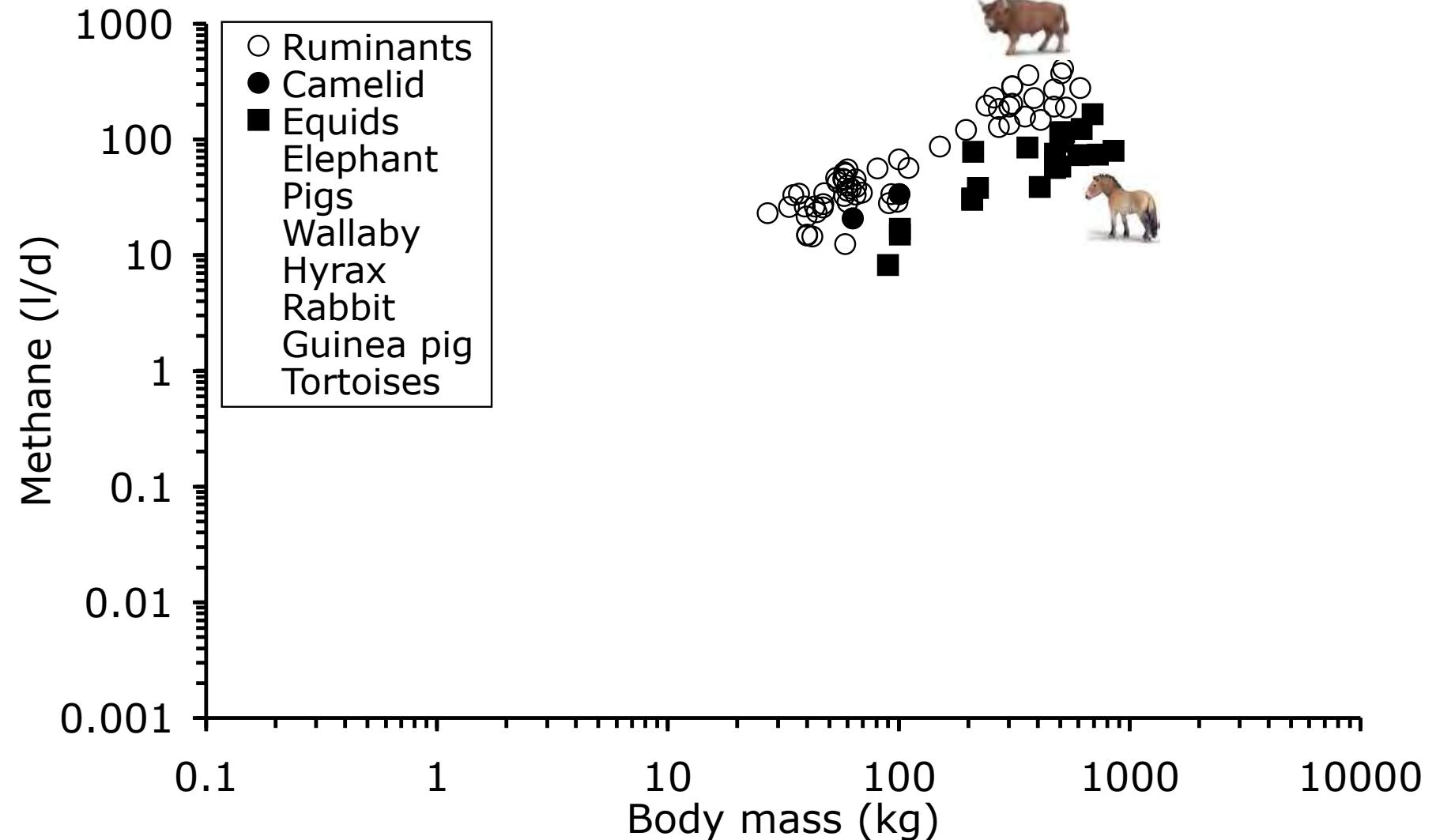
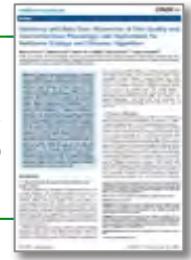
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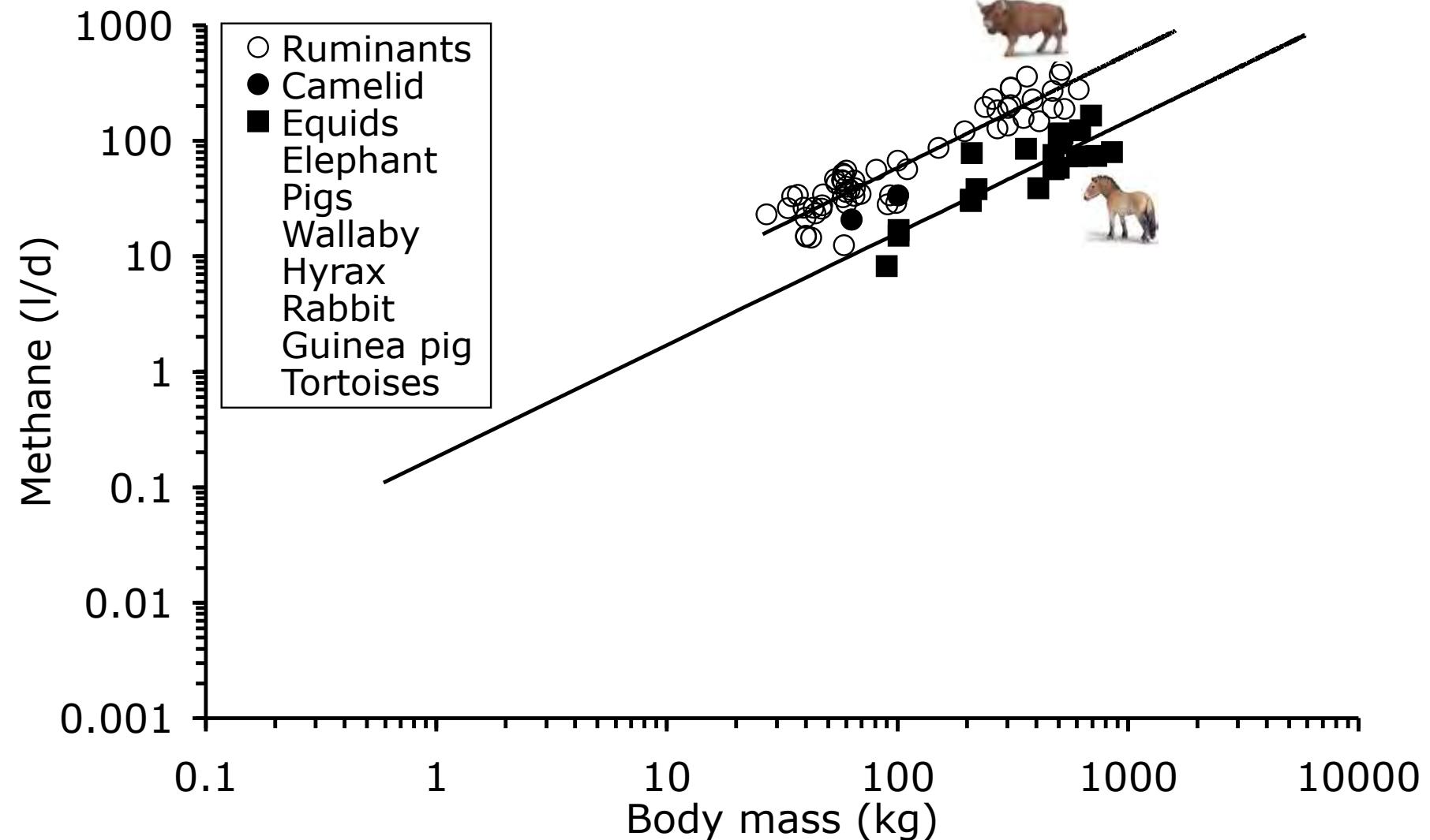
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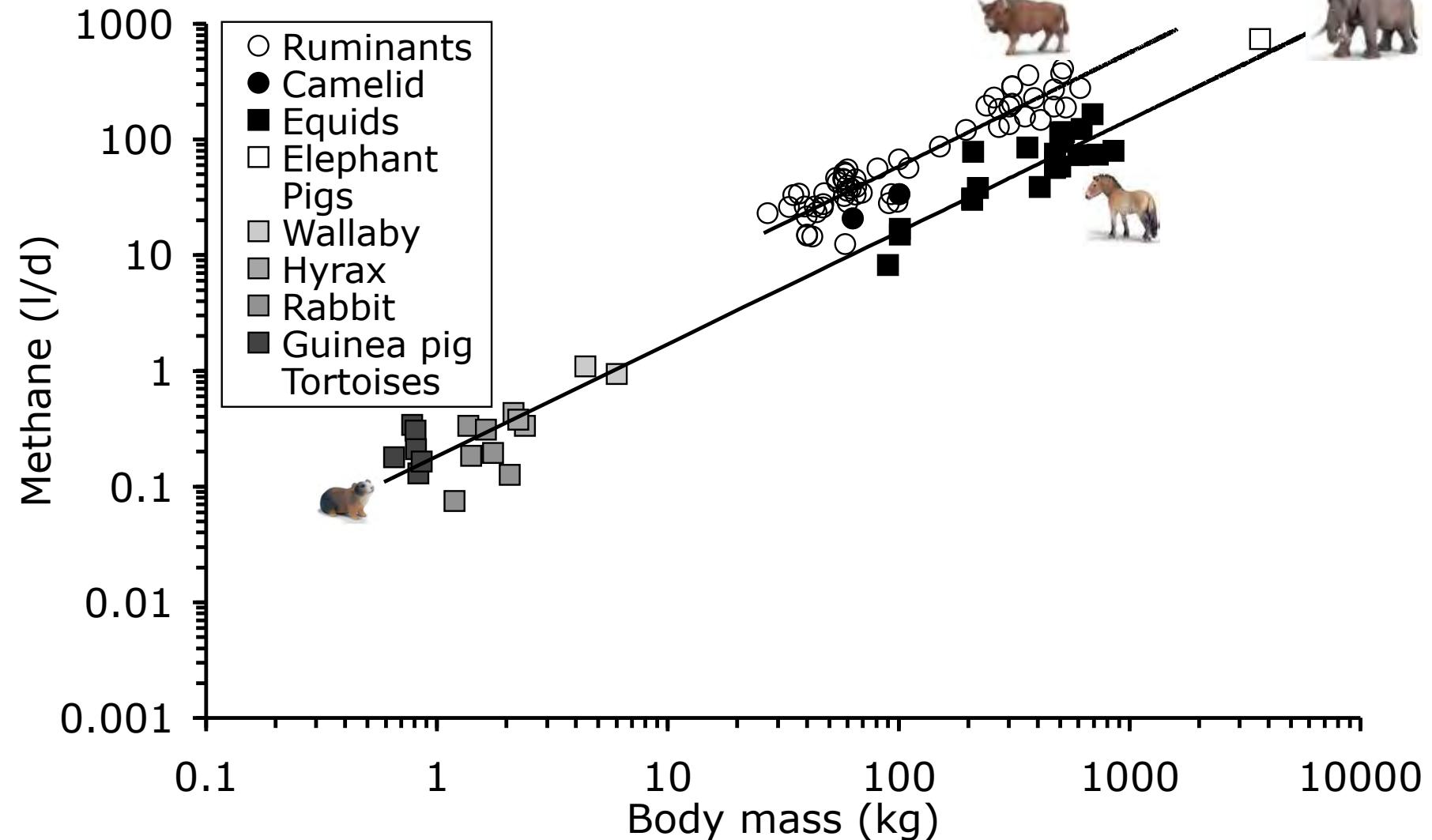
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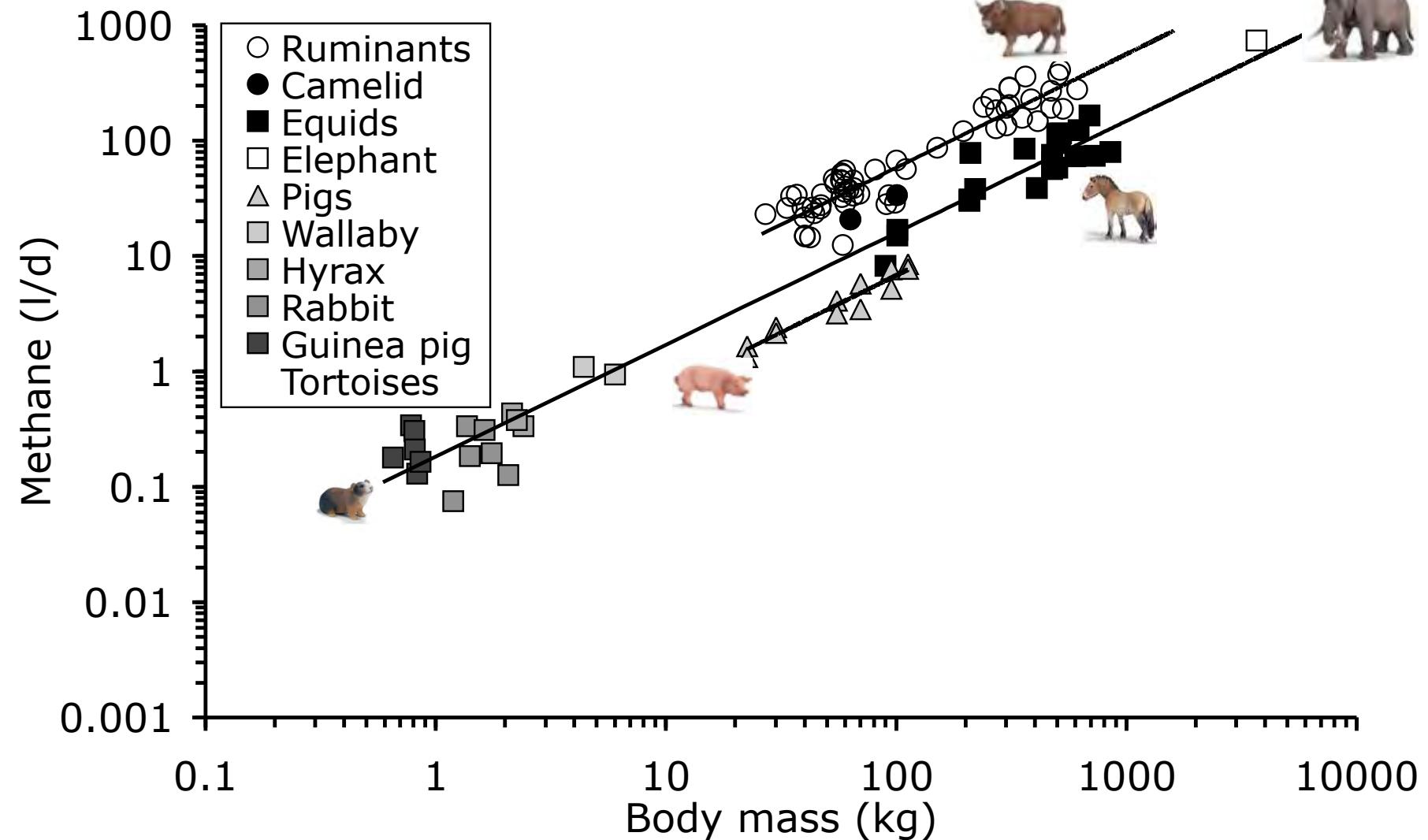
