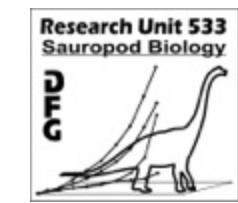




# A playground free-for-all: reconstructing dinosaur biology using data and other means

Marcus Clauss

*Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of  
Zurich, Switzerland  
'Think different' Basle May 2012*

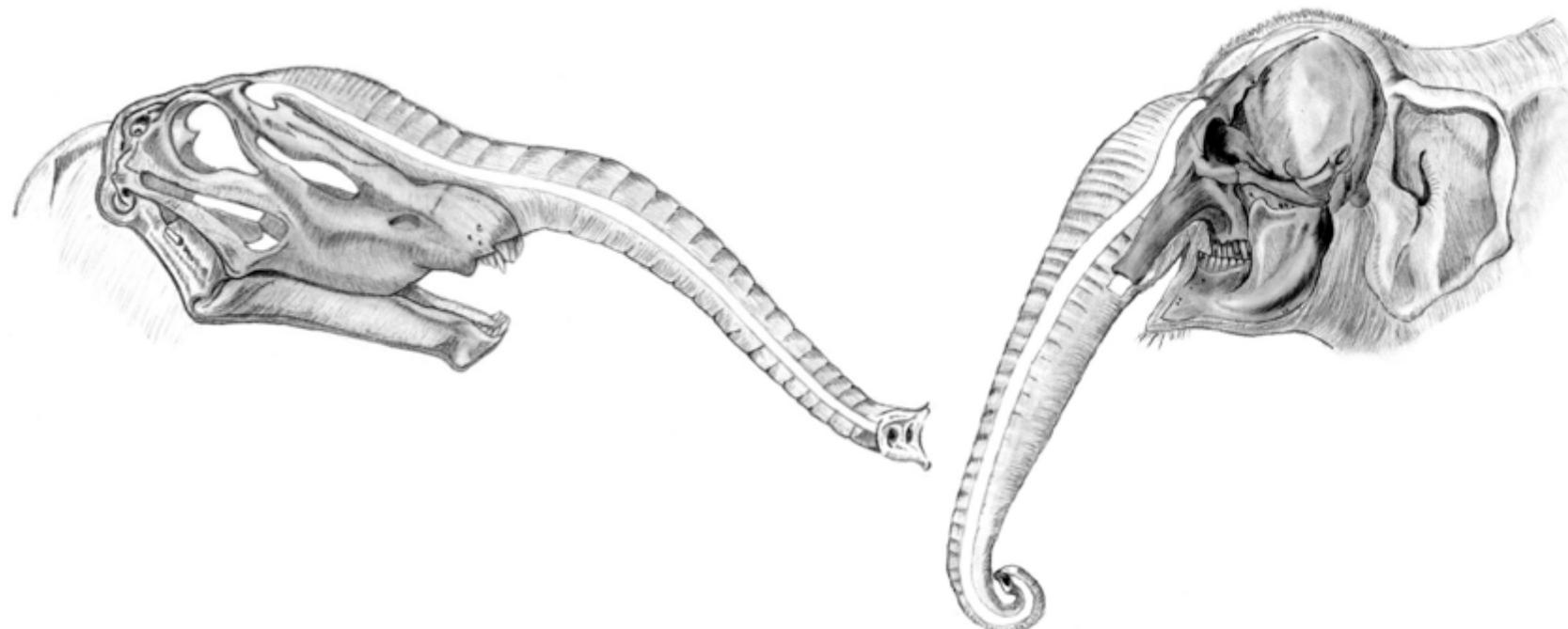




# Paleoneurological evidence against a proboscis in the sauropod dinosaur *Diplodocus*

Fabien Knoll <sup>a,\*</sup>, Peter M. Galton <sup>b</sup>, Raquel López-Antoñanzas <sup>c</sup>

Geobios 39 (2006) 215–221

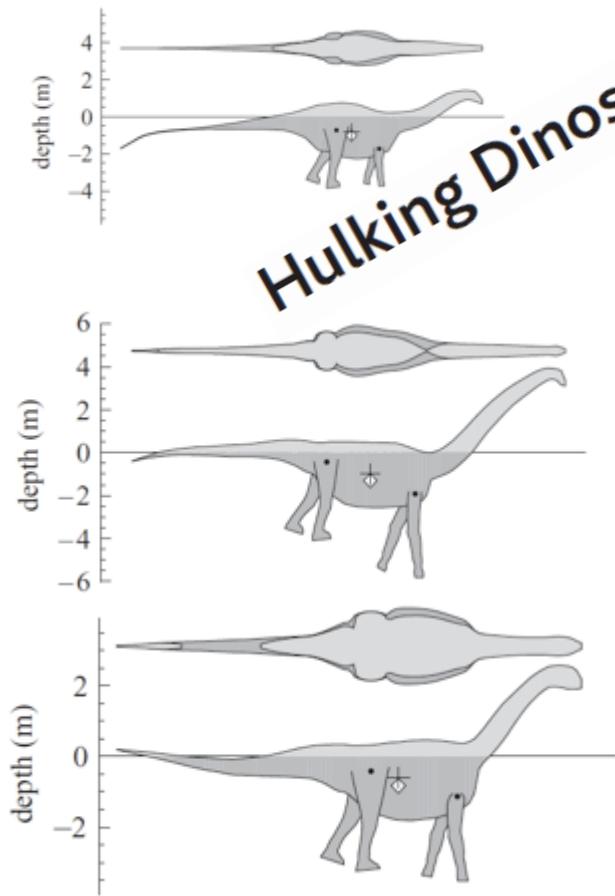




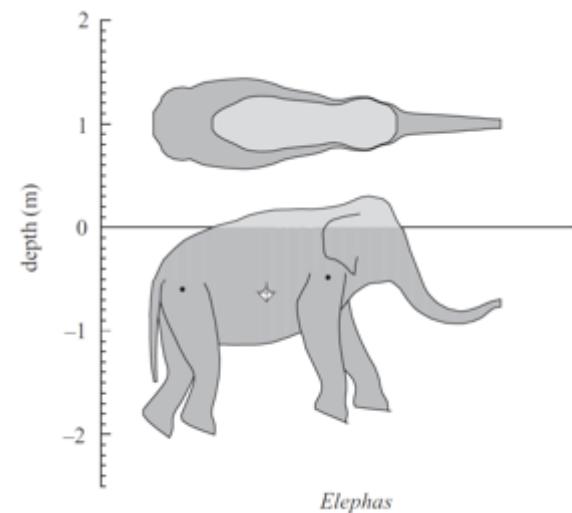
# Topsy punters: sauropod dinosaur pneumaticity, buoyancy and aquatic habits

Donald M. Henderson

*Proc. R. Soc. Lond. B* (Suppl.) 271, S180–S183 (2004)



Hulking Dinosaurs Were Buoyant but Unseaworthy





*based on a true story*



# *based on a true story*

*part of the fascination of scientific writing derives from linking a story to real data*

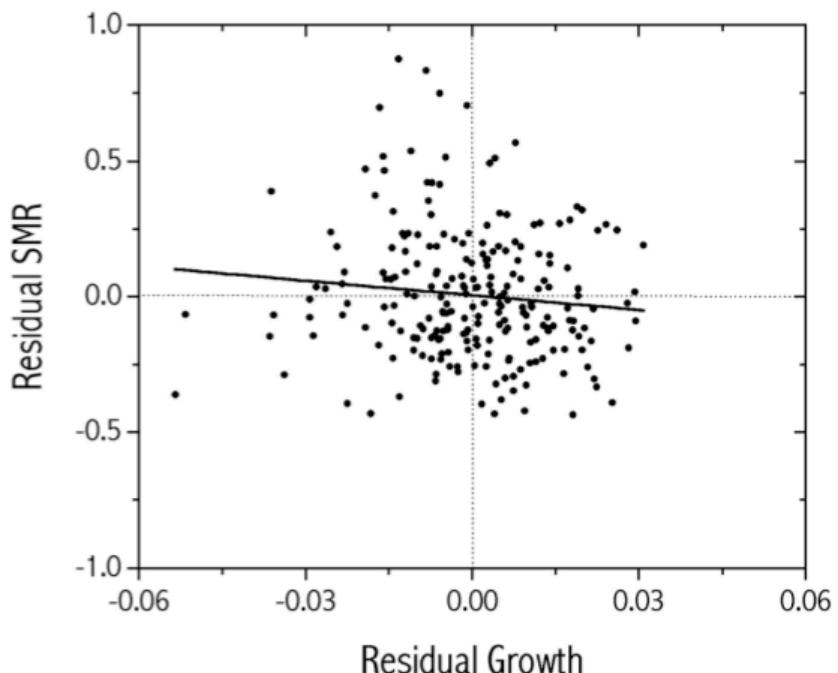


# Basing a story on data

## A high standard metabolic rate constrains juvenile growth

Anthony C. Steyermark\*

Zoology 105 (2002): 147–151



**Fig.1.** A negative relationship exists between the residuals of growth and standard metabolic rate (SMR;  $P = 0.04$ ;  $R = 0.13$ ), indicating a tradeoff in energy expenditure. Growth was measured from hatching to approximately six months of age, and growth rate was calculated as change in body mass per day. Oxygen consumption of each individual was measured immediately after growth measurements ended, and was used to calculate SMR.

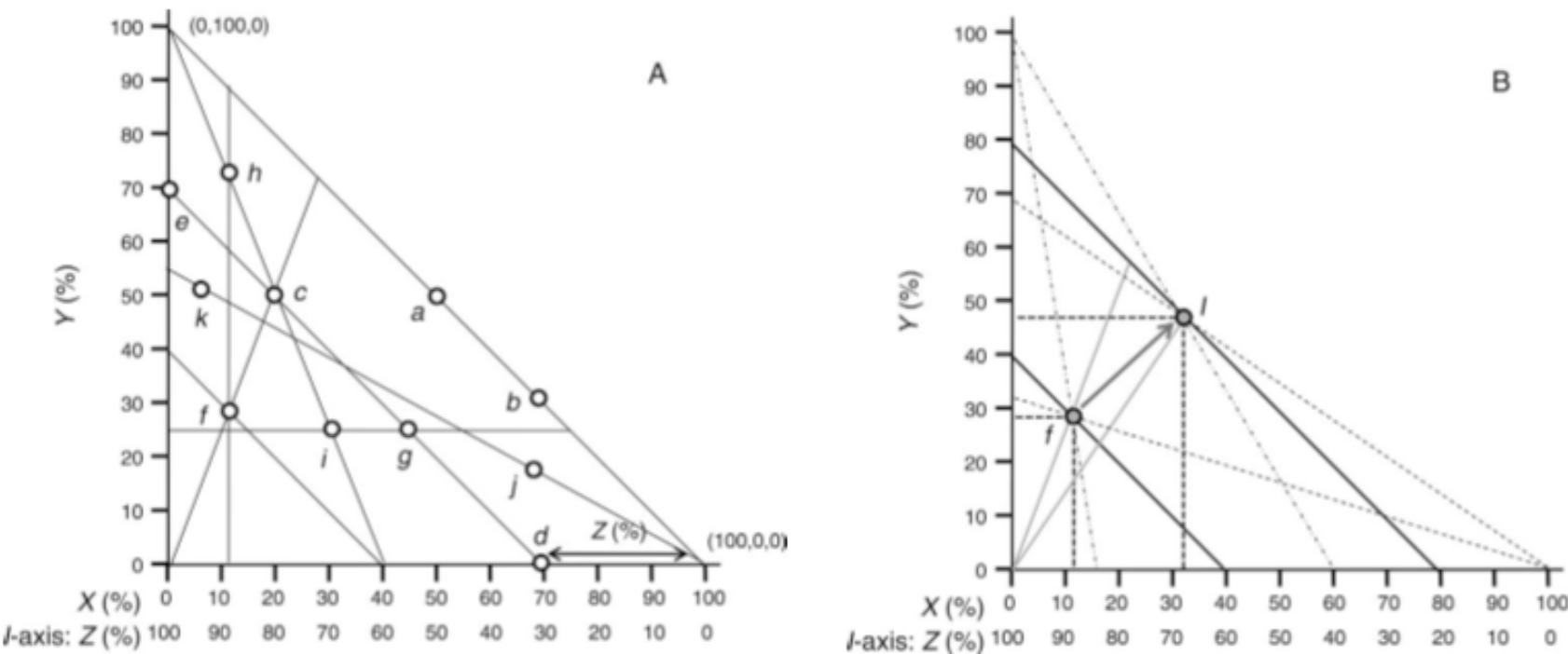


# Basing a story on concept

## Toward a quantitative nutritional ecology: the right-angled mixture triangle

DAVID RAUBENHEIMER<sup>1</sup>

*Ecological Monographs*, 81(3), 2011, pp. 407–427





# Conceptualizing science: two types

## storytellers

historians of all scales:  
history of mankind, all  
life, the universe

explainers of all scales:  
function of atoms,  
concepts, organs,  
organisms, ecosystems,  
the universe

## engineers

applied sciences  
& preparing basic  
research

patents, solutions,  
products,  
procedures

medicine, pharmacists,  
engineers,  
architects,  
agriculturists, lawyers



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the universe

***funding for this ...***

engineers

applied sciences  
& preparing basic  
research

patents, solutions,  
products,  
procedures

medicine, pharmacists,  
engineers,  
architects,  
agriculturists, lawyers

***... by claiming this***



# Conceptualizing science: two types

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patents, solutions,  
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medicine, pharmacists,  
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agriculturists, lawyers

***this is not a distinction between humanities/arts and  
natural sciences***

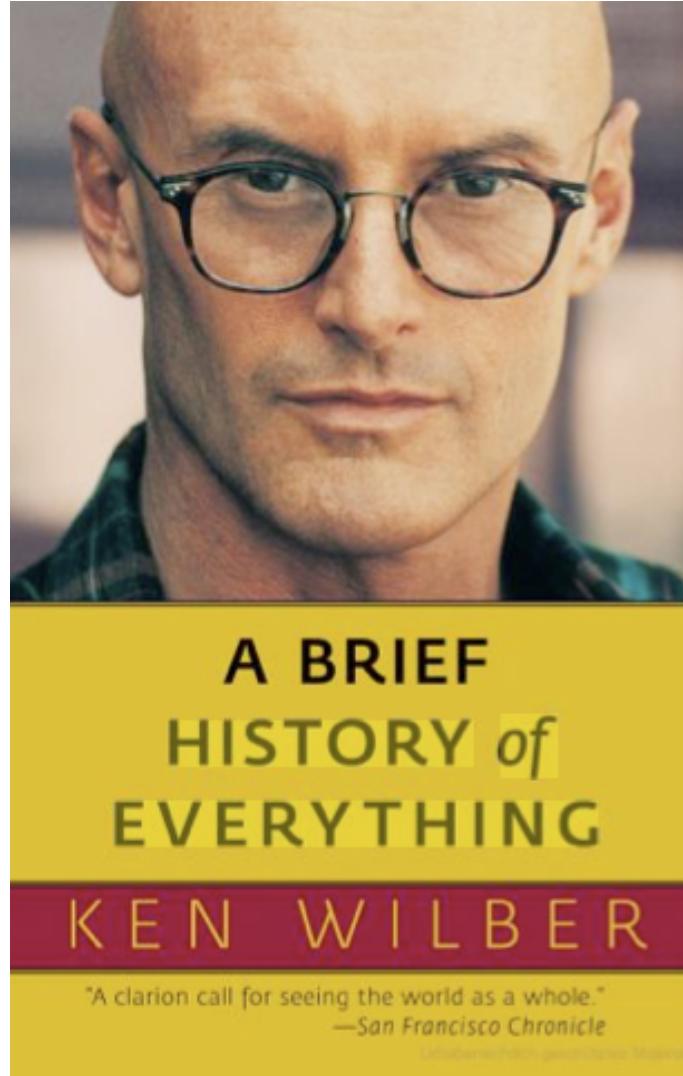


## Storytellers: competing for scope





## Storytellers: competing for scope





# Storytellers: competing for scope

*Ecological Monographs*, 76(1), 2006, pp. 73–92  
© 2006 by the Ecological Society of America

## MANIFOLD INTERACTIVE INFLUENCES ON THE POPULATION DYNAMICS OF A MULTISPECIES UNGULATE ASSEMBLAGE

NORMAN OWEN-SMITH<sup>1,3</sup> AND M. G. L. MILLS<sup>2</sup>

<sup>1</sup>*Centre for African Ecology, School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Wits 2050 South Africa*

<sup>2</sup>*South African National Parks, Endangered Wildlife Trust and Mammal Research Institute, University of Pretoria, Private Bag X402, Skukuza 1350 South Africa*

**Abstract.** The dynamics of animal populations can be influenced directly by prevailing resources, population density, and environmental conditions, and through the delayed effects of trophic interactions and abiotic effects on habitat conditions. For large mammals, lagged effects can extend several years back in time. We attempted to establish the causal processes governing the population changes shown by 11 ungulate species counted annually over a 20-year period in South Africa's Kruger National Park. Kudu, waterbuck, warthog, sable, tsessebe, roan, and eland declined progressively in abundance after 1986, while zebra, wildebeest, impala, and giraffe maintained high abundance levels. To identify lagged influences, we used statistical probes indexing (1) inferred changes in predator abundance as a consequence of past food availability, (2) effects on habitat conditions of prior rainfall, and (3) competitor impacts on shared food resources. Multiple linear regression models were fit to estimates of annual population growth derived from the count totals subdivided among four regions. The temporal pattern of the population declines by five species was most consistent with a lagged effect from past predator food, in addition to the direct effects of seasonal rainfall. However, models including the lagged effect of prior rainfall fit nearly as well. Species that maintained high abundance responded mainly to an immediate or lagged density feedback. Changing rainfall conditions apparently affect the relative susceptibility of ungulate species to predation. Hence, the top-down interaction with predators cannot readily be disentangled from extrinsic influences on population dynamics, mediated through resources. Population declines by some species became extreme because a prolonged period of low rainfall, especially in the dry-season component, followed a doubling in the food base supporting lions, and was coupled with widened prey distribution as a consequence of the augmentation of water points by managers. Changes in population abundance within this multi-prey, generalist predator system arose from a complex interplay between changing climatic conditions, variable food production, shifting habitat conditions, varying vulnerability to predation, and spillover effects on other species.

**Key words:** *climatic influences; density dependence; declining populations; large herbivores; predator-prey interactions; rainfall effects; time-series analysis; trophic interactions.*



# Stories of different scope

## Natural sciences

The rodents of the southern Kalahari

Diversification of desert rodents:  
mechanisms and contingencies

Diversification of desert mammals

Mammalian diversification

Principles of diversification: a comparison of plants and animals

From higgs-bosons to black holes:  
the construction of everything



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From higgs-bosons to black holes: the construction of everything

## Humanities/Arts

The relationships of the Vatican to Poland during WW2

Fundamentals of christian catechism

Human religiosity

Human universals



# Stories of different scope

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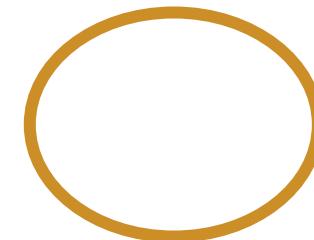
## Humanities/Arts

The relationships of the Vatican to Poland during WW2

Fundamentals of christian catechism

Human religiosity

Human universals



***Humanities/arts cannot compete in the scope-of-the-story race.***



# The greatest story ever told



# The greatest story ever told





# The greatest story ever told

1





# The greatest story ever told

1



1



2





# The greatest story ever told

1



1



1



2



2





# The greatest story ever told

1



1



1



2



2



3



1



2



3





# The greatest story ever told

1



1



1



2



2



3



1



1



2



2



3



3





# The greatest story ever told

1



1



1



2



2



3



1



1



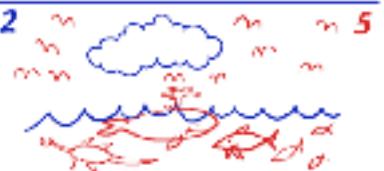
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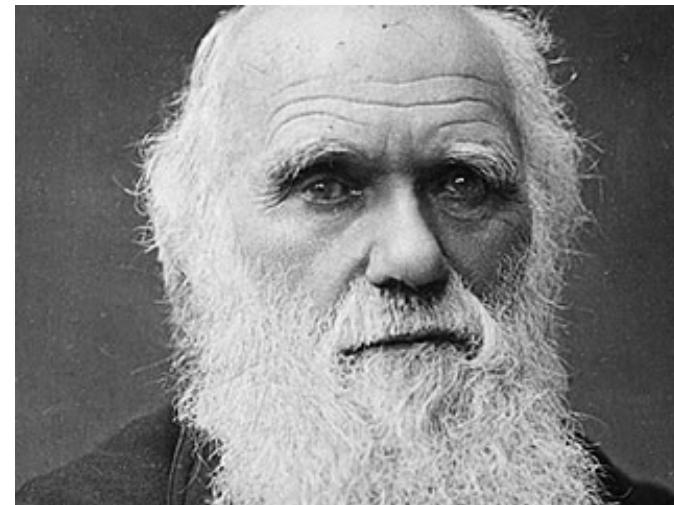
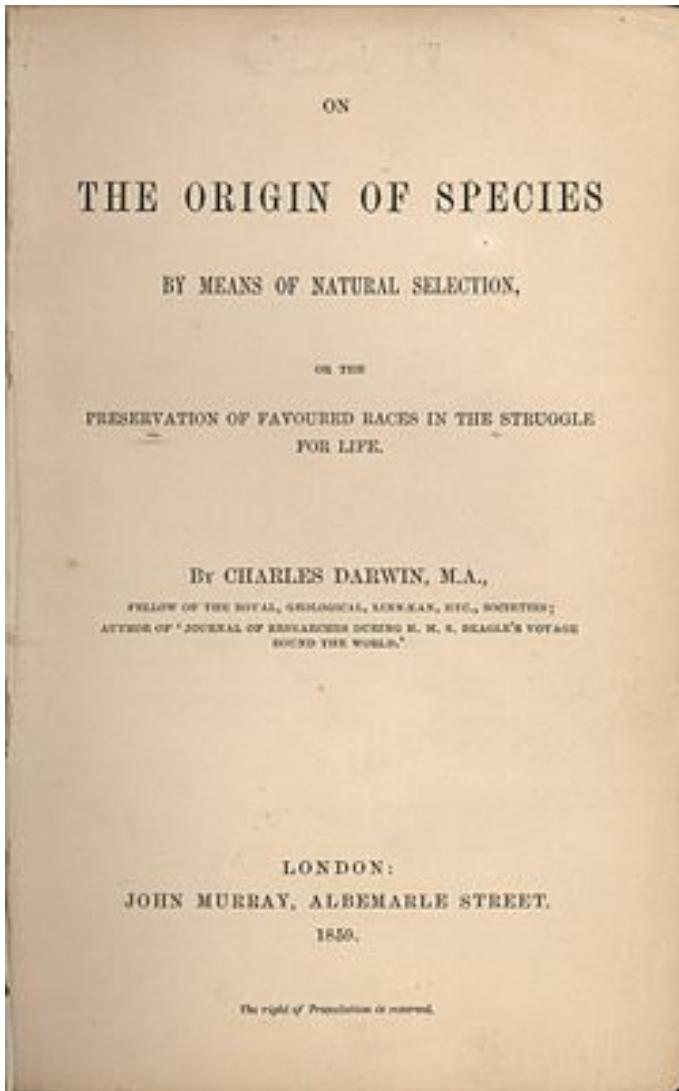


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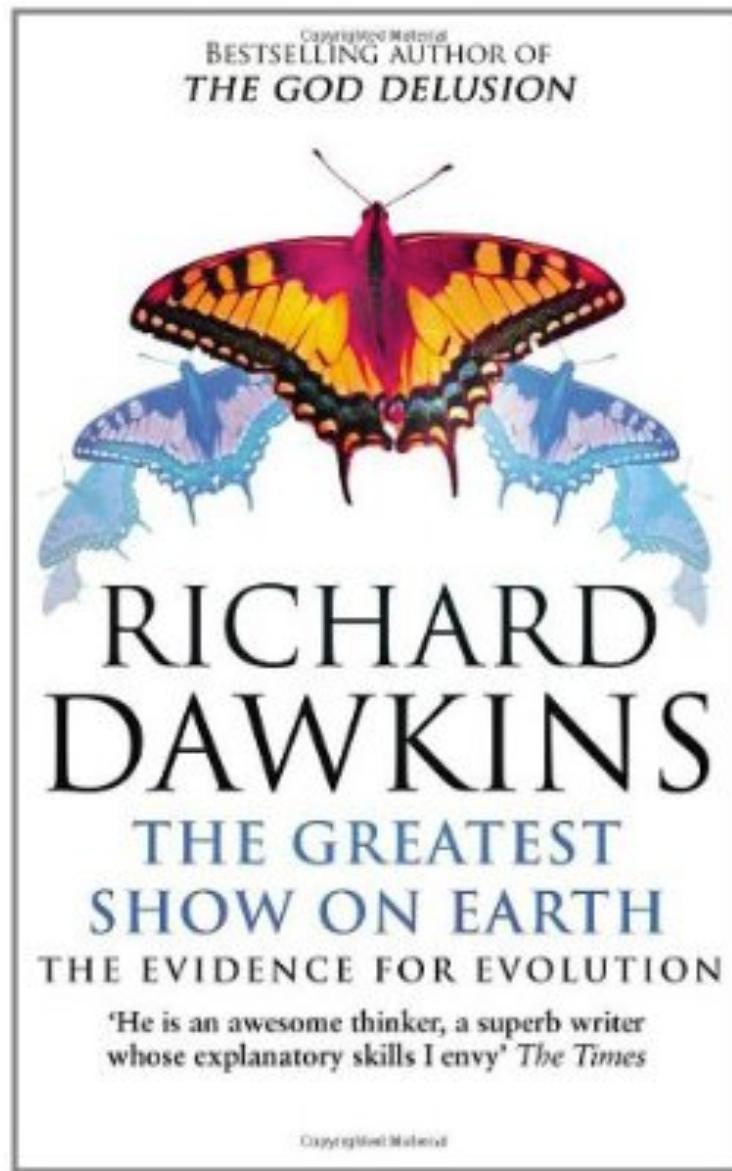


# The greatest story ever told



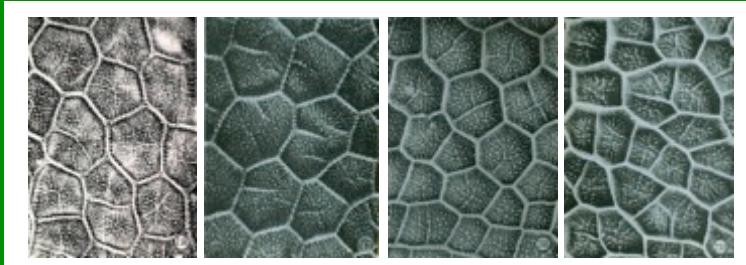


# The greatest story ever told





*Why does the depth of the reticular honeycomb pattern vary among different ruminant species?*



from Hofmann (1969 & 1973)



What  
retirees  
vary  
in  
the  
ern-  
want



from Hofmann (1969 & 1973)

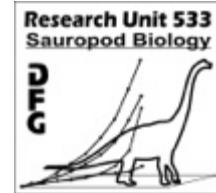


*Why were dinosaurs so large?  
Why did dinosaurs die out?*



# DFG Research Group 533

## Sauropod Biology - the Evolution of Gigantism





# DFG Research Group 533

## Sauropod Biology - the Evolution of Gigantism



### Digestive physiology supervisors

Jürgen Hummel

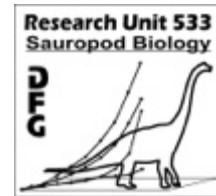


Marcus Clauss



# DFG Research Group 533

## Sauropod Biology - the Evolution of Gigantism



### Digestive physiology supervisors

Jürgen Hummel



Marcus Clauss

### Digestive physiology PhD students & associates



Julia Fritz



Ragna Franz

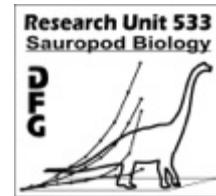


Patrick Steuer



# DFG Research Group 533

## Sauropod Biology - the Evolution of Gigantism



### (Digestive physiology) supervisors

Jürgen Hummel



Chris Carbone



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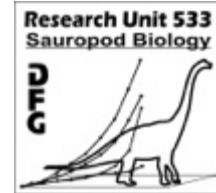


Patrick Steuer



# DFG Research Group 533

## Sauropod Biology - the Evolution of Gigantism



### (Digestive physiology) supervisors

Jürgen Hummel



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Marcus Clauss

### Digestive physiology PhD students & associates



Julia Fritz



Ragna Franz



Patrick Steuer



Dennis Müller



Daryl Codron



Irina  
Nurutdinova



# The plan:



# The plan:

-Think



# The plan:

- Think
- Extrapolate (using data collections that exist or have to be created/supplemented)



# The plan:

- Think
- Extrapolate (using data collections that exist or have to be created/supplemented)
- If possible, link to existing theories



# Different approaches to classify herbage

## The improbable endotherm: the energetics of the sauropod dinosaur *Brachiosaurus*

Jan C. Weaver

*Paleobiology*, 9(2), 1983, pp. 173–182

TABLE 3. Plant genera sampled and hierarchical average (computed by averaging determinations on a plant and then determinations on a species and then determinations on a genus) of plant caloric density for each genus, organized into five groups of plants representative of the Morrison flora. Numbers in parentheses based on single determinations.

Morrison flora	Modern family	Genera	No. spp.	No. determinations	Avg kcal/g
Horsetails	Equisetaceae	<i>Equisetum</i>	1	3	3.347
Ferns	Angiopteridaceae	<i>Angiopteris</i>	1	2	4.294
	Osmundaceae	<i>Osmunda</i>	1	2	4.653
	Cyatheaceae	<i>Cyathea</i>	1	6	4.174
	Polypodiaceae	<i>Sphaeropteris</i>	2	6	4.263
		<i>Asplenium</i>	1	1	(3.369)
		<i>Blechnum</i>	1	2	3.827
		<i>Deinstaedtia</i>	1	2	4.328
		<i>Thelypteris</i>	1	2	4.272
		<i>Drynaria</i>	1	1	(4.158)
	Dicksoniaceae	<i>Dicksonia</i>	1	1	(4.377)
		<i>Cibotium</i>	1	1	(4.540)
Cycads	Cycadaceae	<i>Ceratozamia</i>	1	4	4.754
		<i>Cycas</i>	4	9	4.584
		<i>Dioon</i>	2	9	4.773
		<i>Encephalartos</i>	6	11	4.826
		<i>Lepidozamia</i>	1	4	5.393
		<i>Macrozamia</i>	2	7	5.272
		<i>Stangeria</i>	1	4	4.489
		<i>Zamia</i>	3	9	4.685
Ginkgos	Ginkgoaceae	<i>Ginkgo</i>	1	4	4.218
Conifers	Araucariaceae	<i>Araucaria</i>	5	11	4.423
	Taxodiaceae	<i>Agathis</i>	2	2	4.467
		<i>Taxodium</i>	1	4	4.707
		<i>Cunninghamia</i>	1	1	(4.050)
		<i>Metasequoia</i>	1	4	4.449

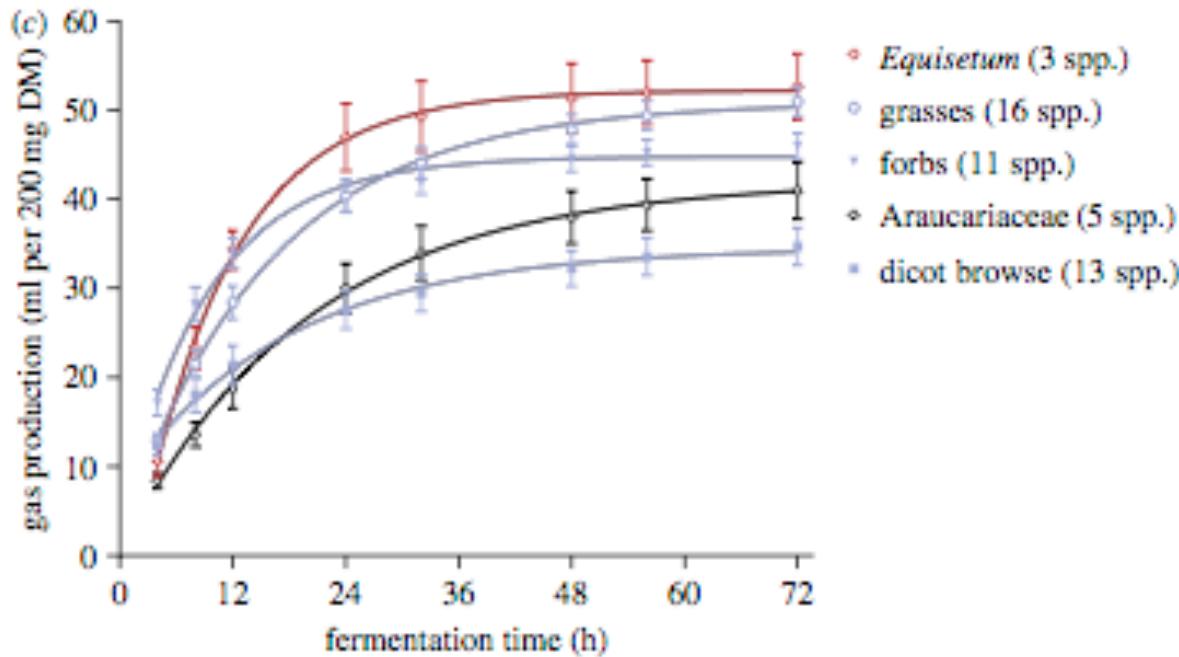


# Different approaches to classify herbage

## ***In vitro* digestibility of fern and gymnosperm foliage: implications for sauropod feeding ecology and diet selection**

Jürgen Hummel<sup>1,\*</sup>, Carole T. Gee<sup>2</sup>, Karl-Heinz Südekum<sup>1</sup>,  
P. Martin Sander<sup>2</sup>, Gunther Nogge<sup>3</sup> and Marcus Clauss<sup>4</sup>

*Proc. R. Soc. B* (2008) 275, 1015–1021



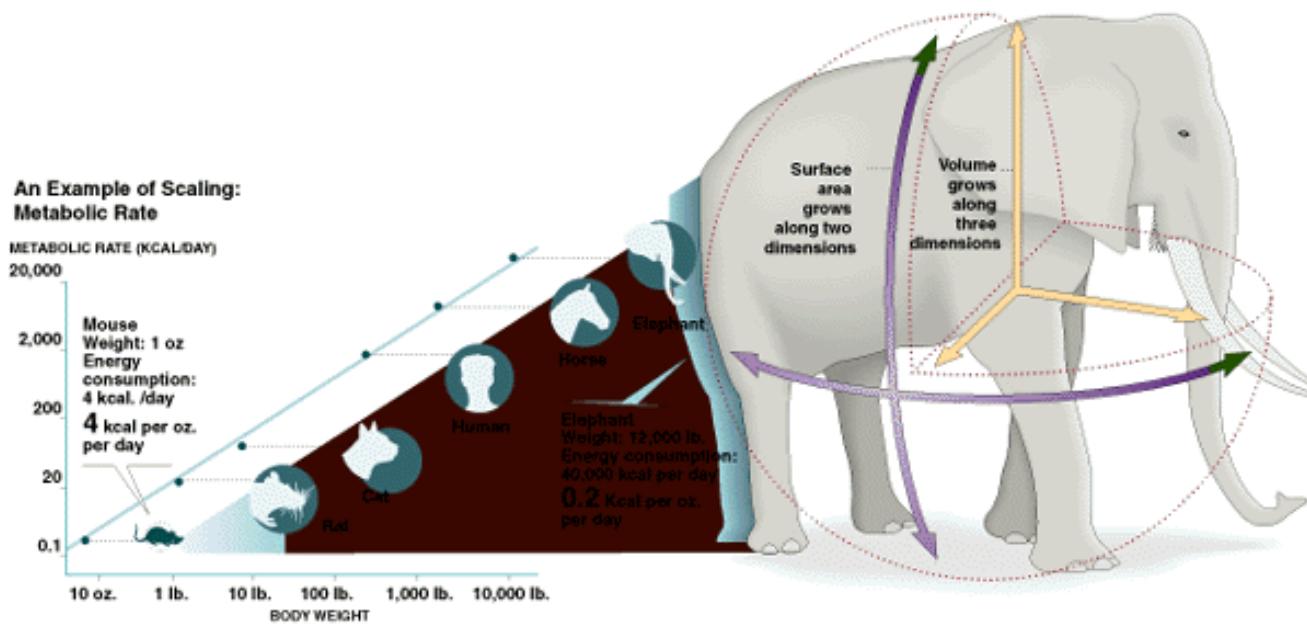


## Scaling: fundamental (conceptual) relevance of body mass

Most biologists consider body mass the most important characteristic of an organism. It is also (mostly) easy to measure.

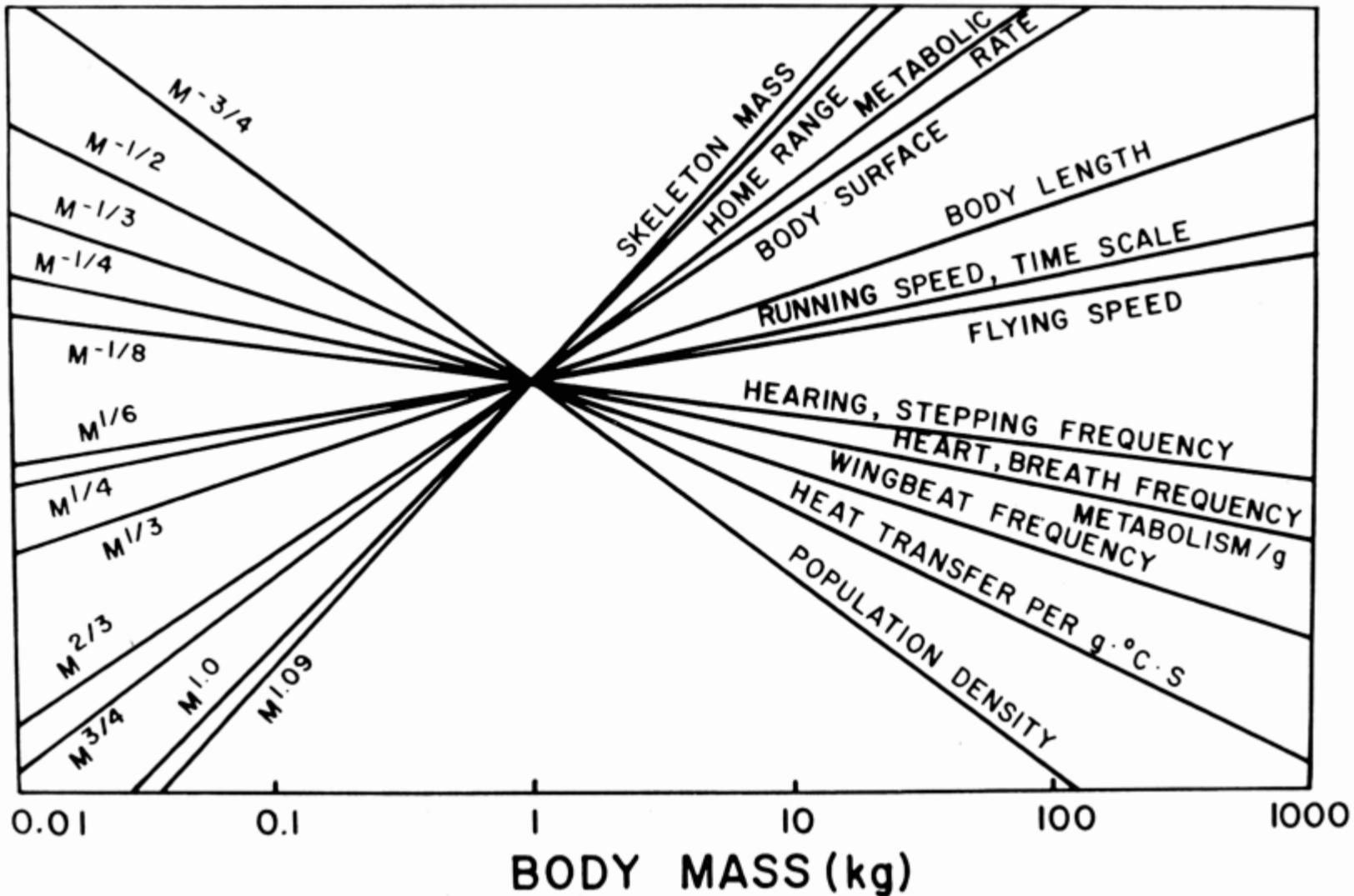
All morphological and physiological traits scale somehow with body mass.

*"Scaling is interesting because, aside from natural selection, it is one of the few laws we really have in biology."* John Gittleman





# Scaling: fundamental (conceptual) relevance of body mass



(Calder 1983)



## Organ allometry

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

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

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

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

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

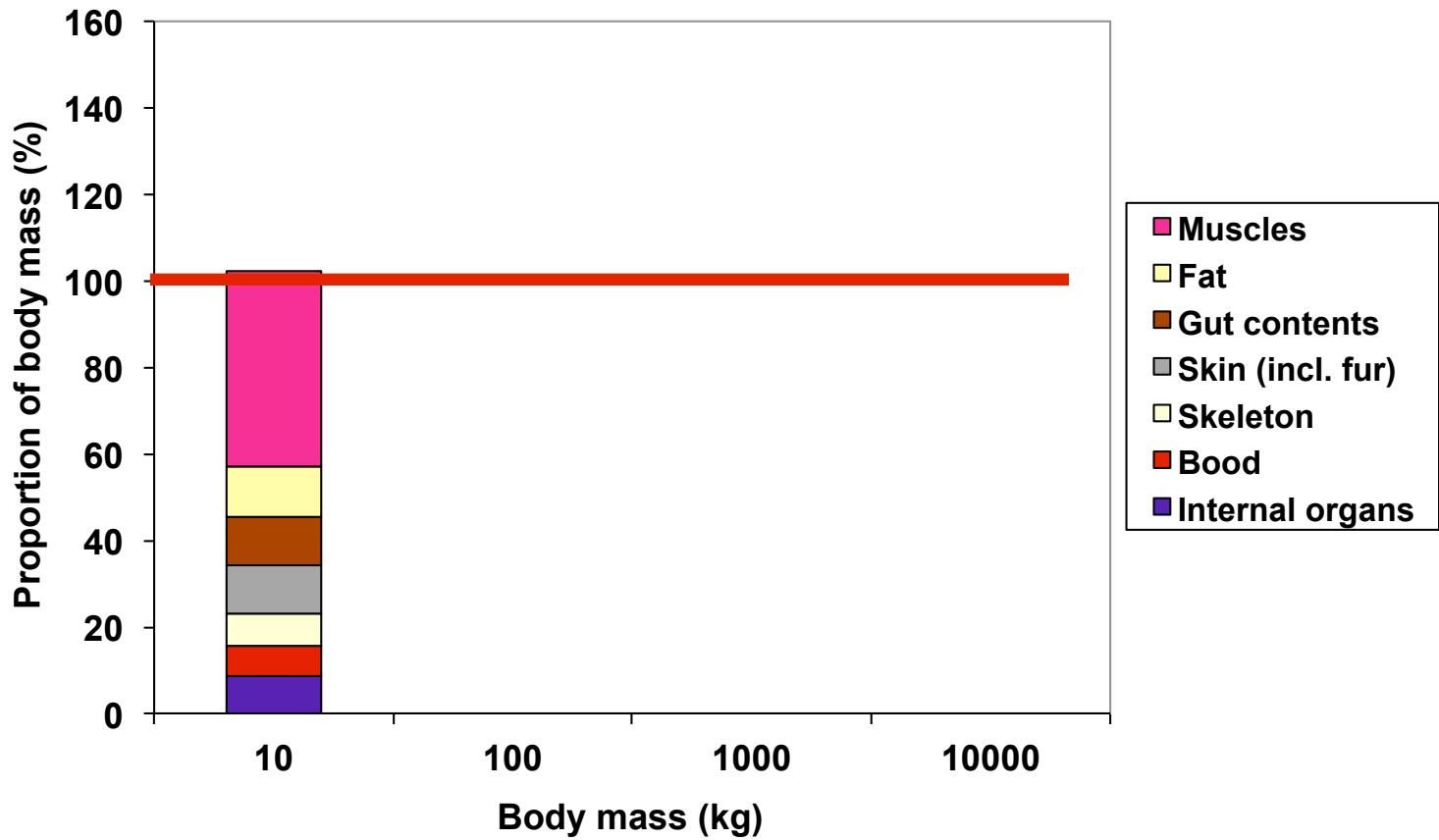
$$\textit{Integument (kg)} = \mathbf{0.134} \textit{BW}^{0.92}$$

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

(Parra 1978, Calder 1983)



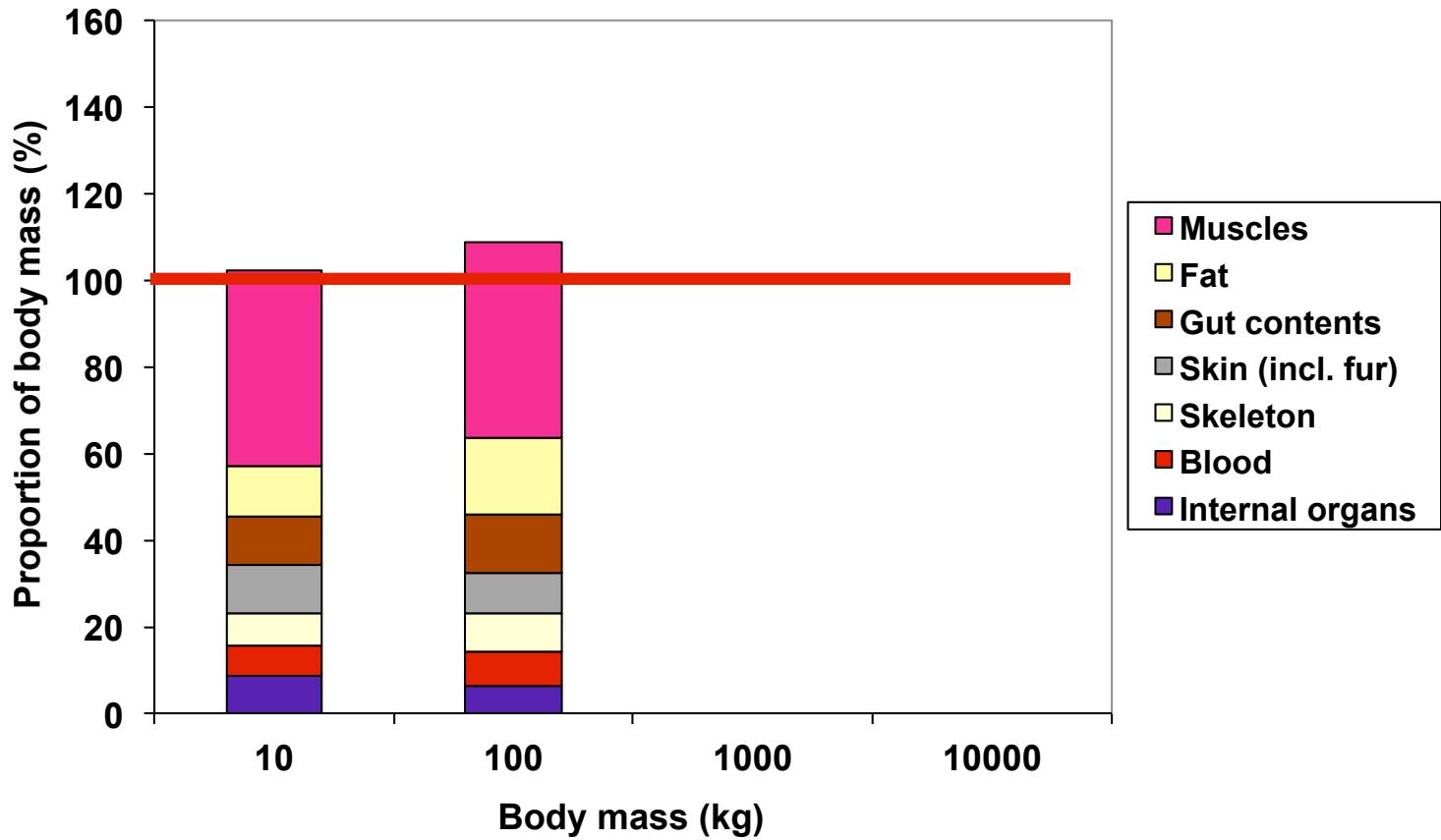
## Allometry of body composition



from Hummel and Clauss (2010)