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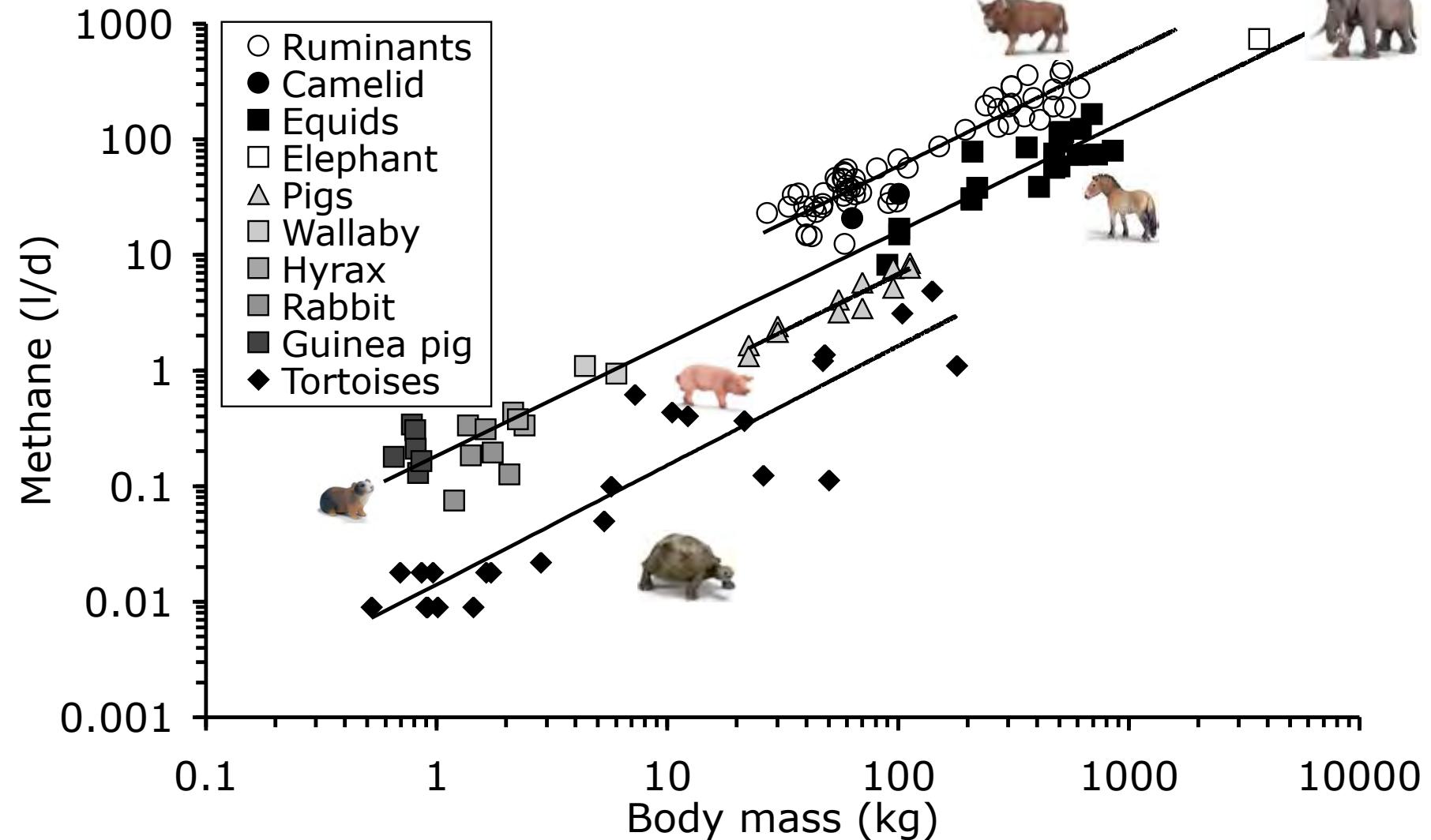
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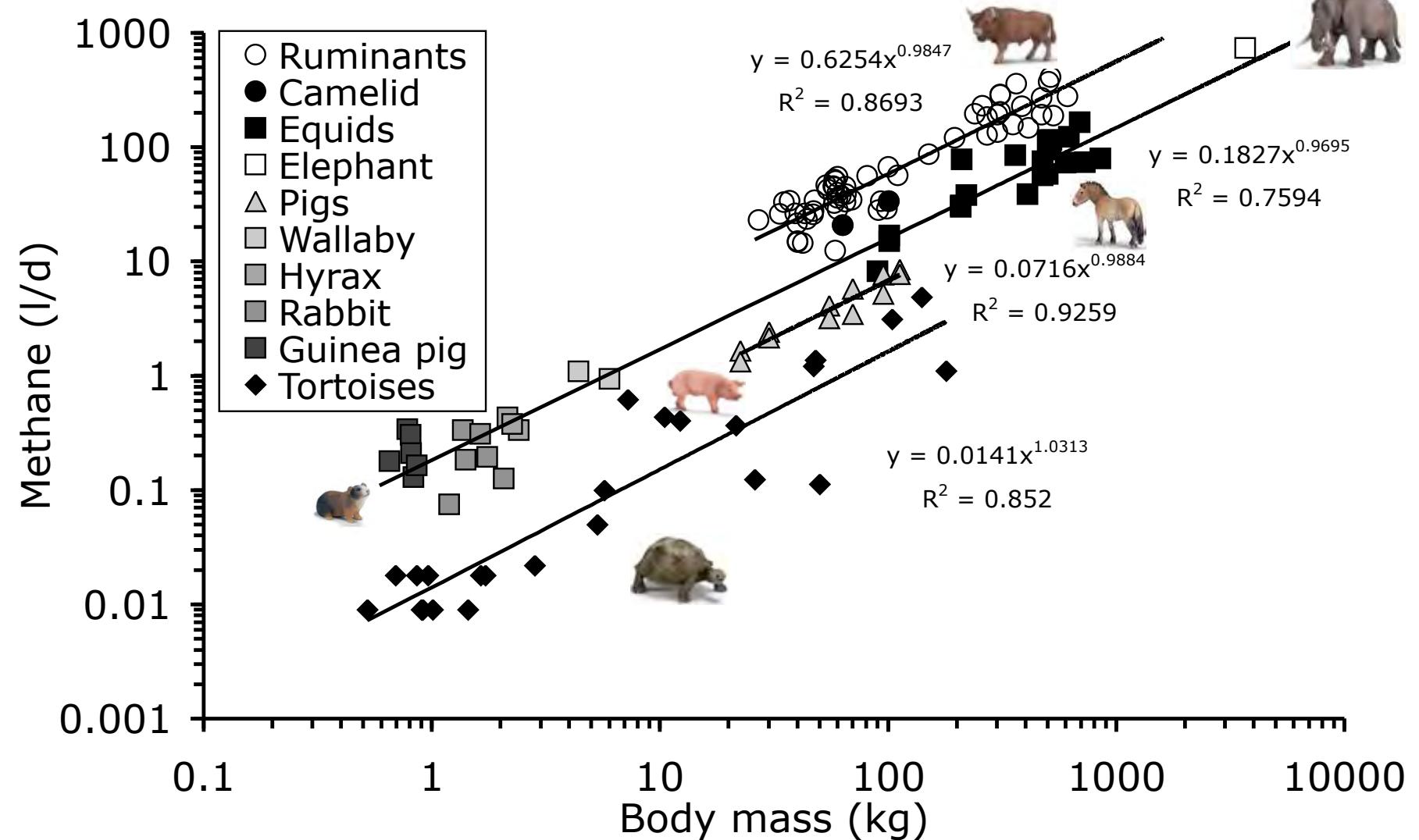
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Conceptual problems

2. What about other, potential digestive disadvantages linked to larger body size – such as
 - digesta particle size – **less with higher BM**
 - methane losses – **more with higher BM**



Jarman-Bell: solution

3. Possible reactions if diet quality decreases with body mass:



Jarman-Bell: solution

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 - a) if intake scales as requirements, then digestive efficiency must increase



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 - b) if digestive efficiency can't increase, then intake must scale higher than requirements to compensate for the lower food quality



Jarman-Bell: solution

3. Possible reactions if diet quality decreases with body mass:
 - a) if intake scales as requirements, then digestive efficiency must increase ***– not in accord with other concepts and empirical data!***
 - b) if digestive efficiency can't increase, then intake must scale higher than requirements to compensate for the lower food quality
 - dry matter intake $BM^{0.89}$
 - requirements $BM^{0.75}$



Ecological opportunity rather than physiological necessity

Don't say:

Small animals cannot afford to eat low quality diets because of body mass-related physiological laws ('higher mass-specific requirements').

Try:

Small animals can afford to live on high-quality diets (because such diets come in densities and package sizes sufficient for small animals) – so some of them could afford to lose the capacity to digest low-quality diets.