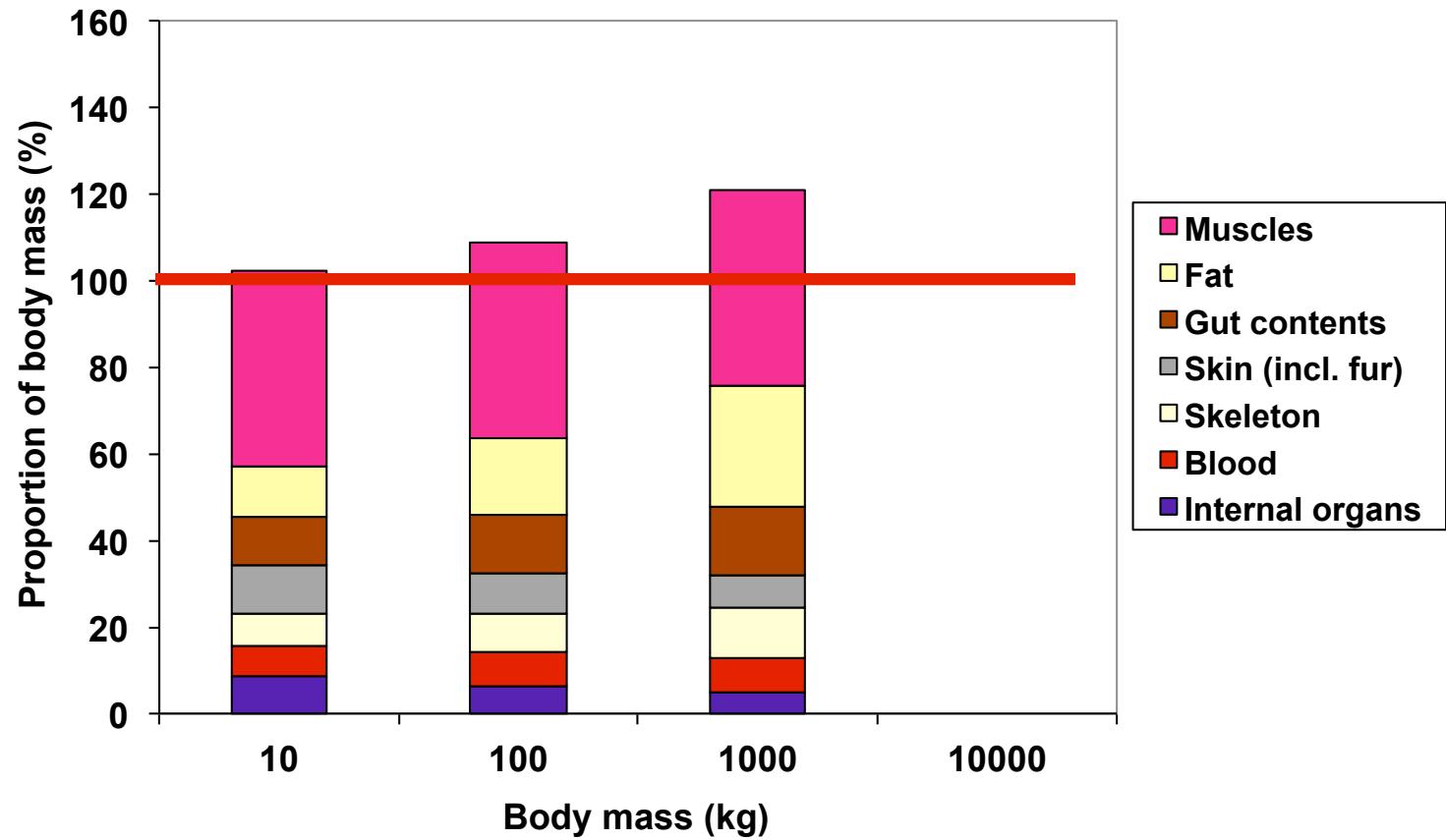
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from Hummel and Clauss (2010)



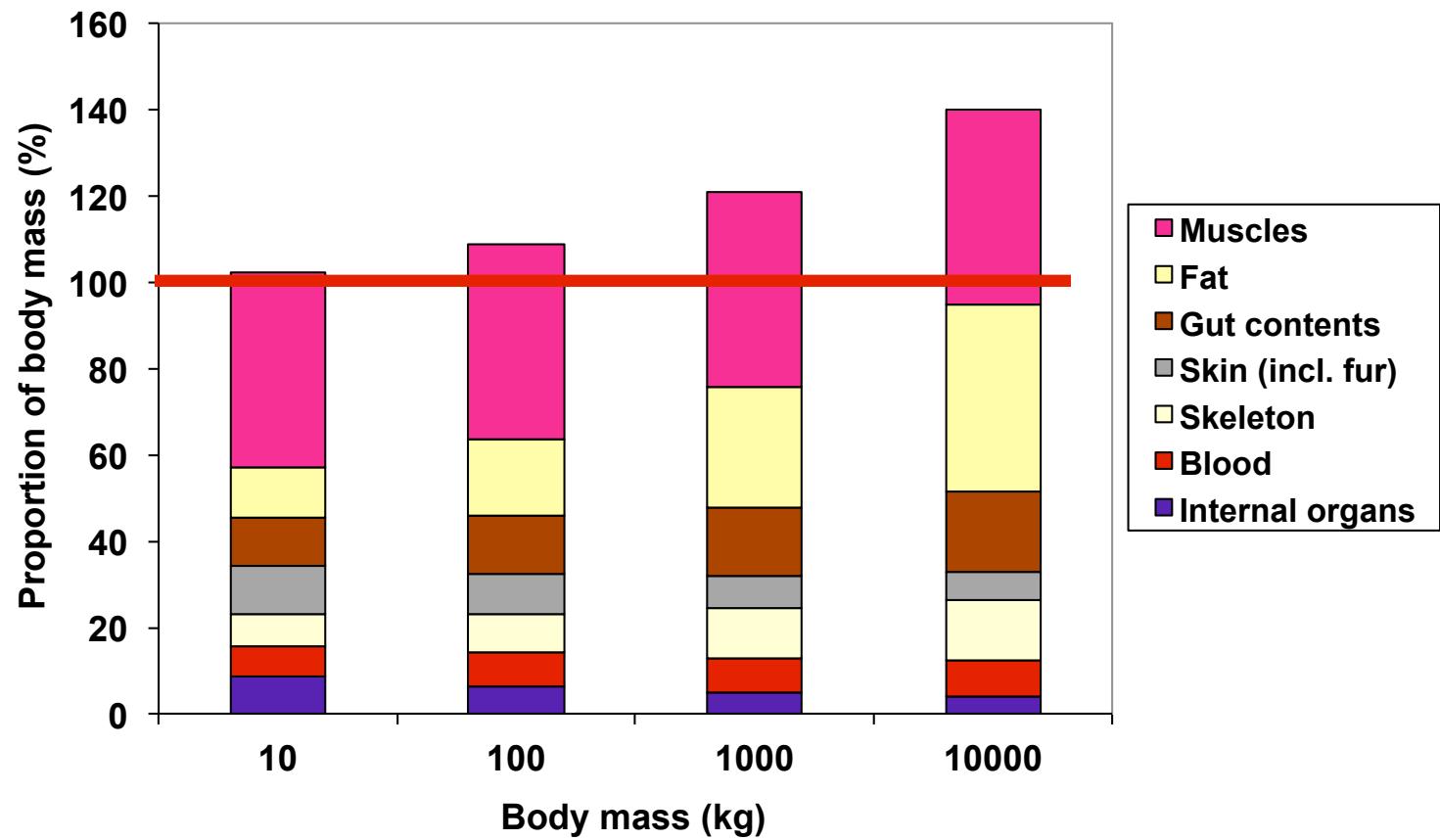
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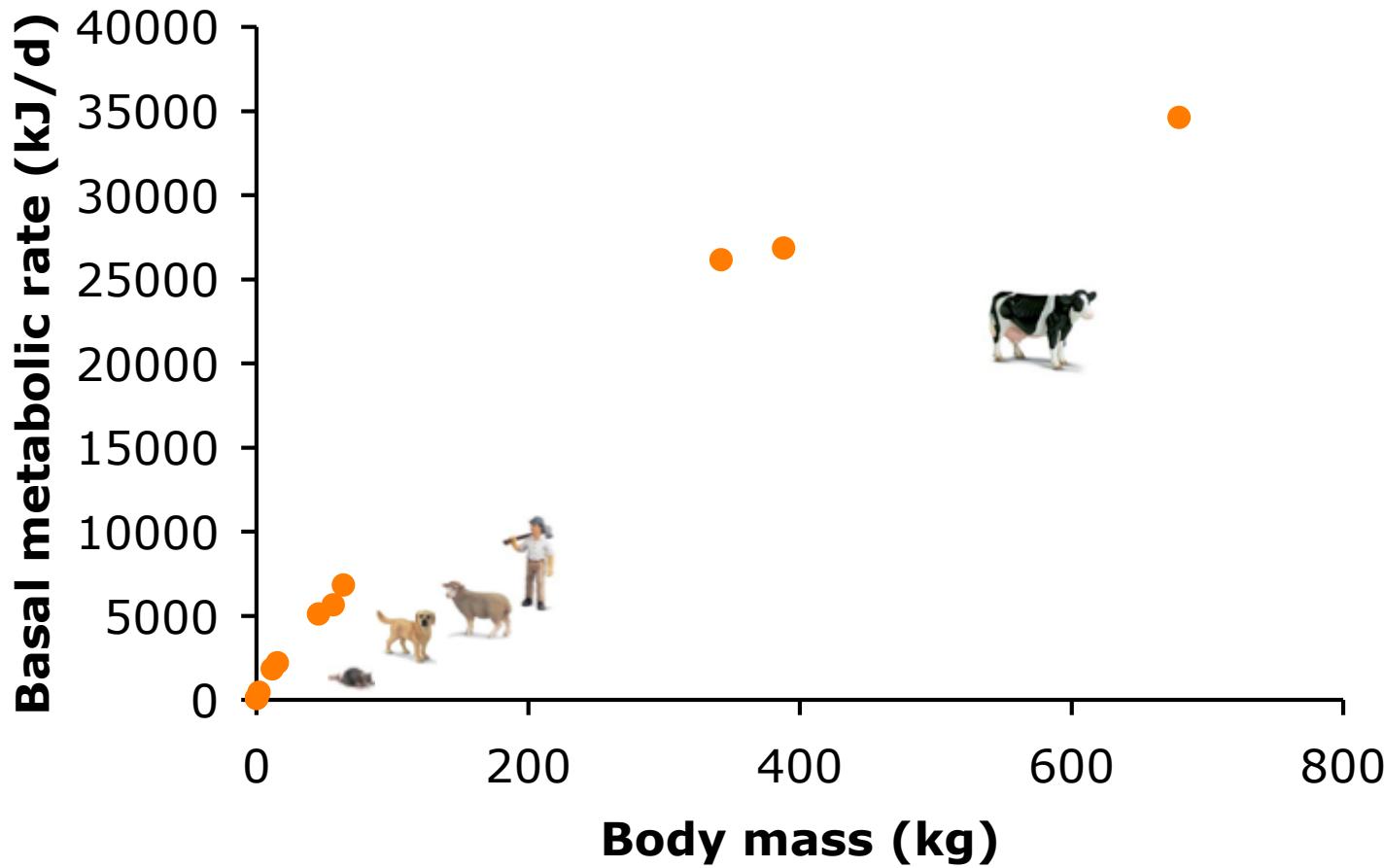
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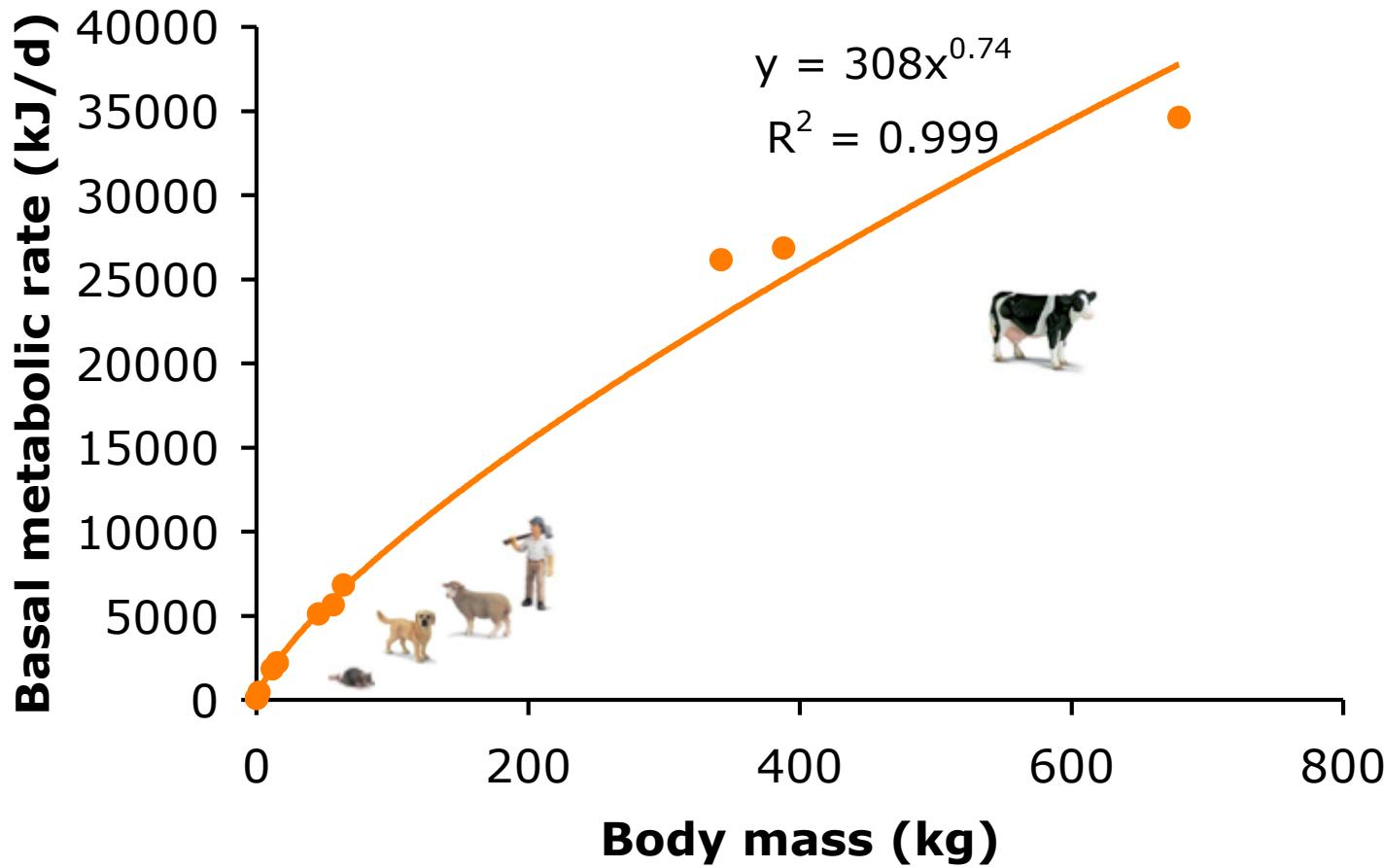
## Displaying allometries



from Kleiber (1932)



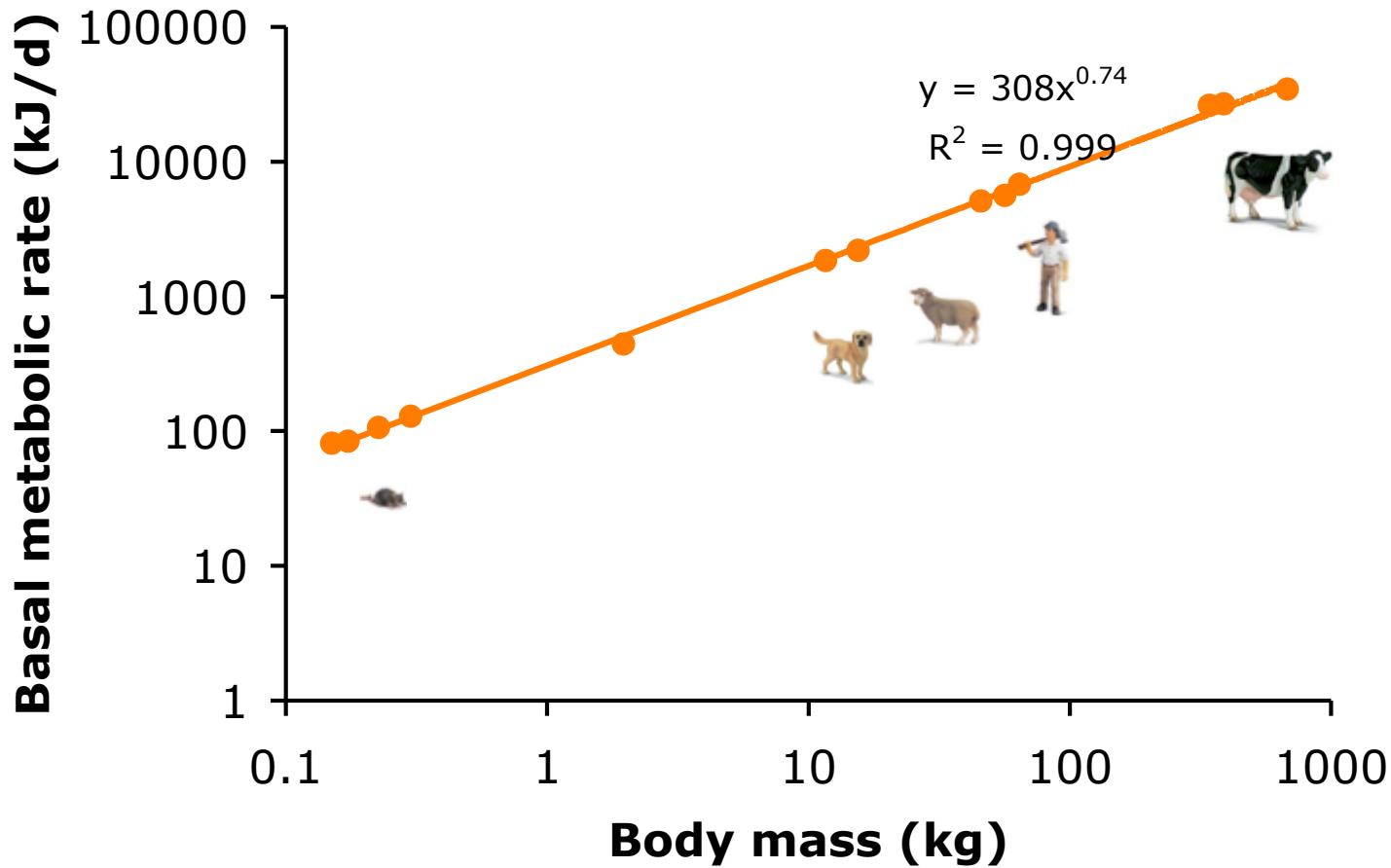
## Displaying allometries



from Kleiber (1932)



## Displaying allometries



from Kleiber (1932)



# General allometric considerations

Metabolic allometry - the influence of the exponent

Mammals  $BM^{0.75}$

Reptiles  $BM^?$



# General allometric considerations

Metabolic allometry - the influence of the exponent

Mammals  $BM^{0.75}$

Reptiles  $BM^?$

Reptiles  $BM^{0.89}$



from Nagy et al. (1999)



# General allometric considerations

Metabolic allometry - the influence of the exponent

Mammals  $BM^{0.75}$

Reptiles  $BM^?$

Reptiles  $BM^{0.89}$

Reptiles  $BM^{0.77}$



from Nagy et al. (1999)

from Bennett & Dawson (1976)



# General allometric considerations

Metabolic allometry - the influence of the exponent

Mammals:  $a \text{ BM}^{0.75}$

Reptiles:  $a/10 \text{ BM}^?$

Reptiles  $\text{BM}^{0.89}$

Reptiles  $\text{BM}^{0.77}$



{

{

from Nagy et al. (1999)

from Bennett & Dawson (1976)



# General allometric considerations

Metabolic allometry - the influence of the exponent

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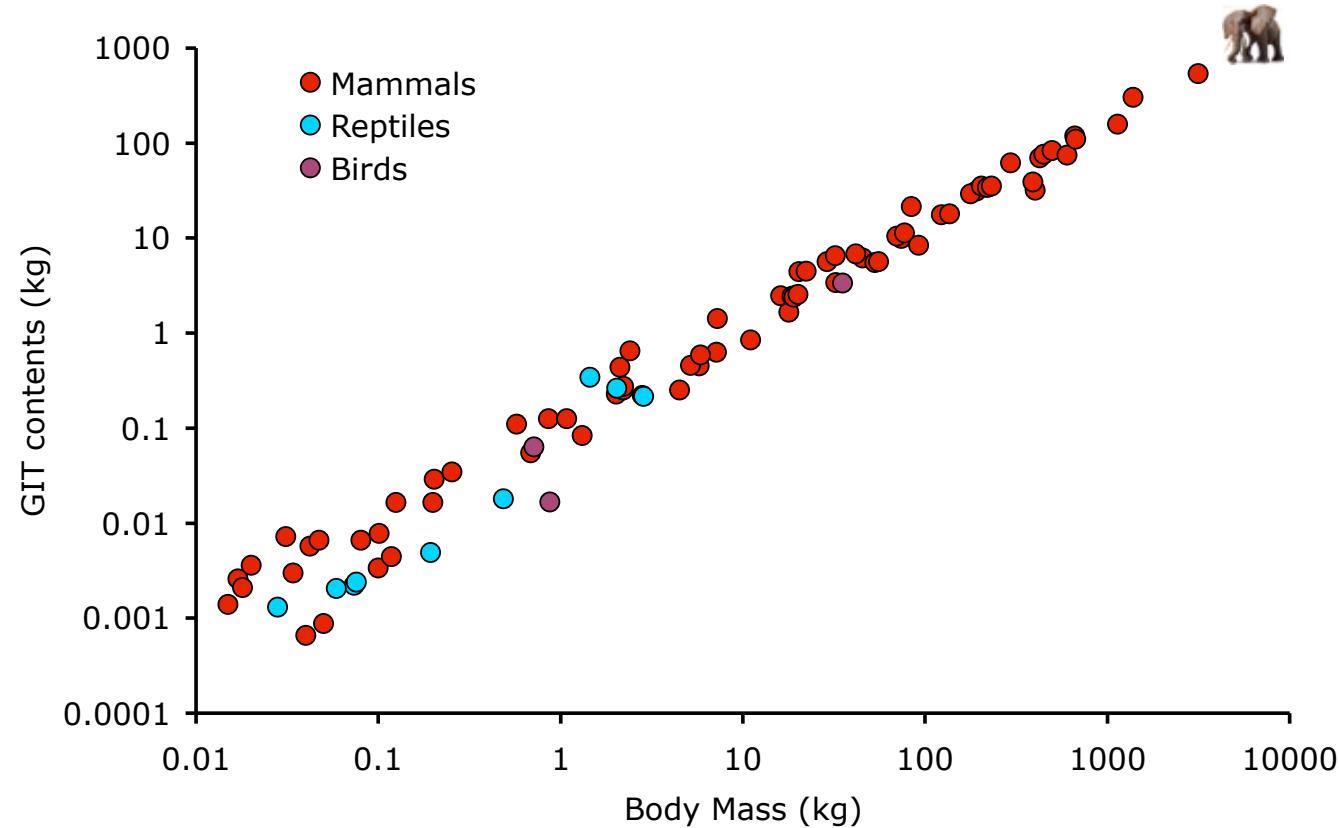
from Nagy et al. (1999)

from Bennett & Dawson (1976)



# General allometric considerations

## Gut capacity

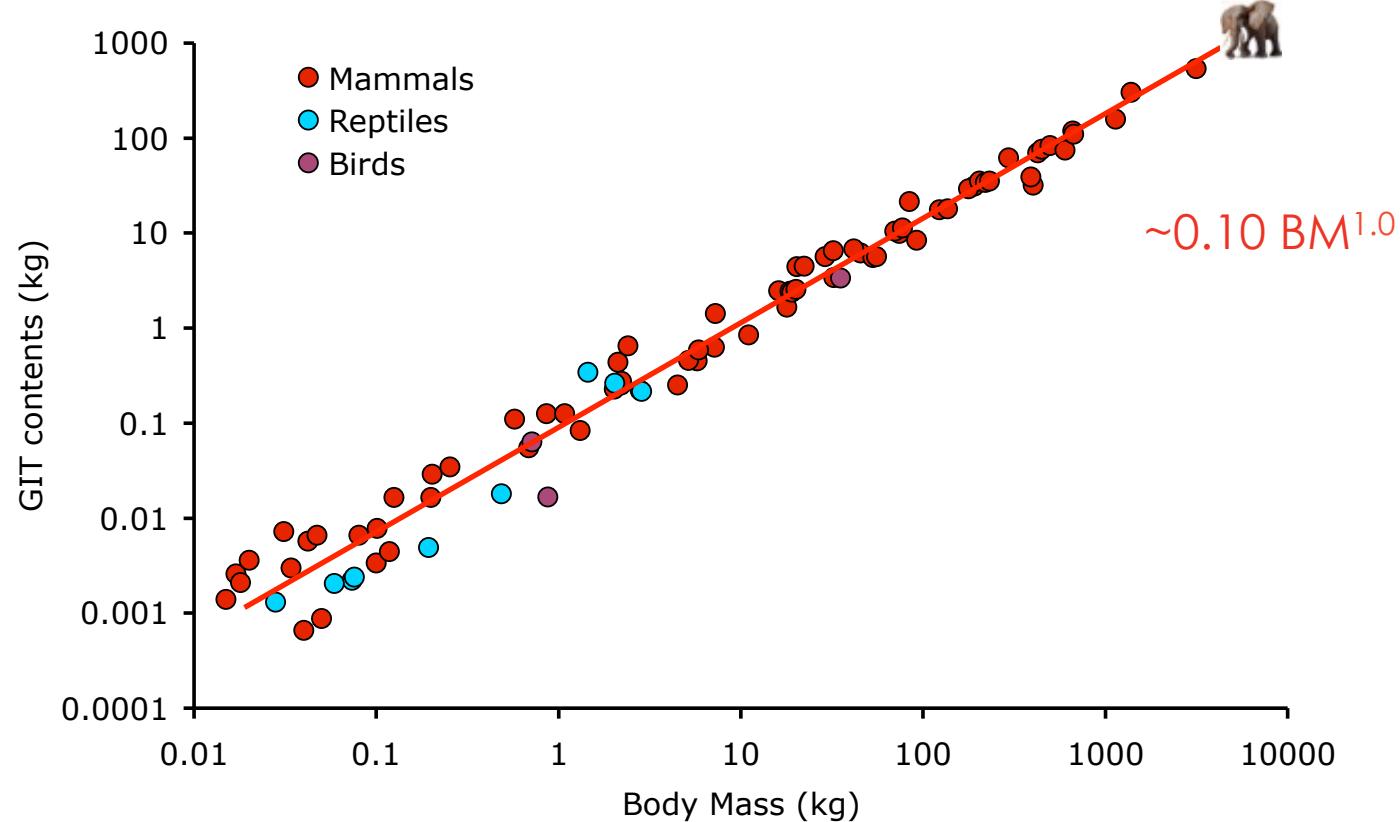


from Franz et al. (2009)



# General allometric considerations

## Gut capacity

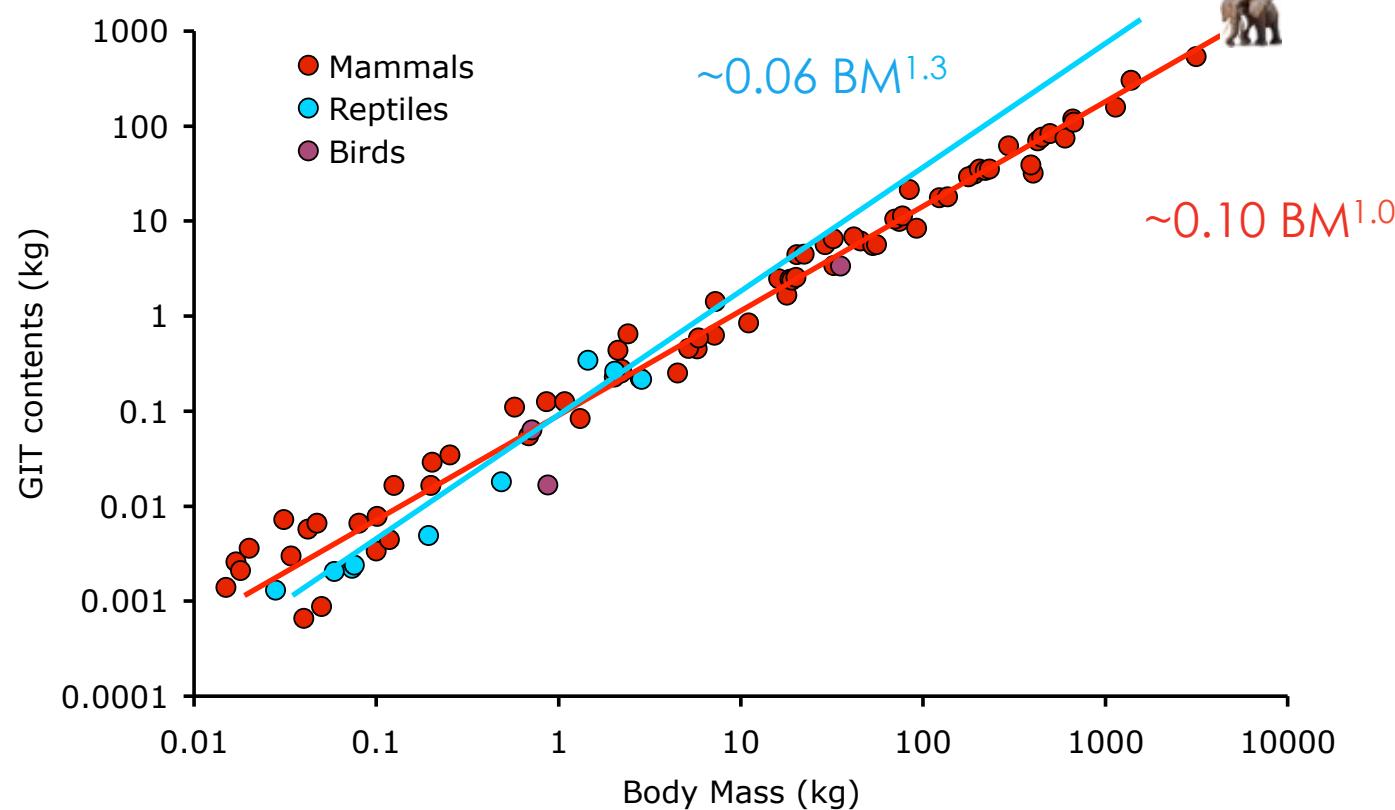


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# General allometric considerations

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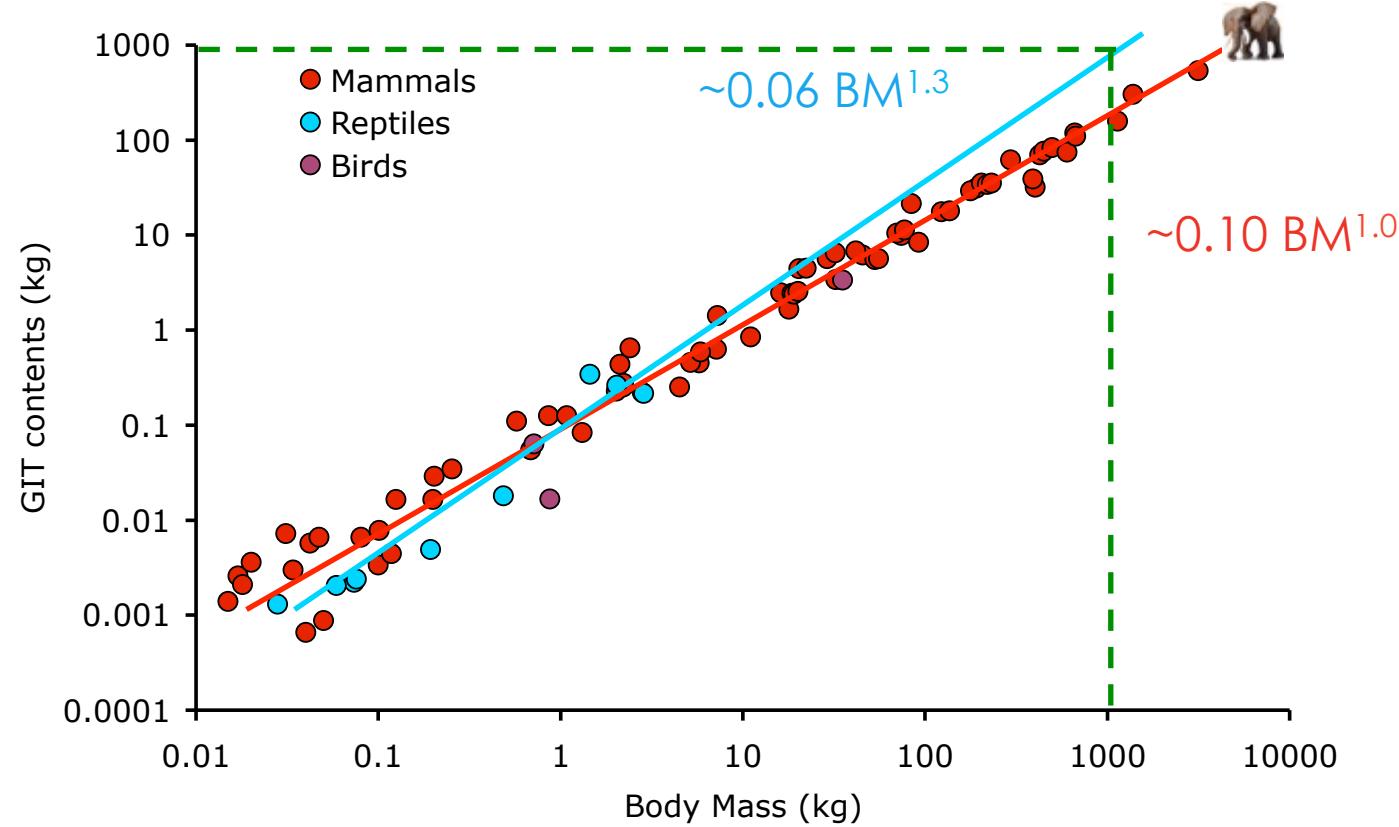


from Franz et al. (2009)



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## Gut capacity

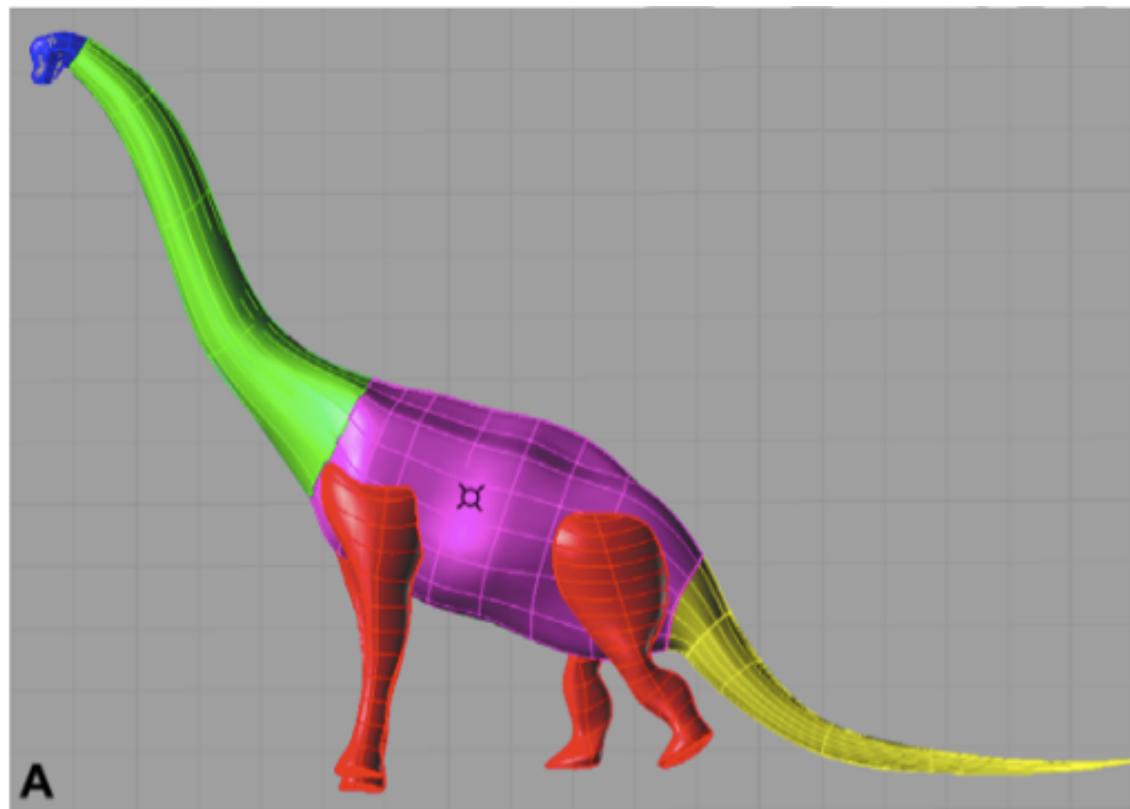


from Franz et al. (2009)



## Are there functional constraints?

- Comparing (extrapolated) organ size with the capacity of the (reconstructed) coelomic cavity



from Gunga et al. (2008)



# Organ allometry

38 ton brachiosaurus - coelomic cavity ~32 m<sup>2</sup>

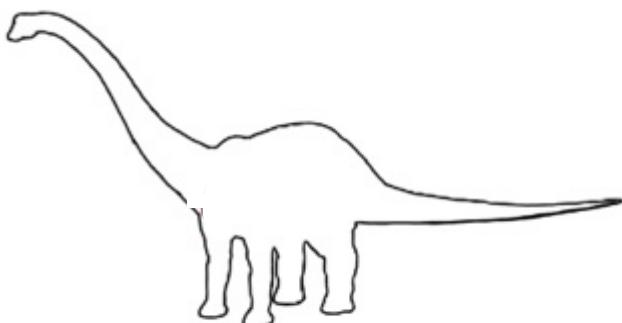
from Franz et al. (2009)



# Organ allometry

38 ton brachiosaurus - coelomic cavity ~32 m<sup>2</sup>

	Reptile $m^3$	Mammal $m^3$
Heart		
Kidney		
Liver		
GIT tissue		
Gut content		
Total		

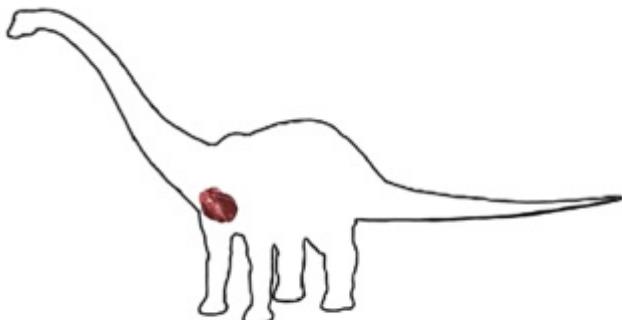
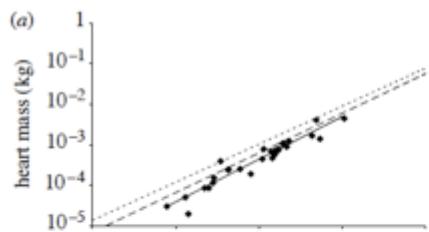


from Franz et al. (2009)



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38 ton brachiosaurus - coelomic cavity ~32 m<sup>2</sup>



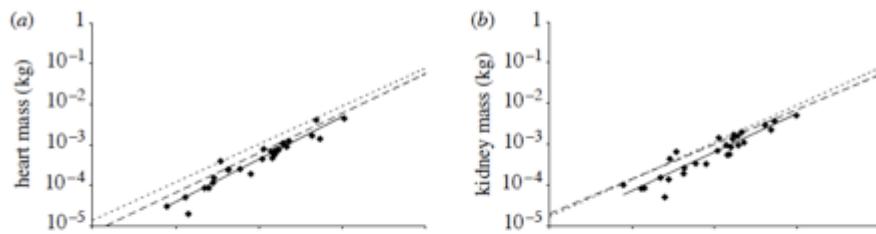
	Reptile $m^3$	Mammal $m^3$
Heart	0.238	0.236
Kidney		
Liver		
GIT tissue		
Gut content		
Total		

from Franz et al. (2009)



# Organ allometry

38 ton brachiosaurus - coelomic cavity ~32 m<sup>2</sup>



	Reptile m <sup>3</sup>	Mammal m <sup>3</sup>
Heart	0.238	0.236
Kidney	0.285	0.069
Liver		
GIT tissue		
Gut content		
Total		

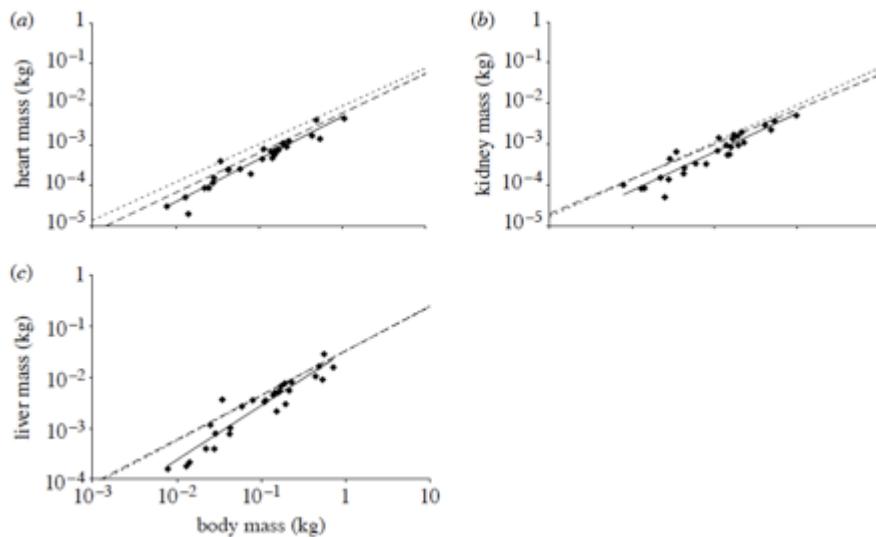


from Franz et al. (2009)



# Organ allometry

38 ton brachiosaurus - coelomic cavity ~32 m<sup>2</sup>



	Reptile m <sup>3</sup>	Mammal m <sup>3</sup>
Heart	0.238	0.236
Kidney	0.285	0.069
Liver	1.568	0.398
GIT tissue		
Gut content		
Total		

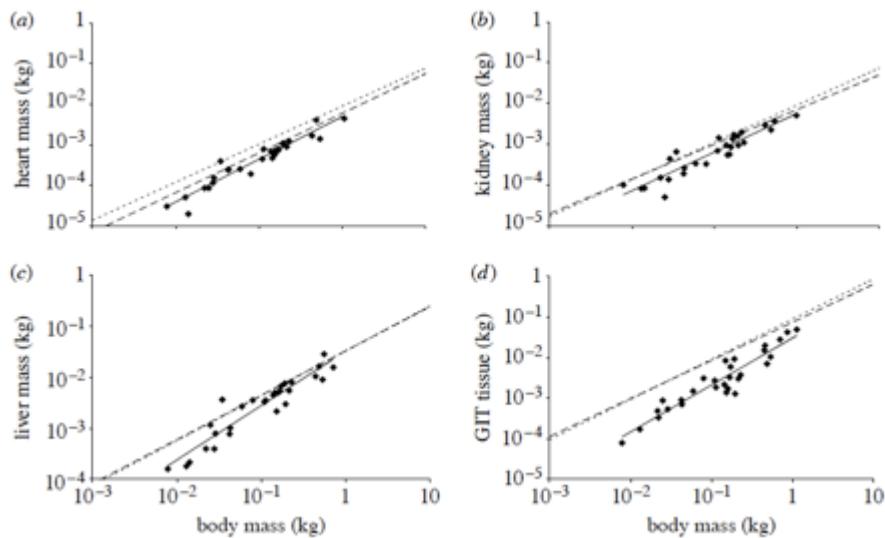


from Franz et al. (2009)

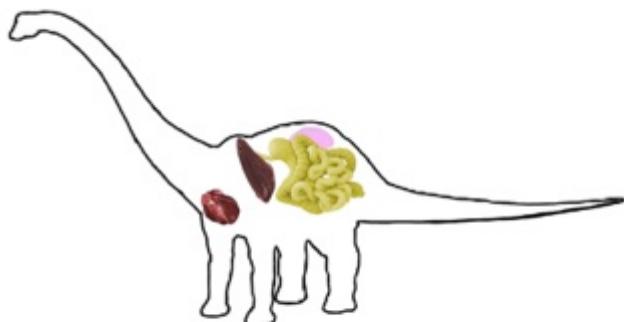


# Organ allometry

38 ton brachiosaurus - coelomic cavity ~32 m<sup>2</sup>



	Reptile m <sup>3</sup>	Mammal m <sup>3</sup>
Heart	0.238	0.236
Kidney	0.285	0.069
Liver	1.568	0.398
GIT tissue	1.473	3.109
Gut content		
Total		

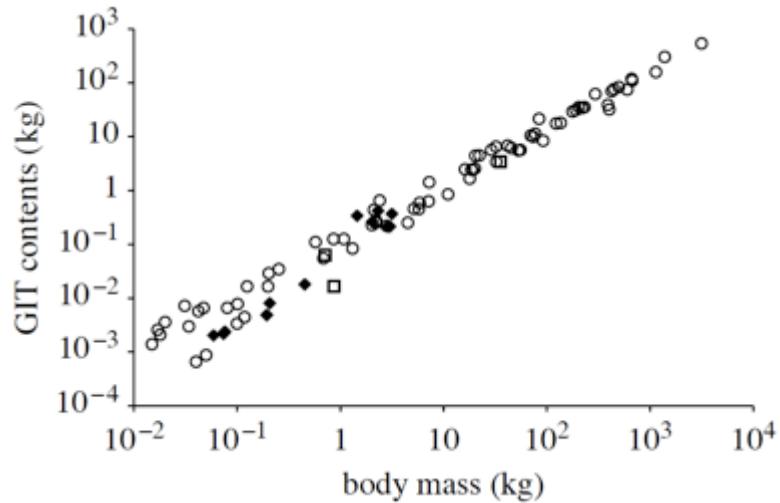


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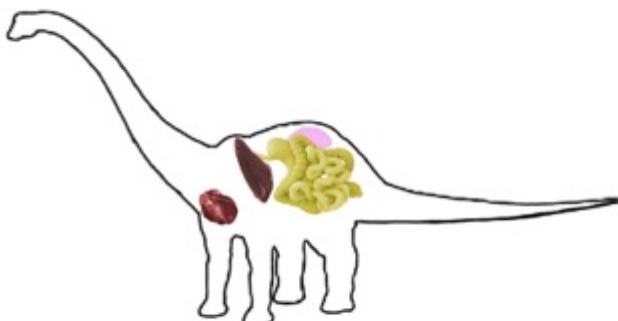


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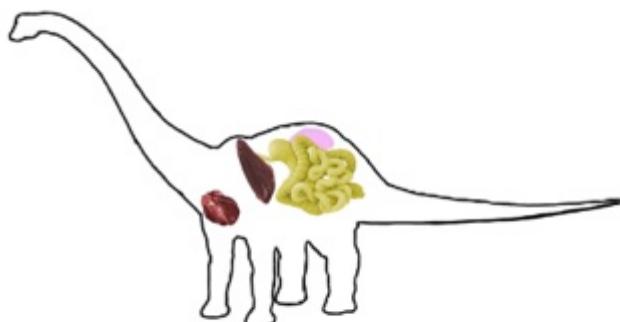
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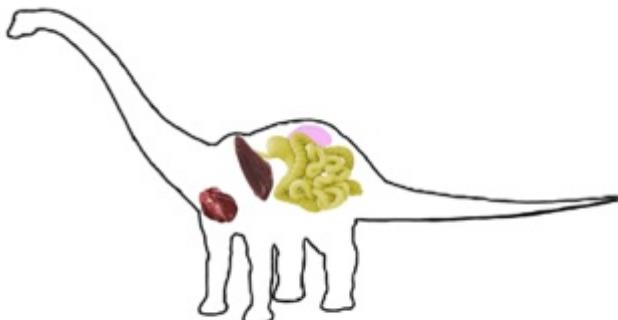


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Gut content	5.083	7.429
Total	<b>8.645</b>	<b>11.240</b>
+		
proportion of the blood volume, lung skeleton and muscle mass	8.921	10.040
	<b>17.566</b>	<b>21.280</b>

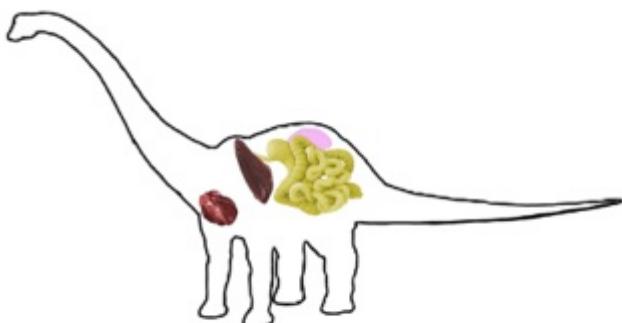
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	8.921	10.040
	<b>17.566</b>	<b>21.280</b>



Organs (excl. mesenteries and reproduction) 16-21 m<sup>2</sup>

⇒ Ample leeway for any 'larger organ size' necessary?

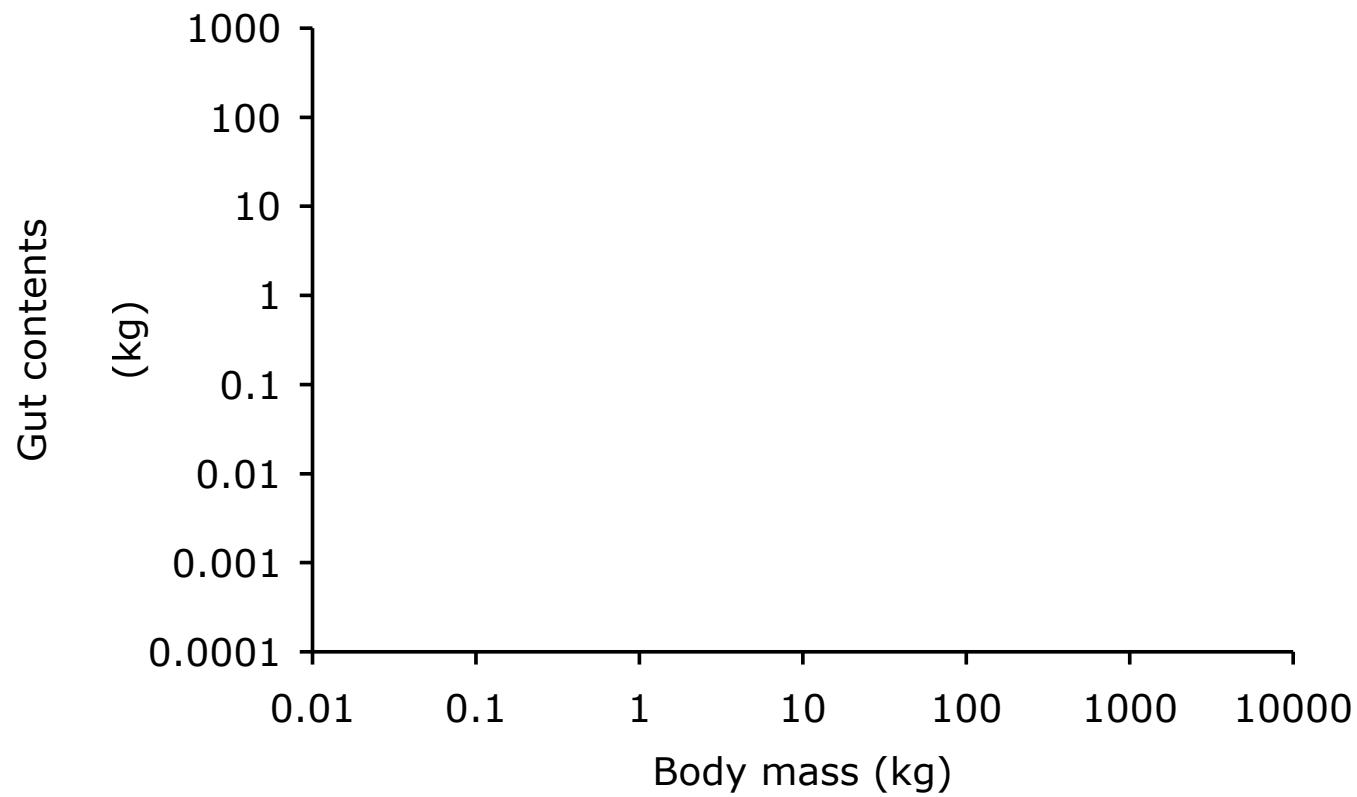
from Franz et al. (2009)



The ‘Jarman-Bell-principle’:  
Larger herbivores have a digestive  
advantage  
because of allometric principles



# General allometric considerations

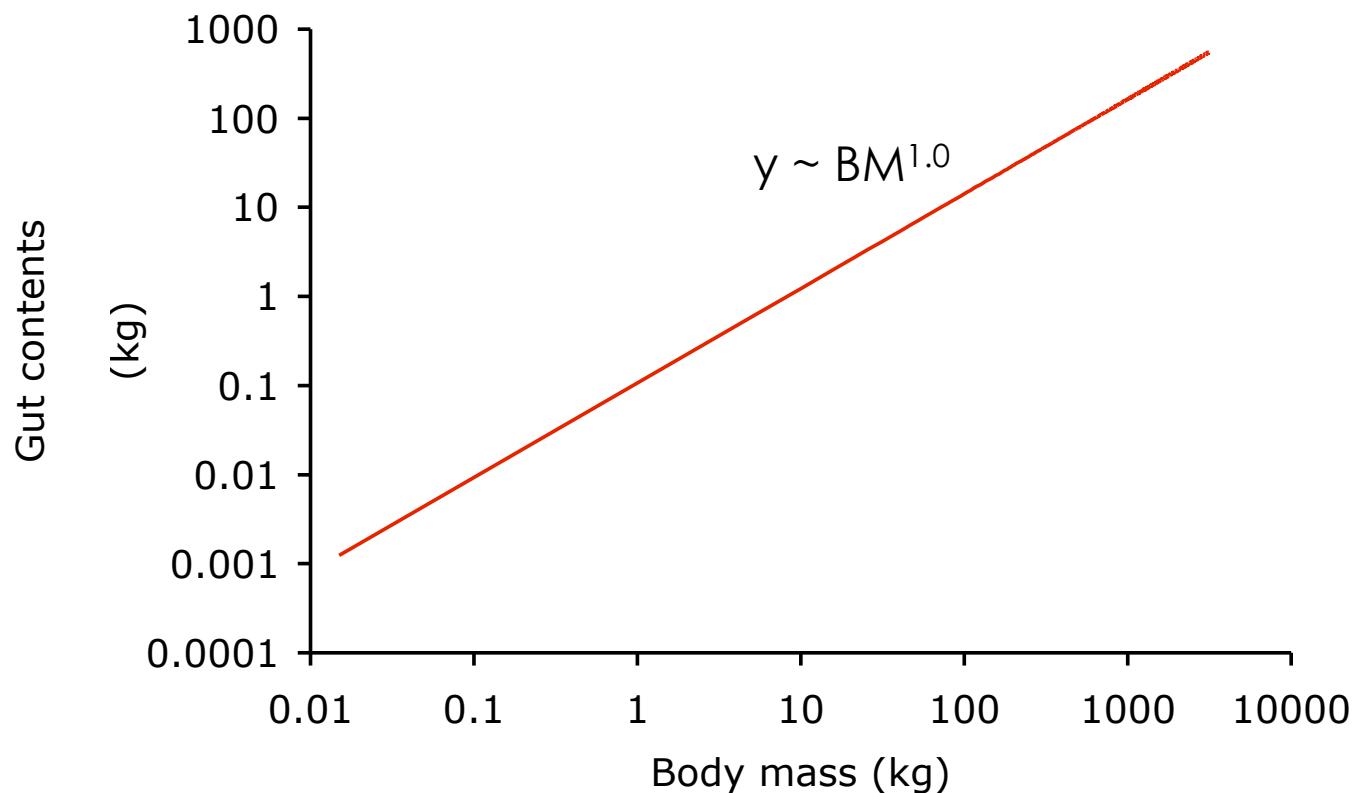


from Parra (1978), Demment & Van Soest (1985), Illius & Gordon (1992); McNab (2002)



## General allometric considerations

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

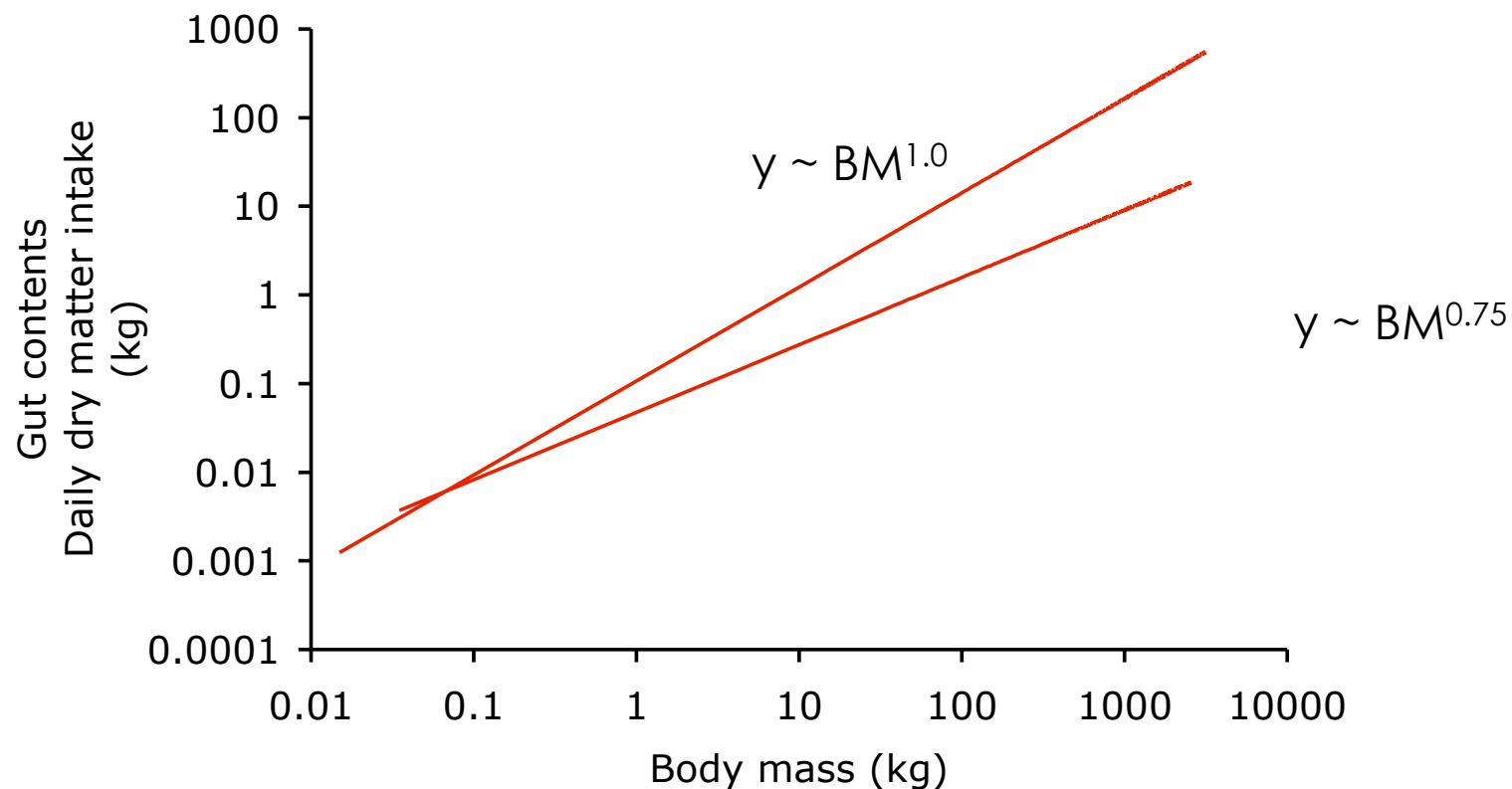


from Parra (1978), Demment & Van Soest (1985), Illius & Gordon (1992); McNab (2002)



# General allometric considerations

Food intake (relating to energy requirements) scales to metabolic body mass (body mass<sup>0.75</sup>)

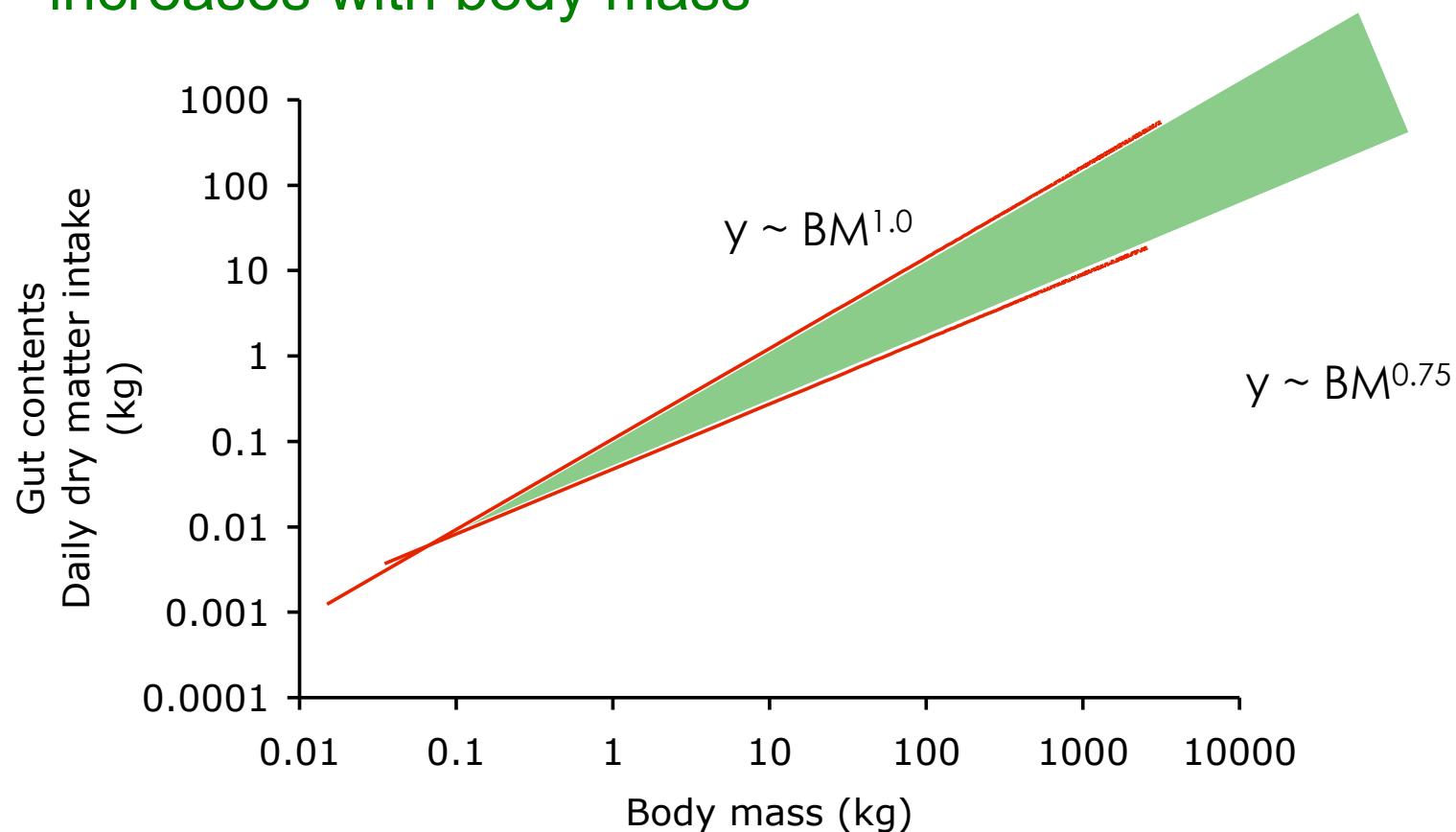


from Parra (1978), Demment & Van Soest (1985), Illius & Gordon (1992); McNab (2002)



# General allometric considerations

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



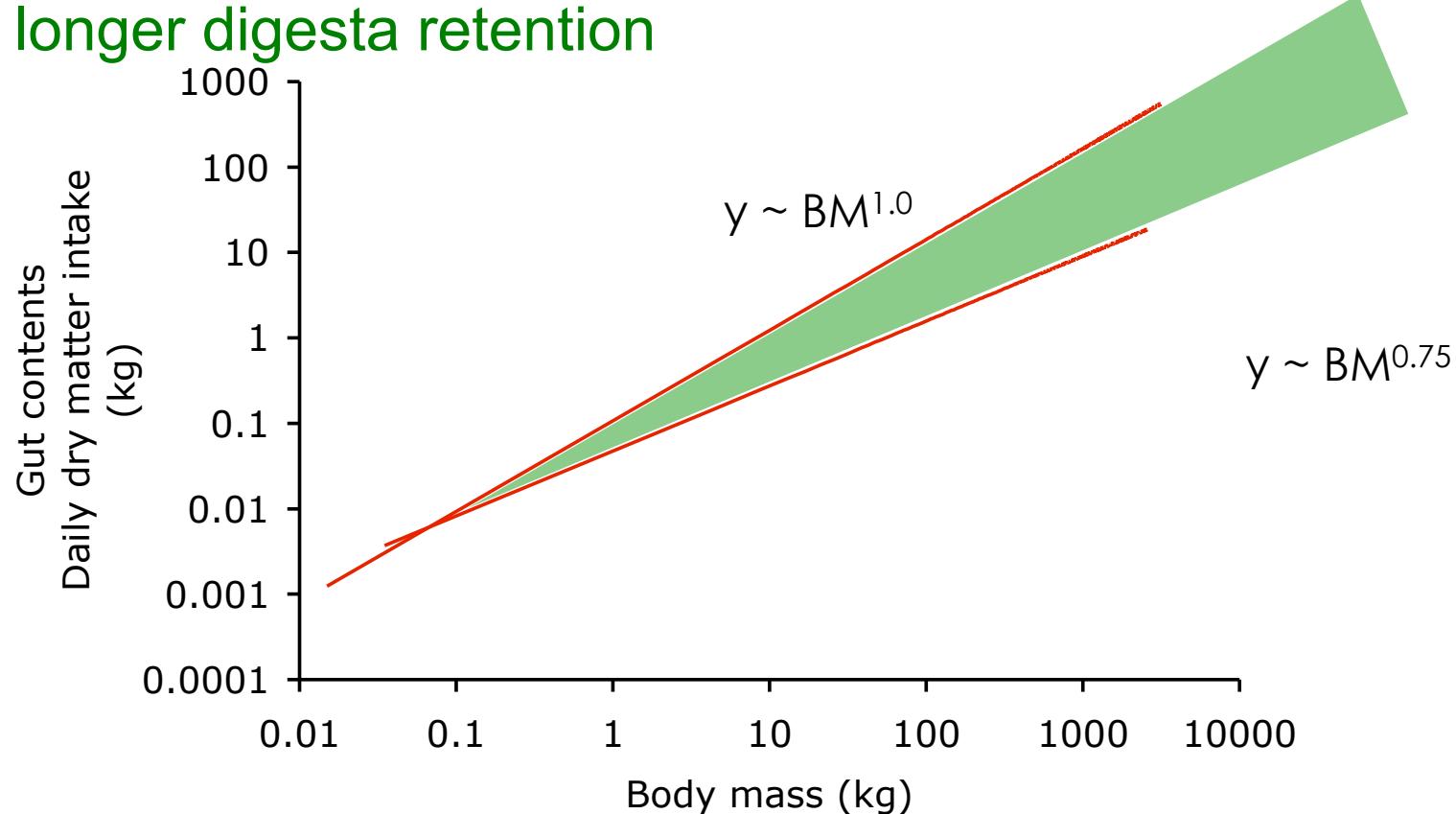
from Parra (1978), Demment & Van Soest (1985), Illius & Gordon (1992); McNab (2002)



## General allometric considerations

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

=> longer digesta retention

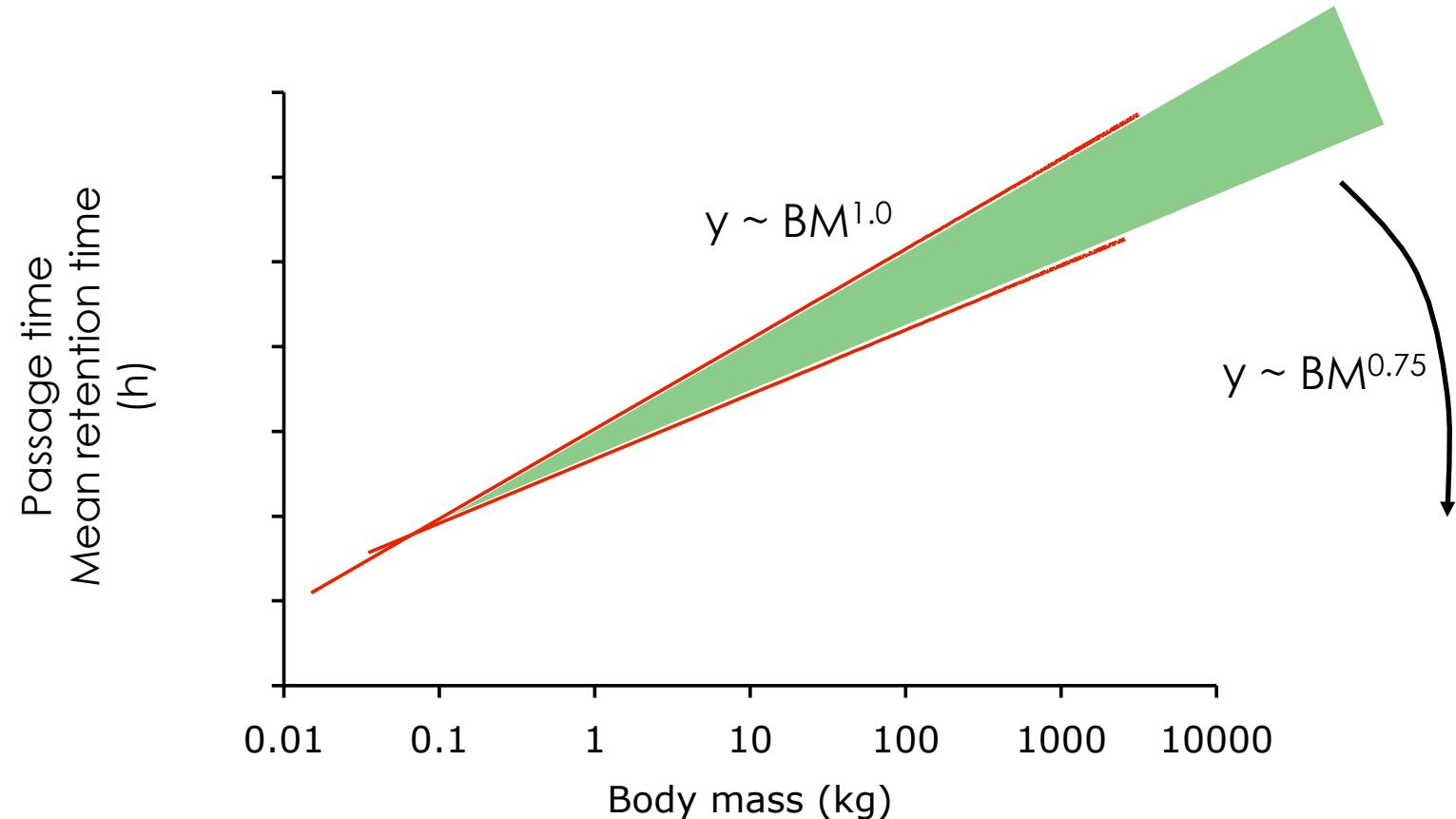


from Parra (1978), Demment & Van Soest (1985), Illius & Gordon (1992); McNab (2002)



# General allometric considerations

Digesta retention scales to body mass ...

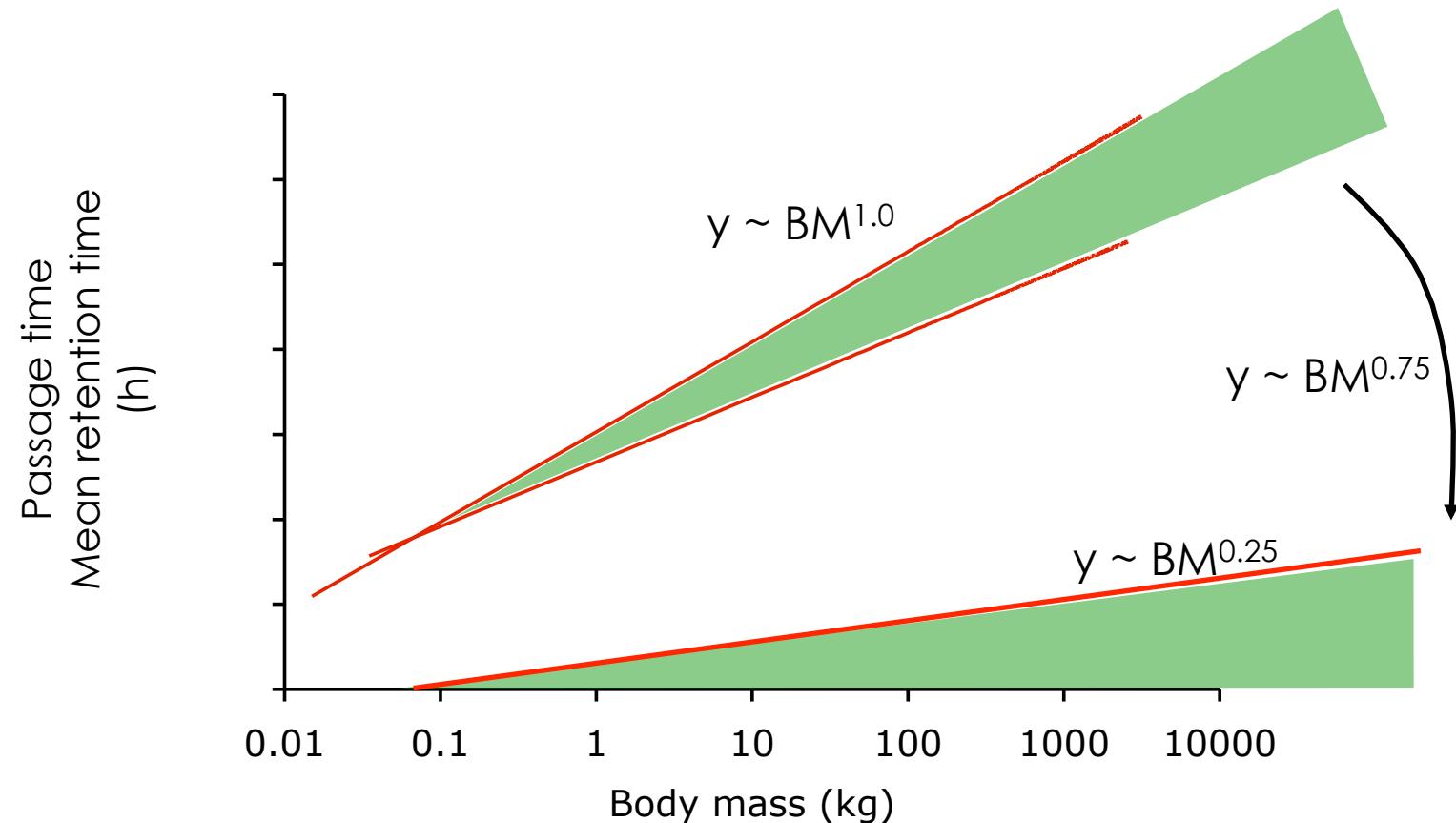


from Parra (1978), Demment & Van Soest (1985), Illius & Gordon (1992); McNab (2002) -



# General allometric considerations

... to the power of 0.25

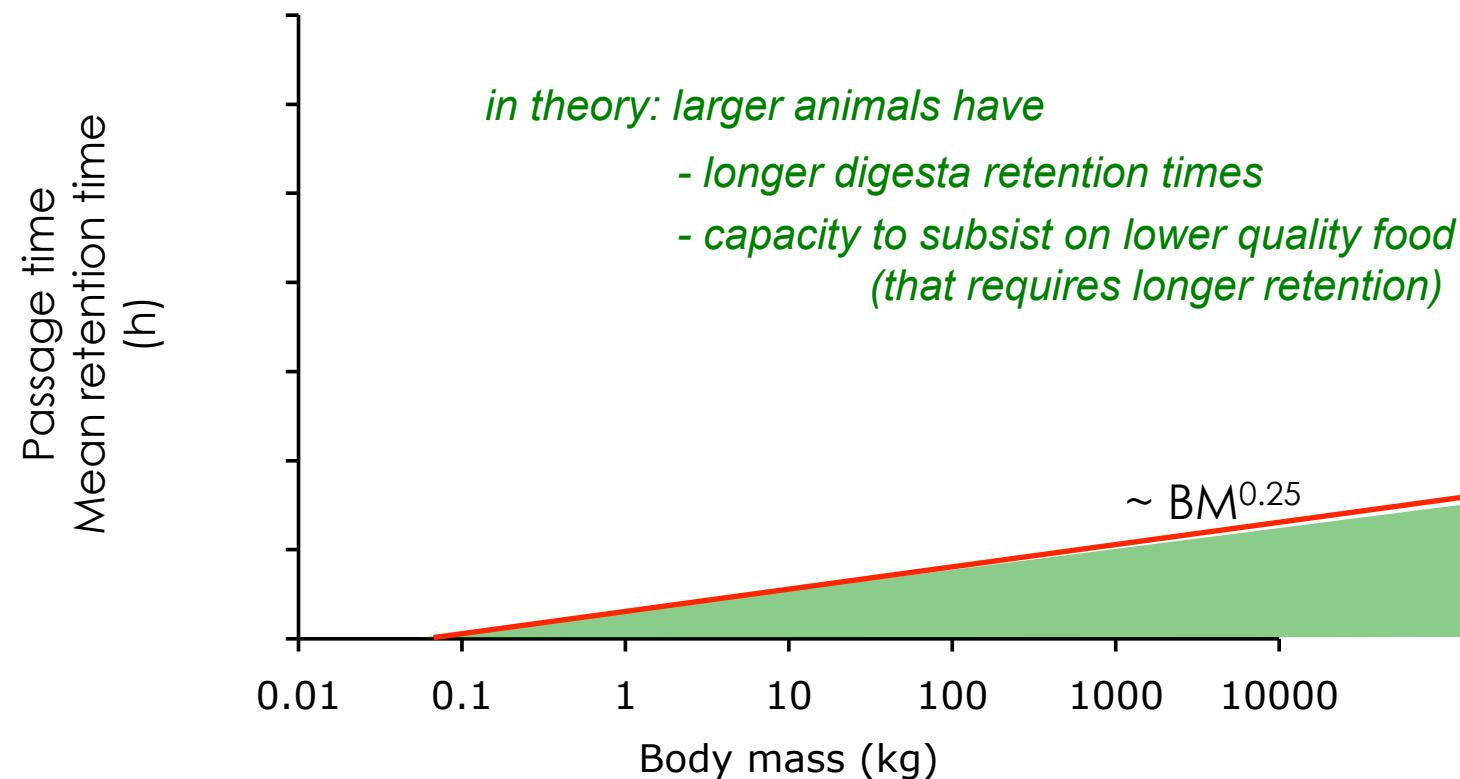


from Parra (1978), Demment & Van Soest (1985), Illius & Gordon (1992); McNab (2002)



# 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)





# our premise



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

MARCUS CLAUSS\* and JÜRGEN HUMMEL

*Mammal Rev.* 2005, Volume 35, No. 2, 174–187.



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- JBP disregards potentially important negative effects of increasing body mass
  - GIT geometry (longer diffusion ways)
  - Chewing efficiency (particle size reduction)
  - Methane losses



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A case of non-scaling in mammalian physiology? Body size, digestive capacity, food intake, and ingesta passage in mammalian herbivores<sup>☆</sup>

Marcus Clauss<sup>a,\*</sup>, Angela Schwarm<sup>b</sup>, Sylvia Ortmann<sup>b</sup>, W. Jürgen Streich<sup>b</sup>, Jürgen Hummel<sup>c</sup>  
Comparative Biochemistry and Physiology, Part A 148 (2007) 249–265



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- JBP-scaling apparently correct for gut capacity and food intake, but ...
- ... no empirical evidence for a consistent scaling of digesta retention with body mass



Assess principles (as much as possible) in parallel in different vertebrate herbivore groups  
- mammals, reptiles and birds.





# Workload: Allometries



Gut contents

Müller

Franz(\*)

Fritz(\*)

Food intake

Müller/Steuer\*

Franz(\*)

Fritz(\*)

Retention time

Müller/Steuer\*

Franz(\*)

Fritz(\*)

Particle size

Fritz\*

Fritz\*

Fritz\*

Digestibility

Müller/Steuer\*

Franz(\*)

Fritz(\*)

Methane production

Franz(\*)

Franz\*

?



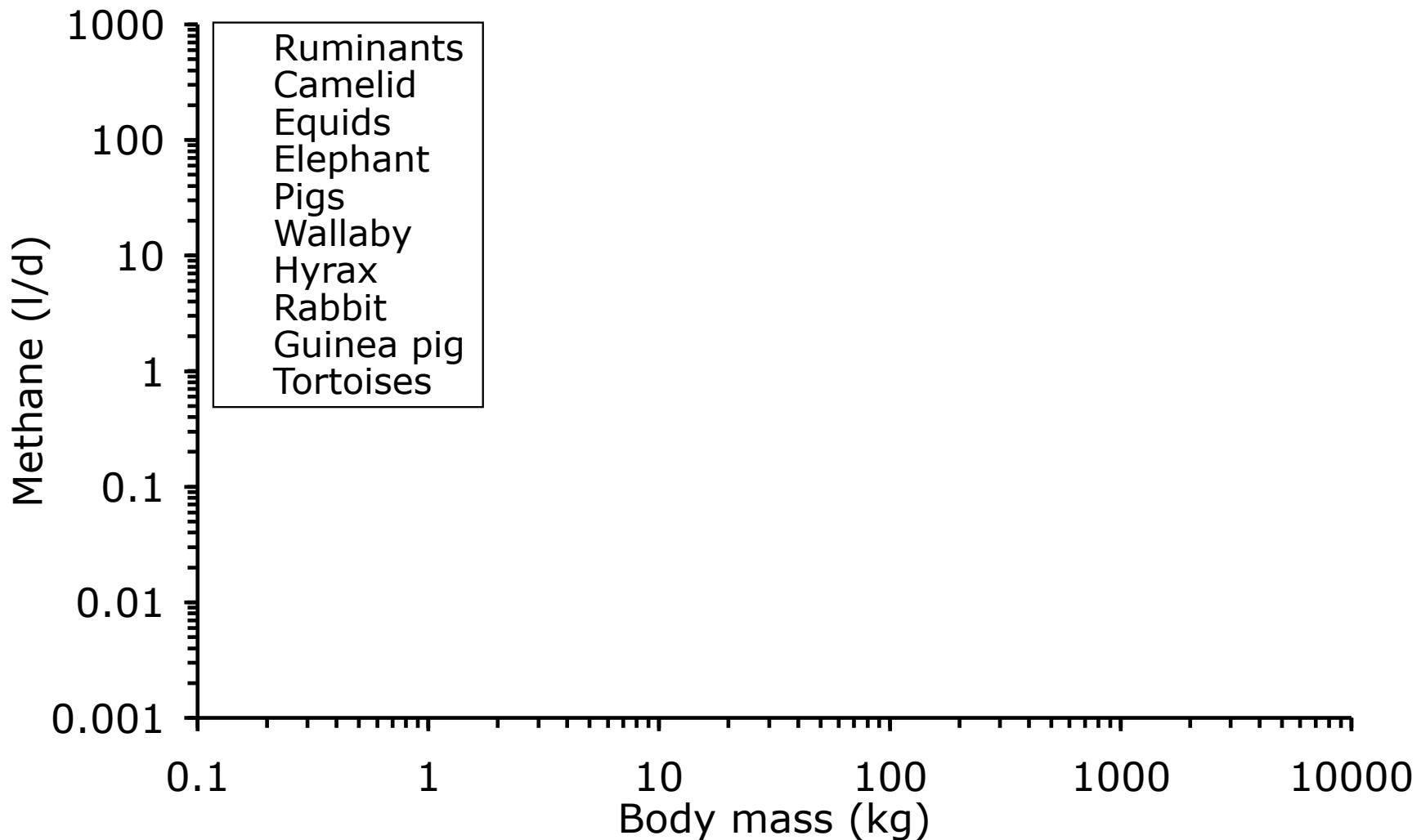
# Results



# Methane



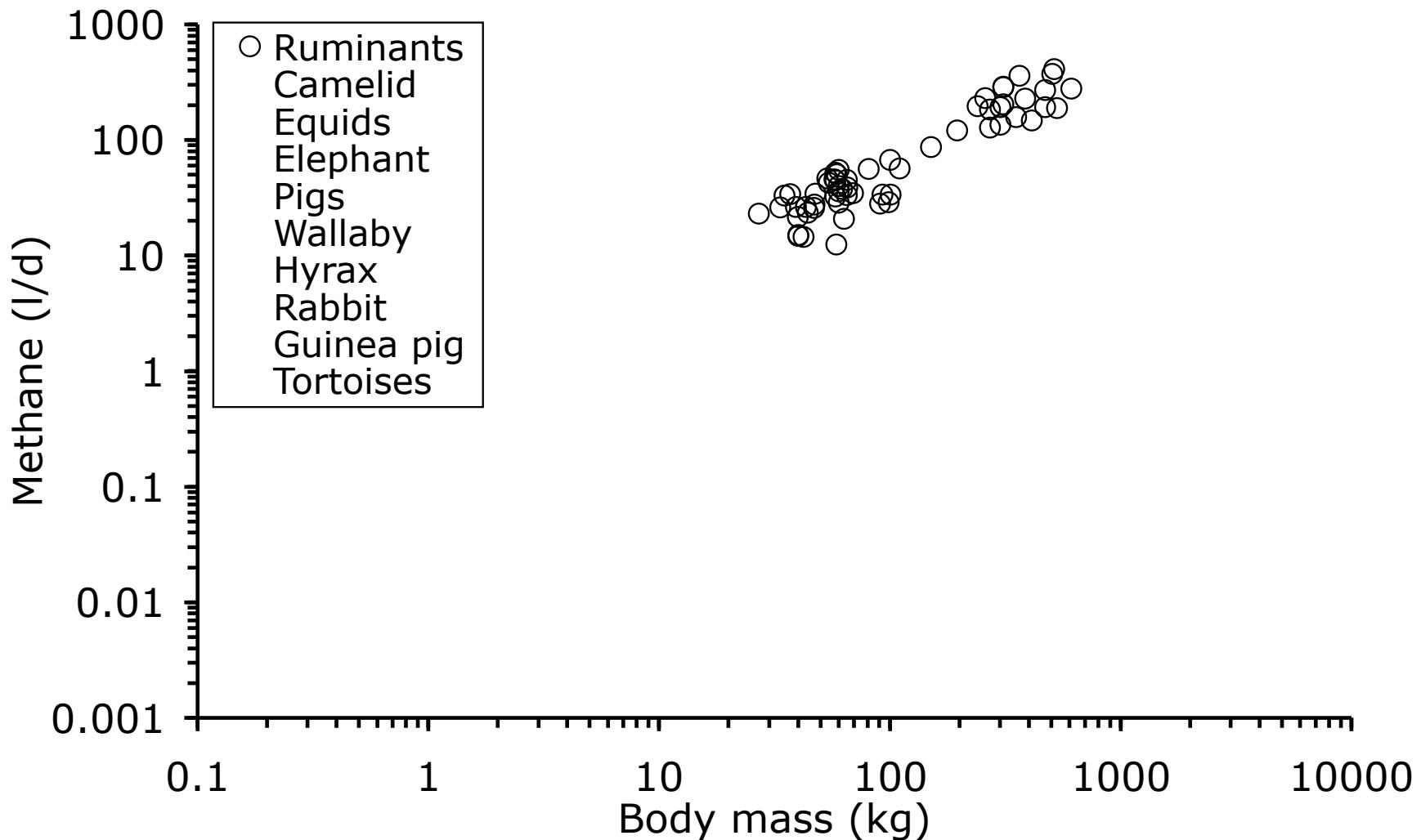
# Methane allometry in herbivores



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



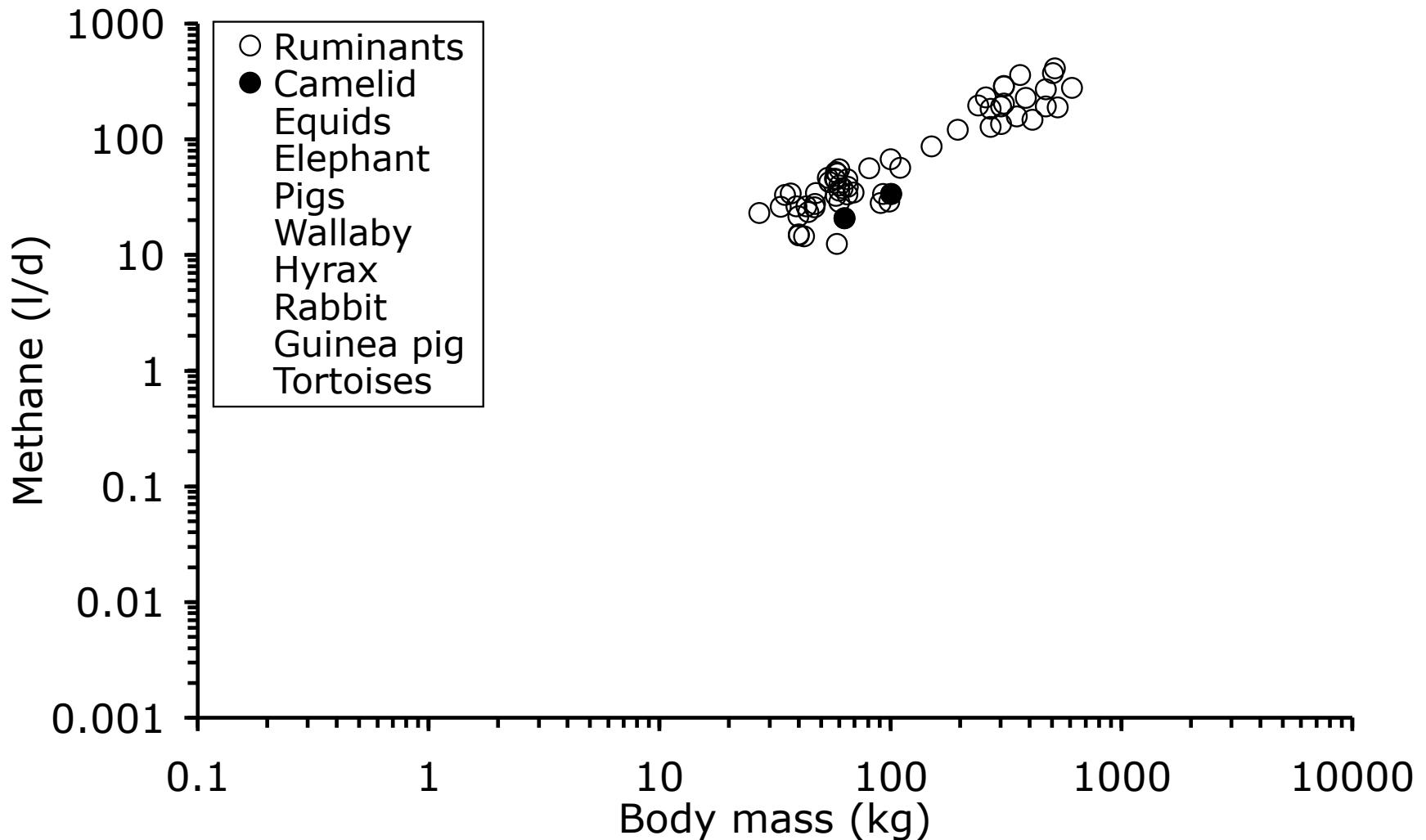
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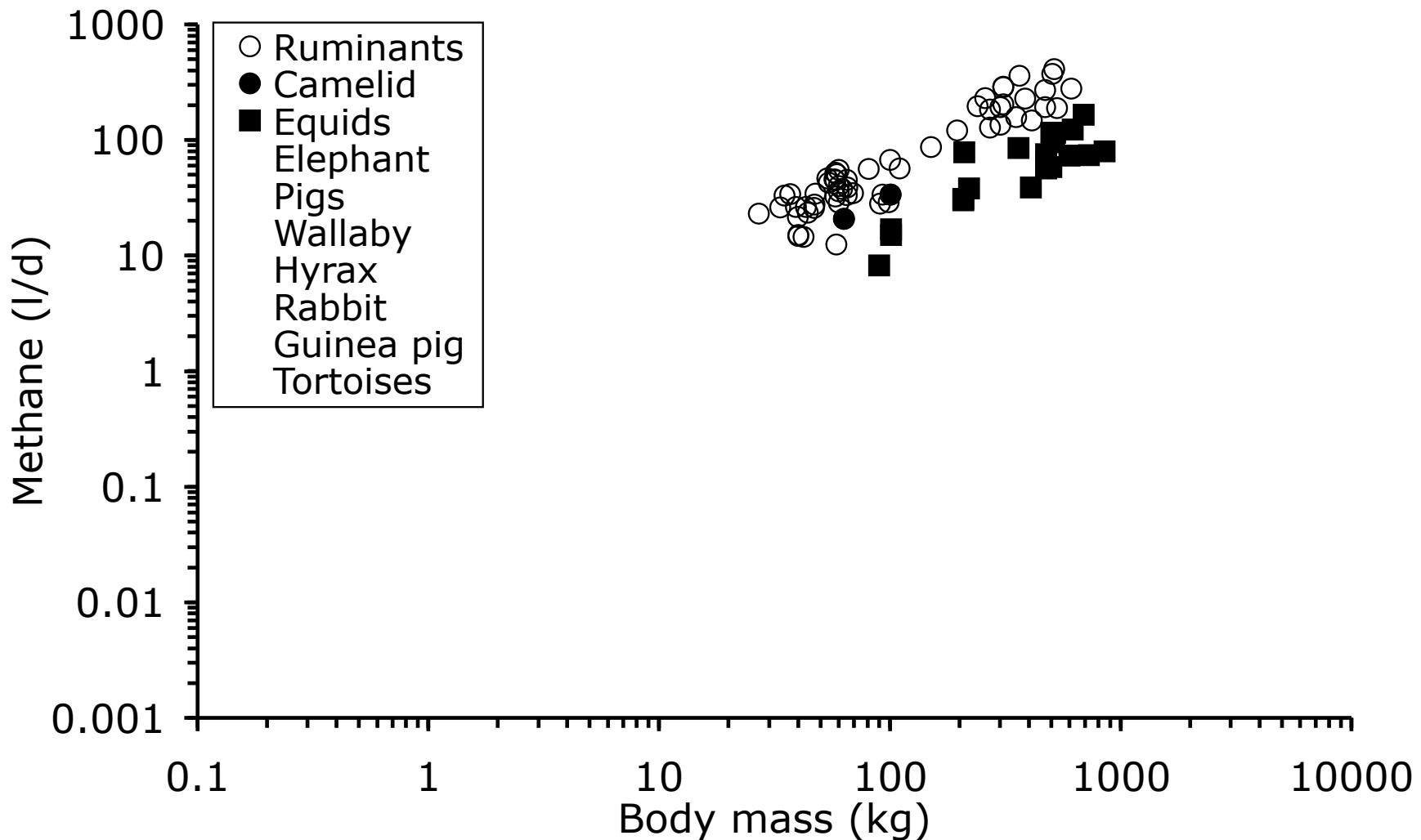
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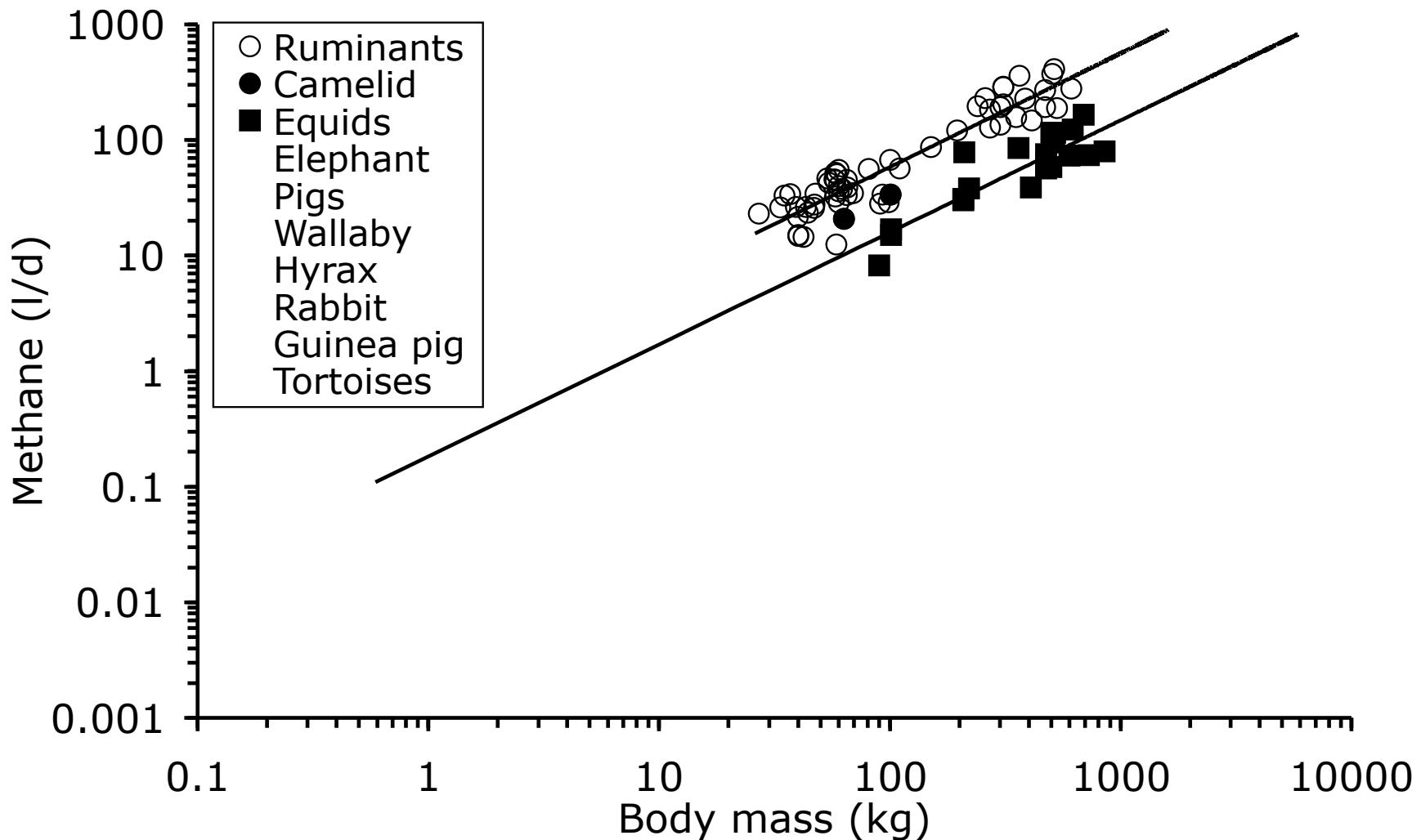
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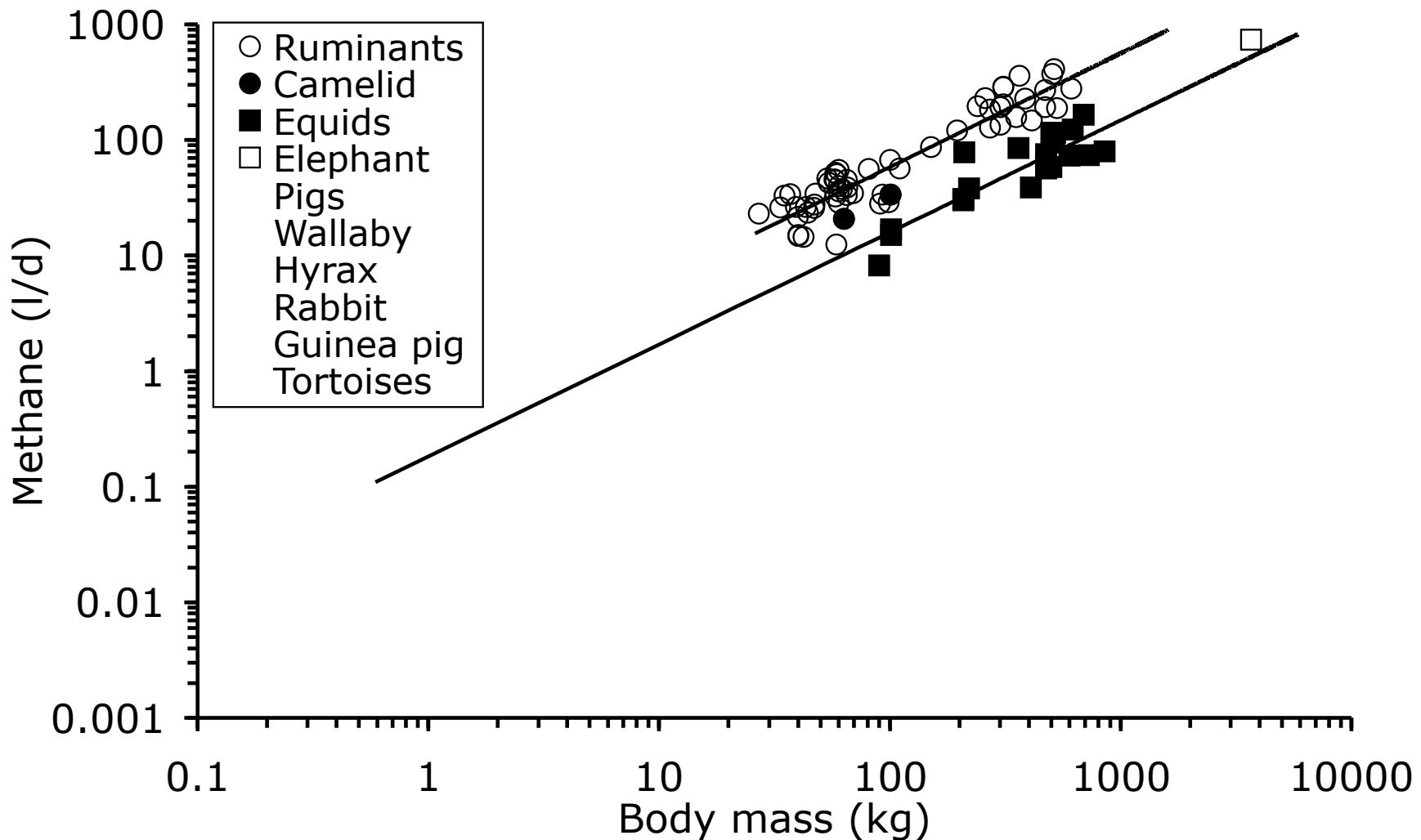
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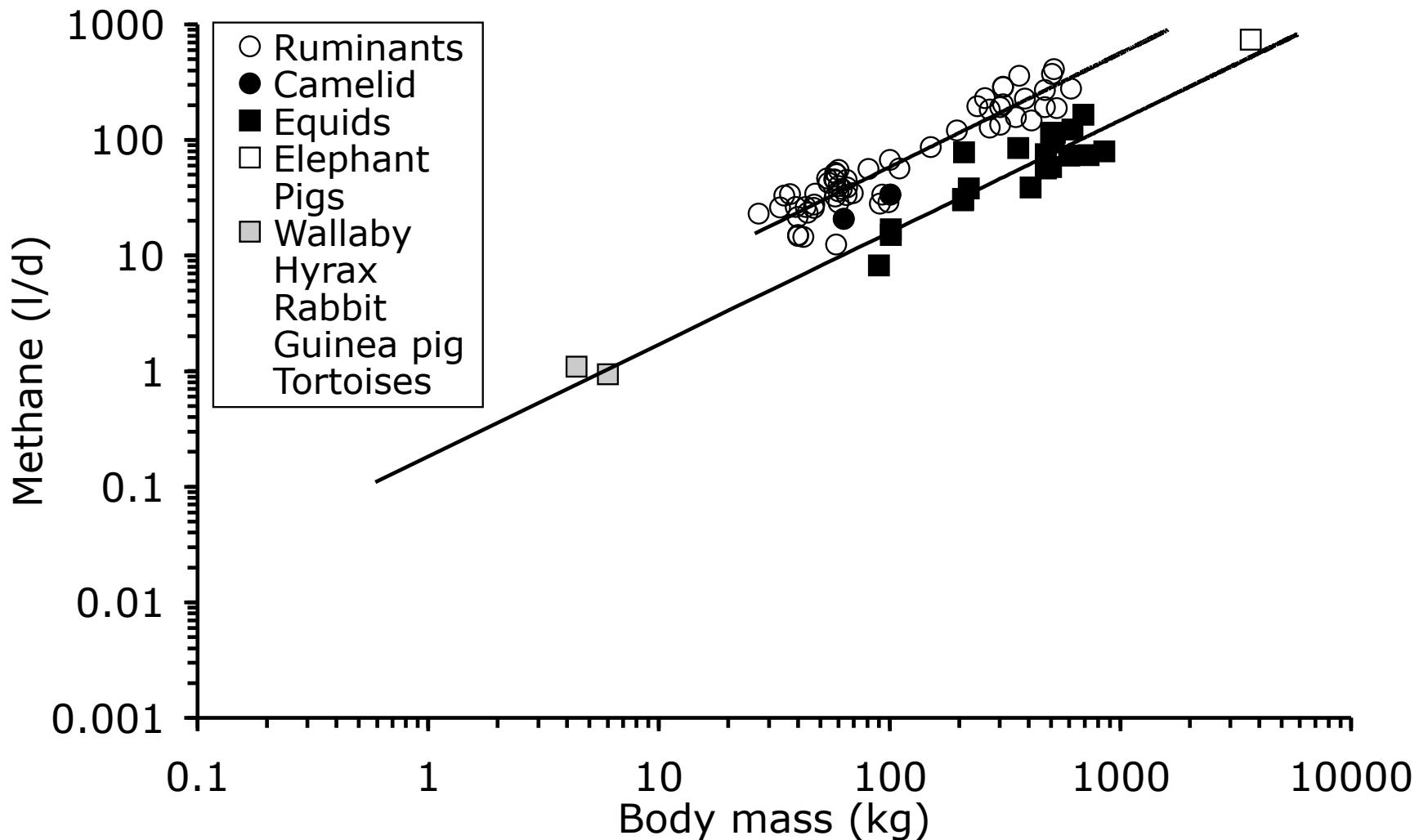
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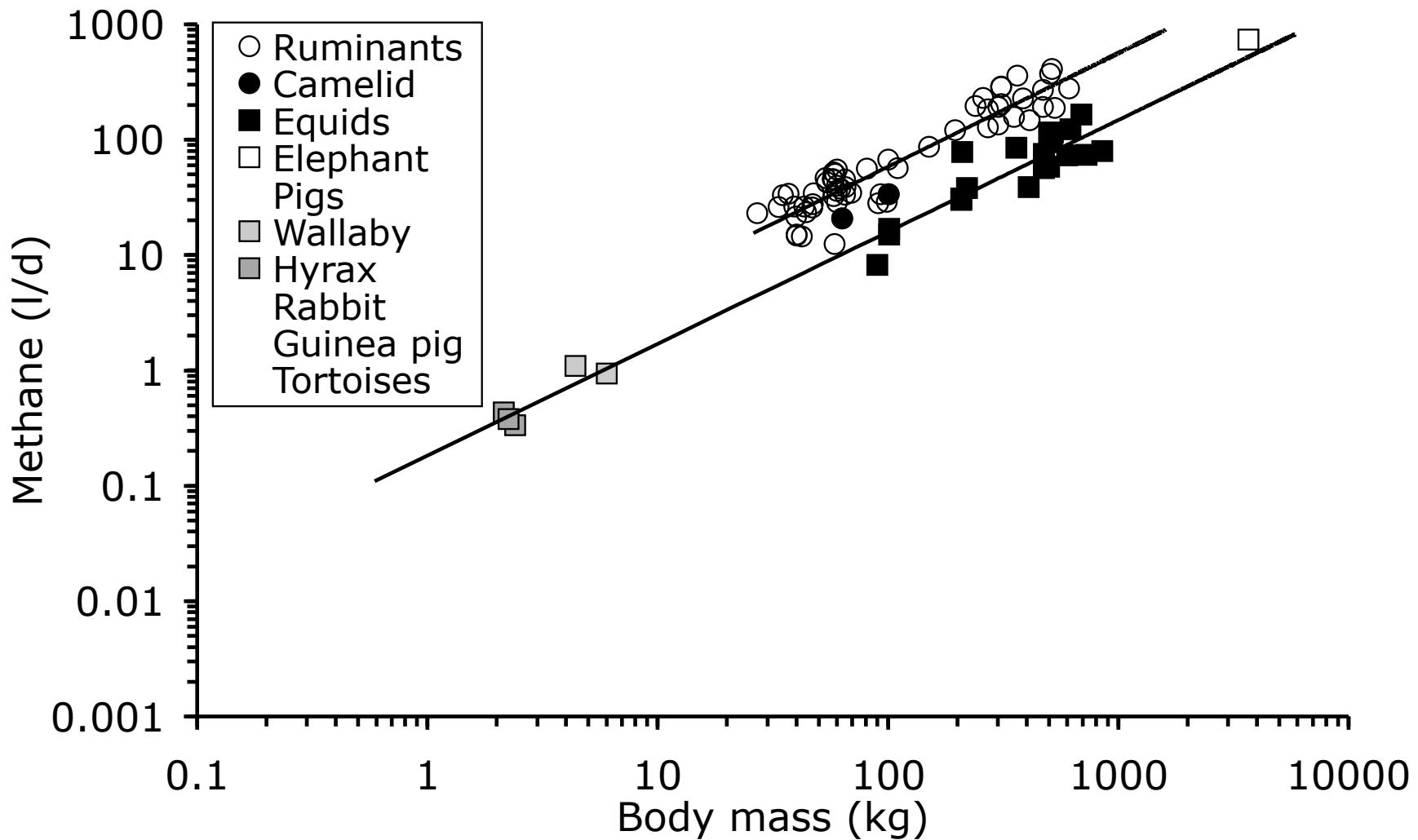
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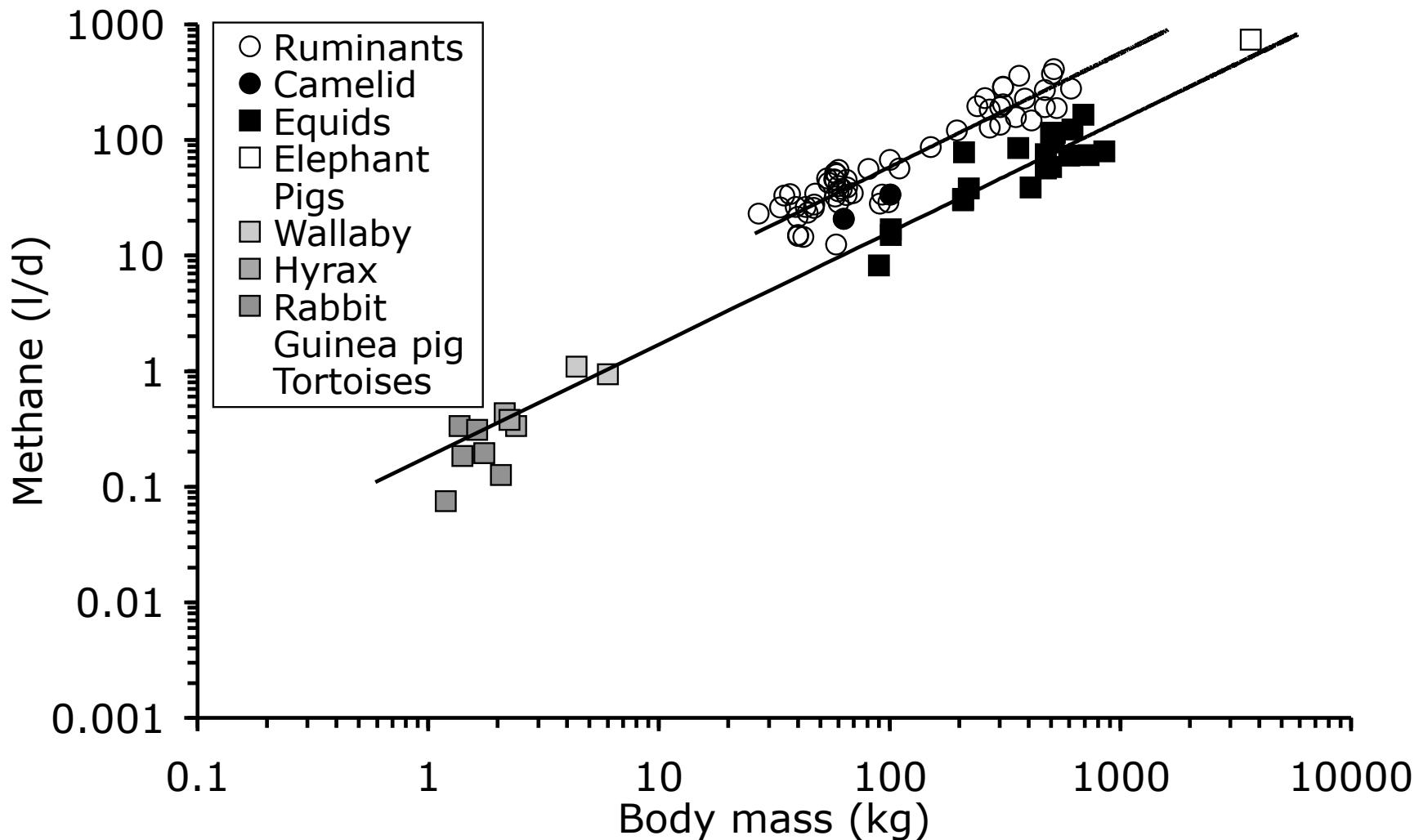
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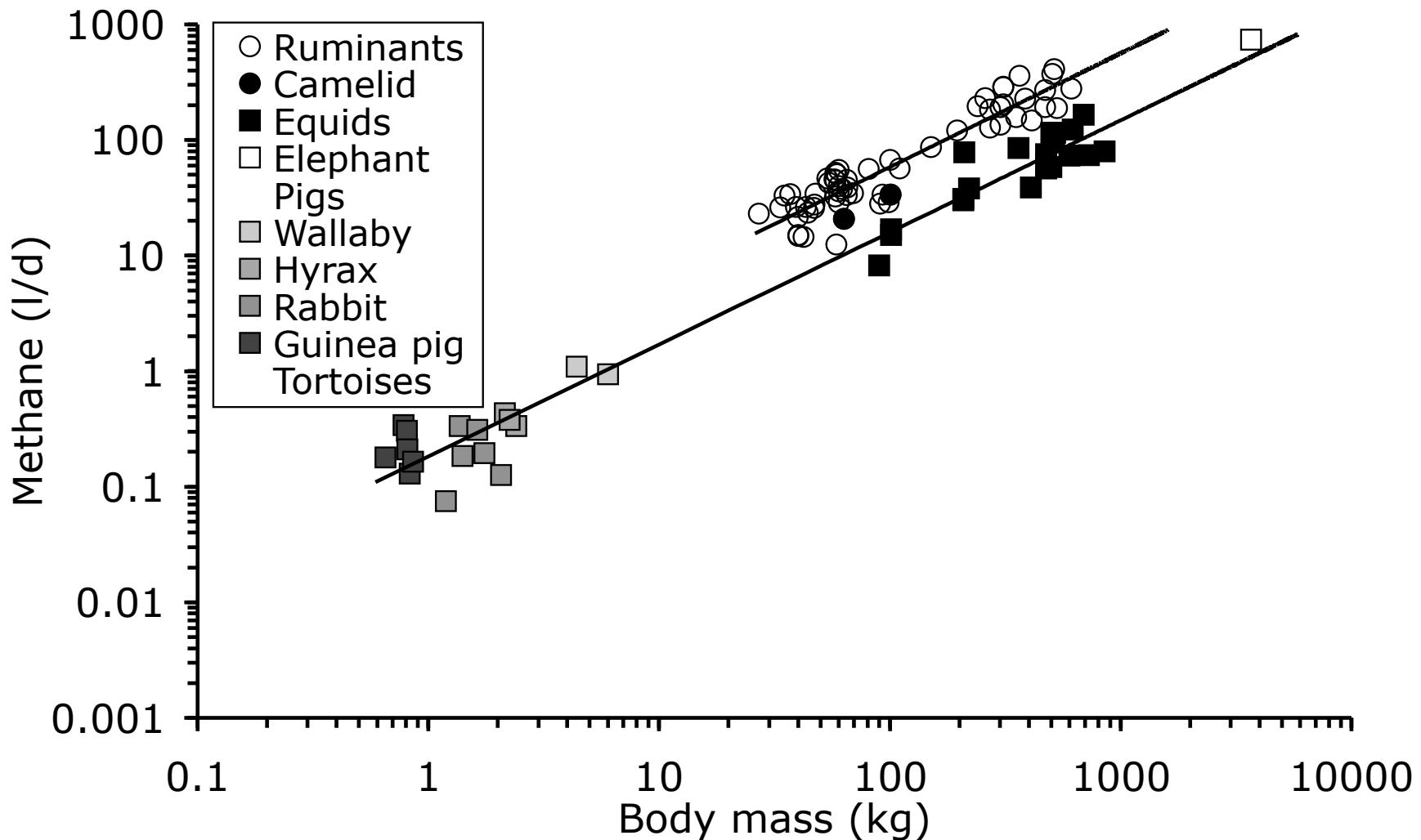
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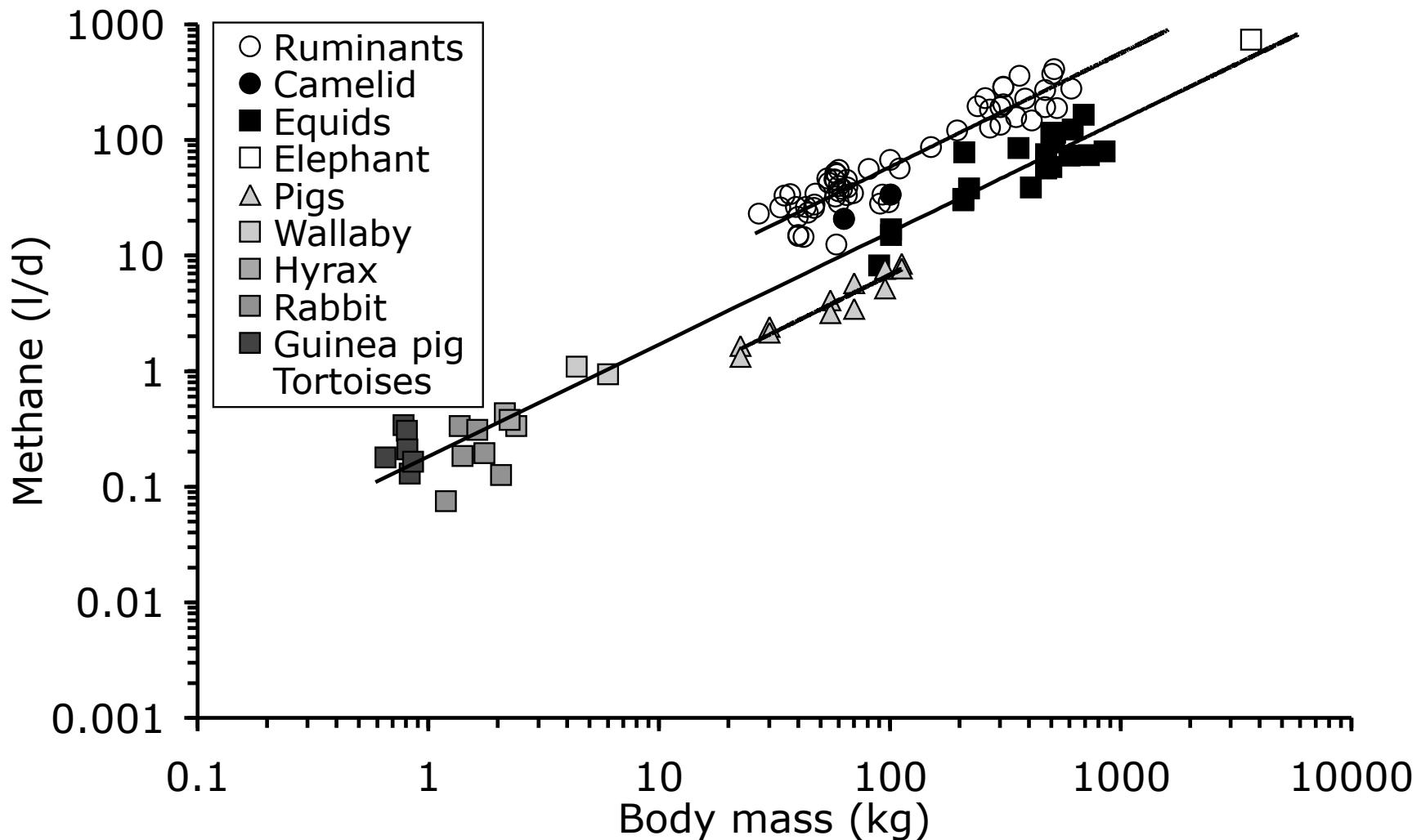
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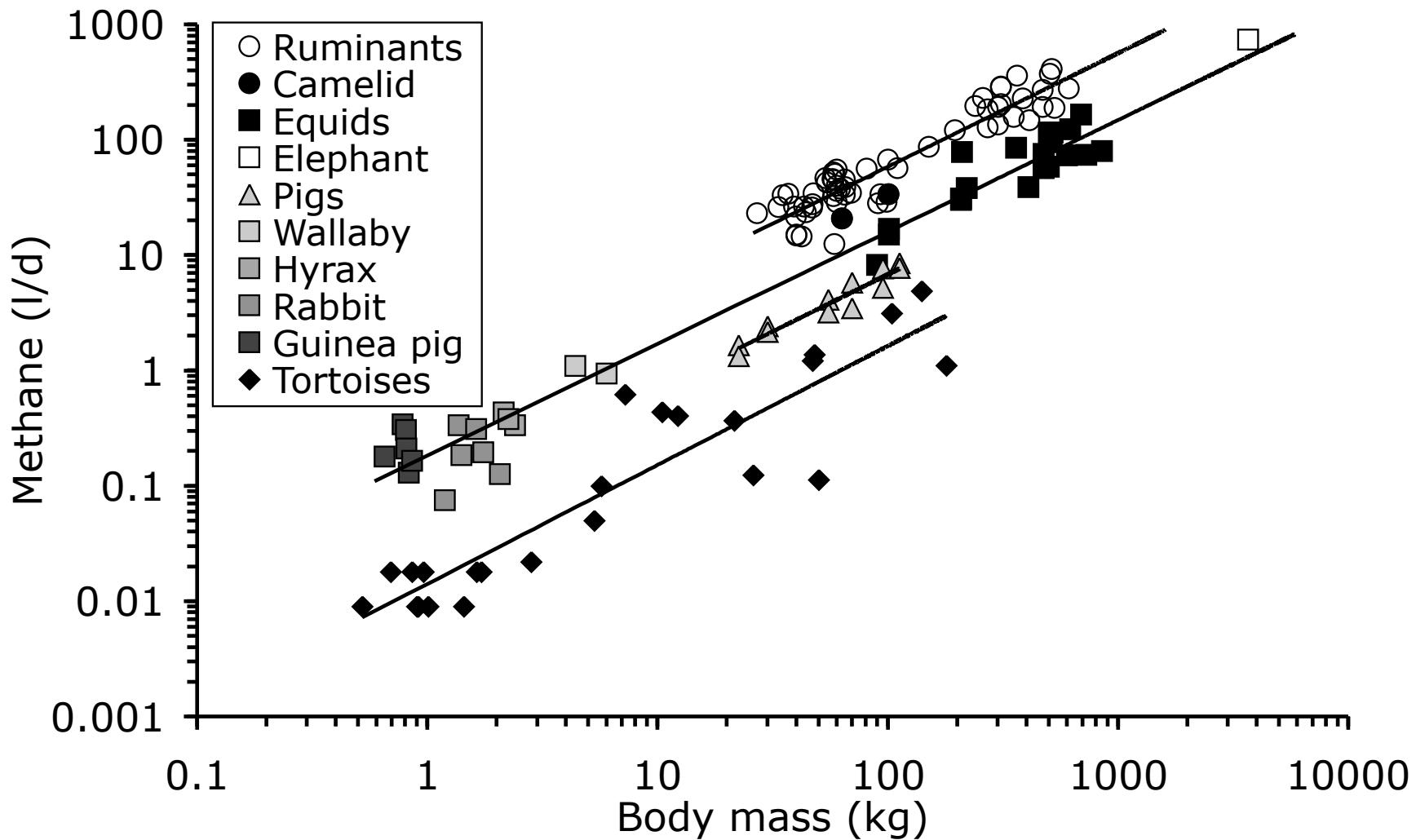
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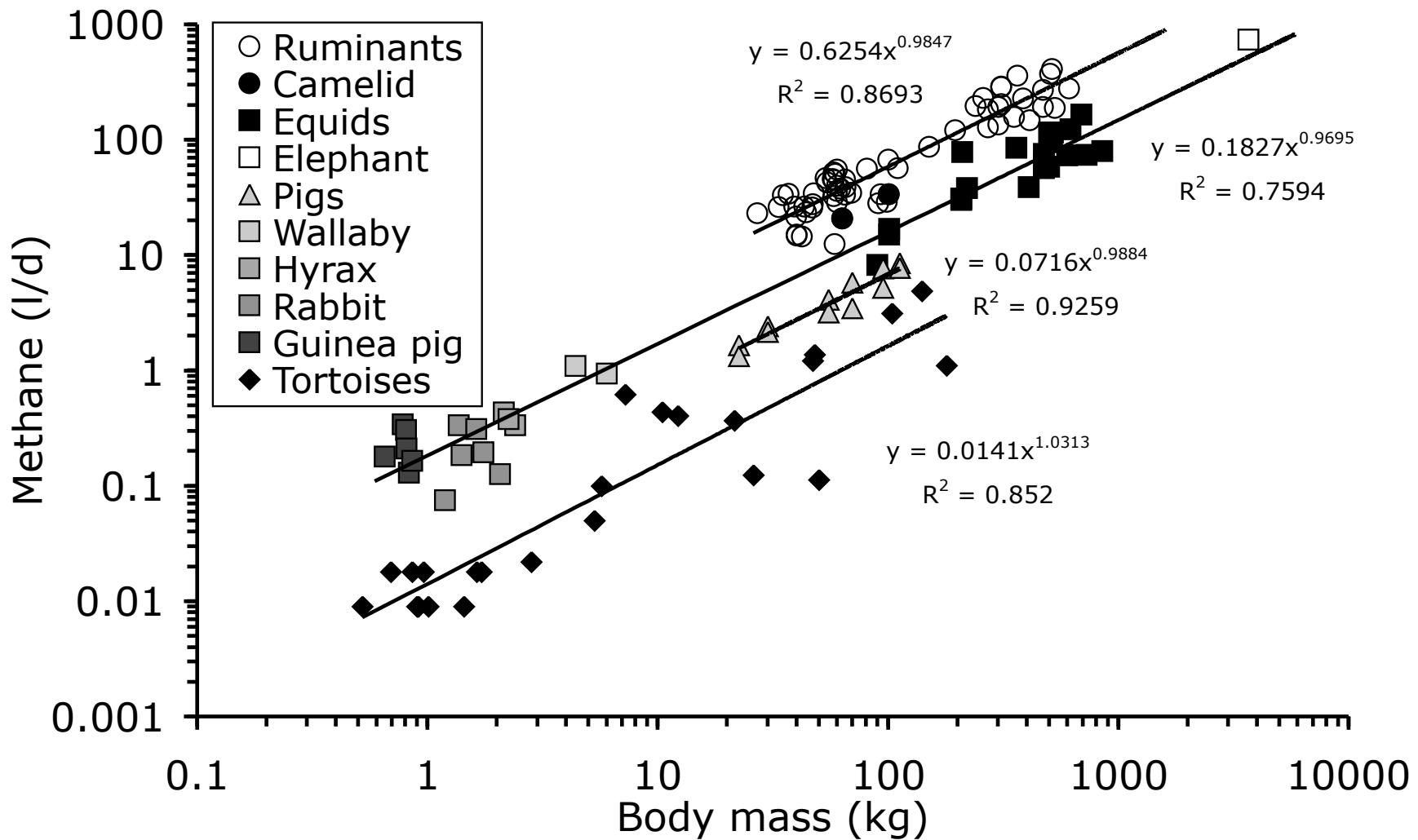
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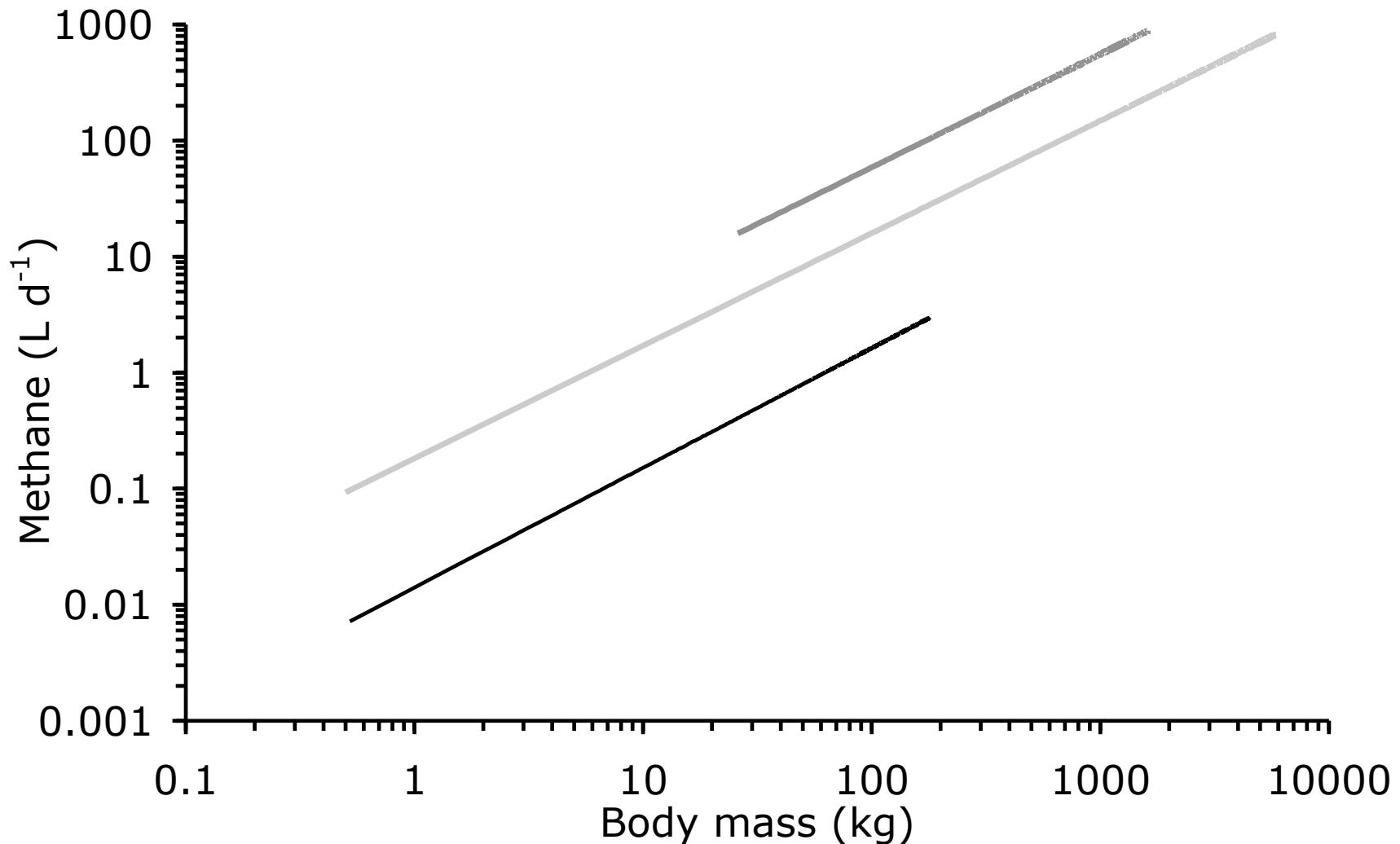
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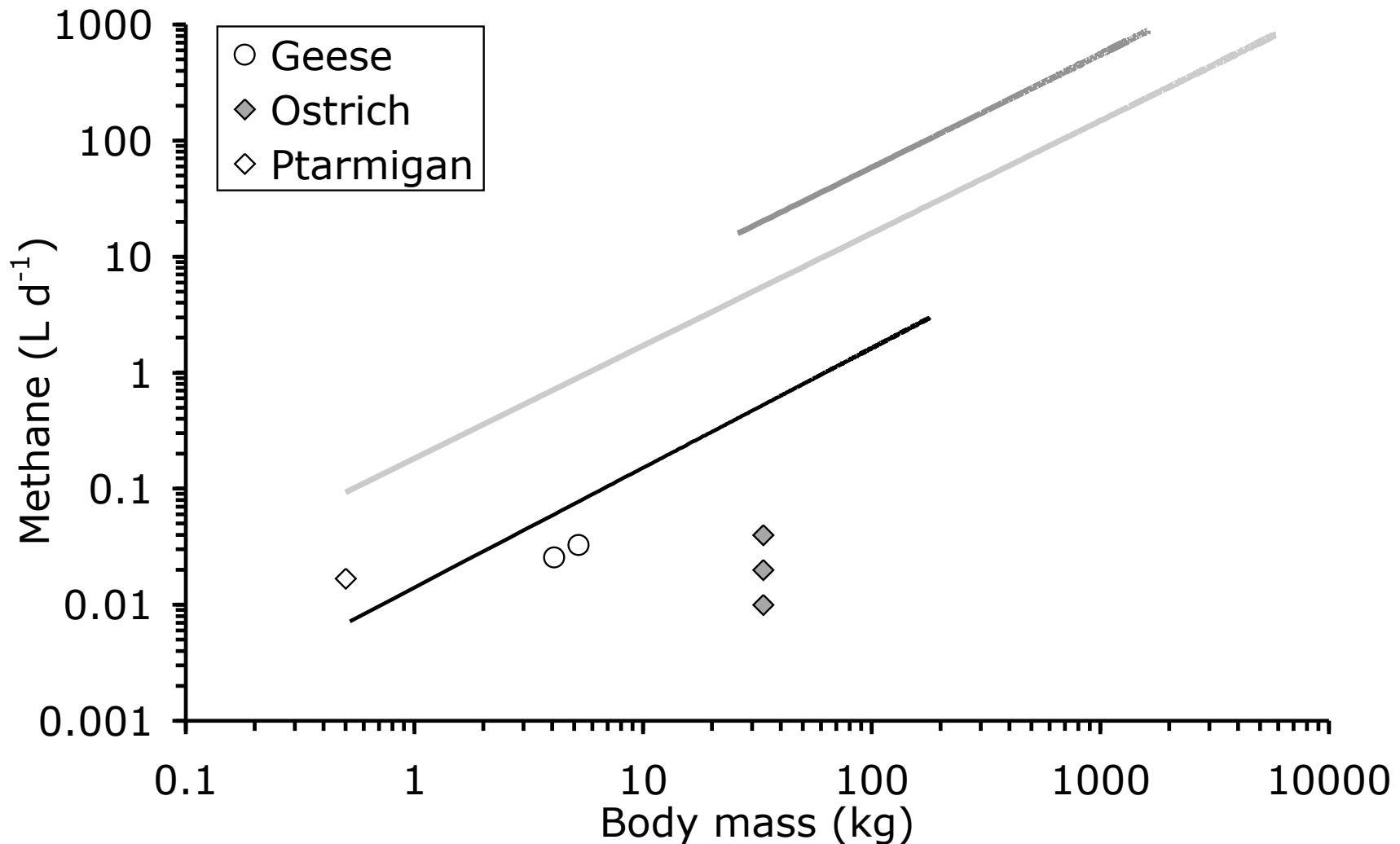
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Literature collection (Fritz et al., subm.) and own data (Franz et al. 2010, 2011ab)



# Methane allometry in herbivores



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



# Particle size



# Faecal particle size allometry in herbivores

(Fritz et al. 209, 2010, 2011)



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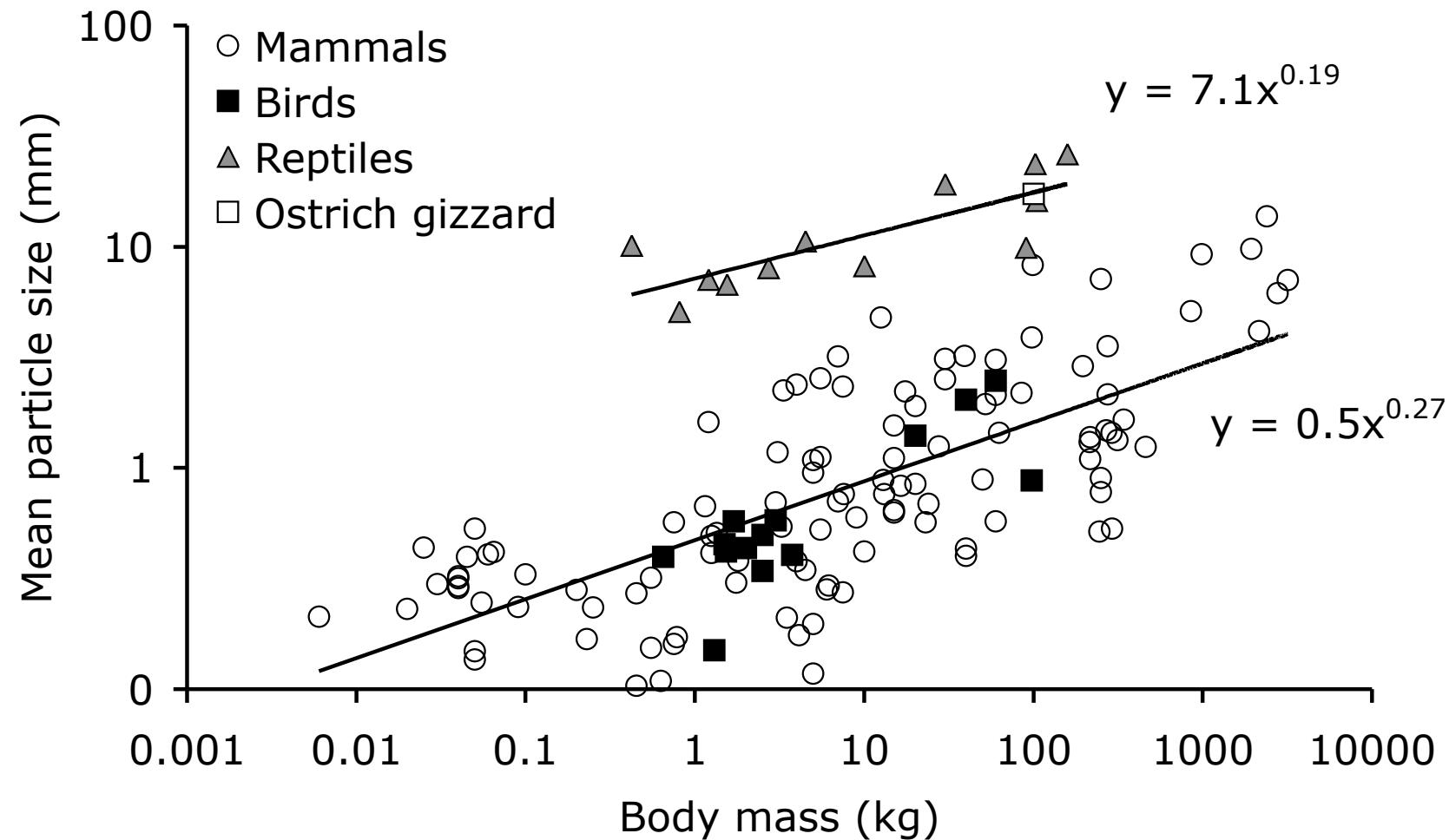


# Faecal particle size allometry in herbivores

(Fritz et al. 209, 2010, 2011)



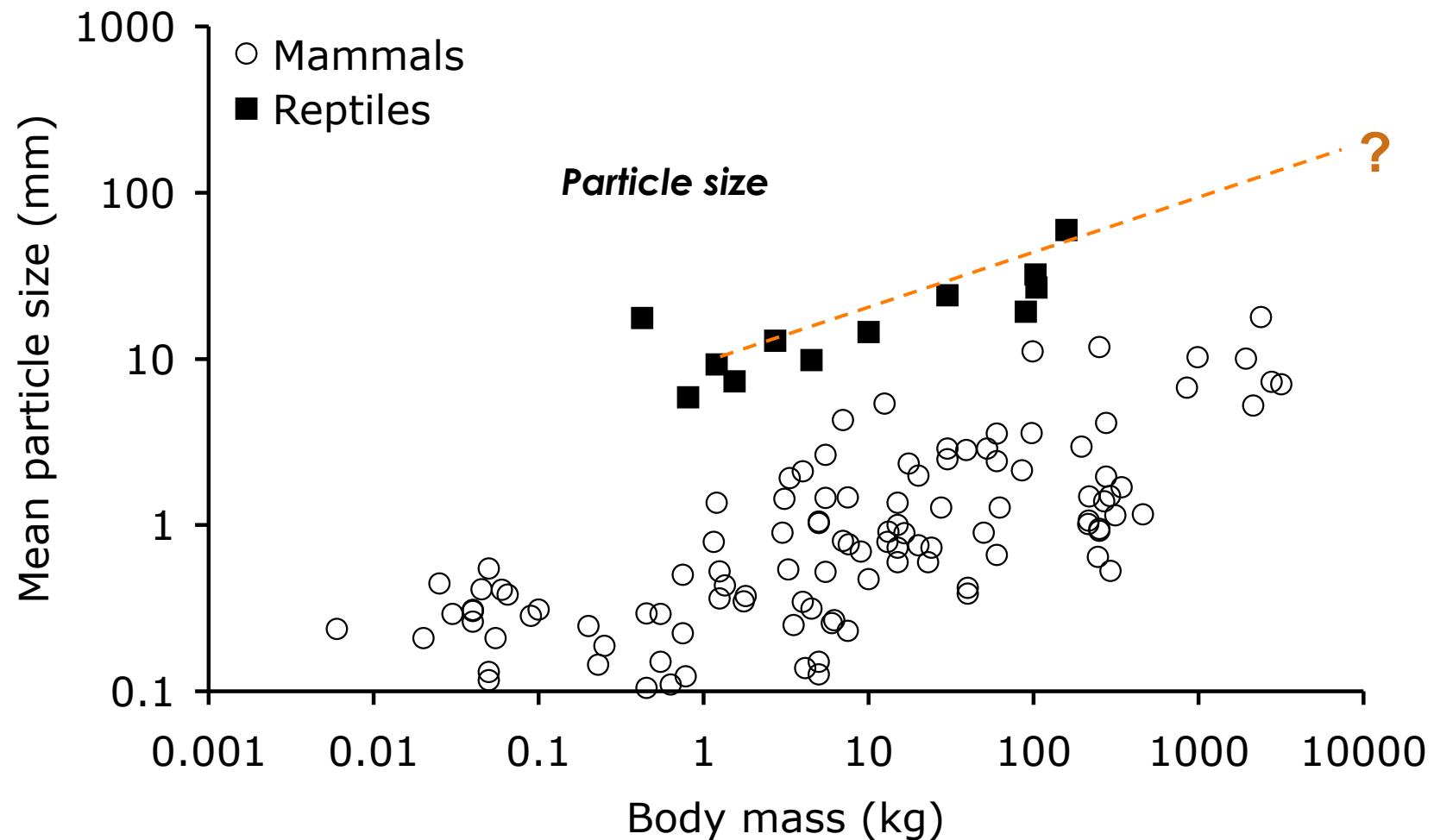
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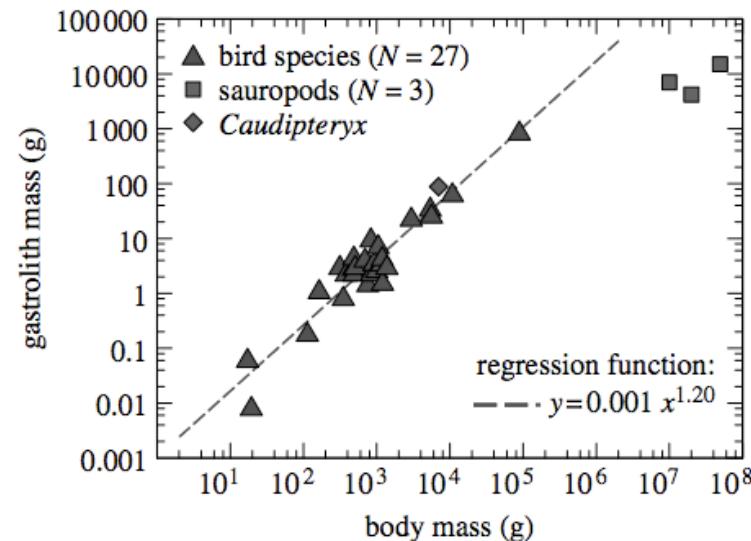
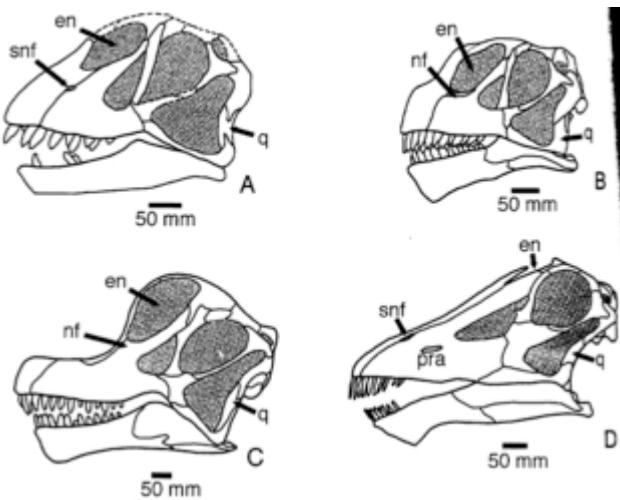
# Extrapolating to sauropods





# Sauropods

Absence of mastication apparatus (no grinding teeth, no cheeks) and absence of gastric mill



*sauropods are special - they did not comminute their food*

from Calvo (1994)

from Wings & Sander (2007)



## General allometric considerations

At a certain body mass, ingesta particle size will only depend on plant morphology





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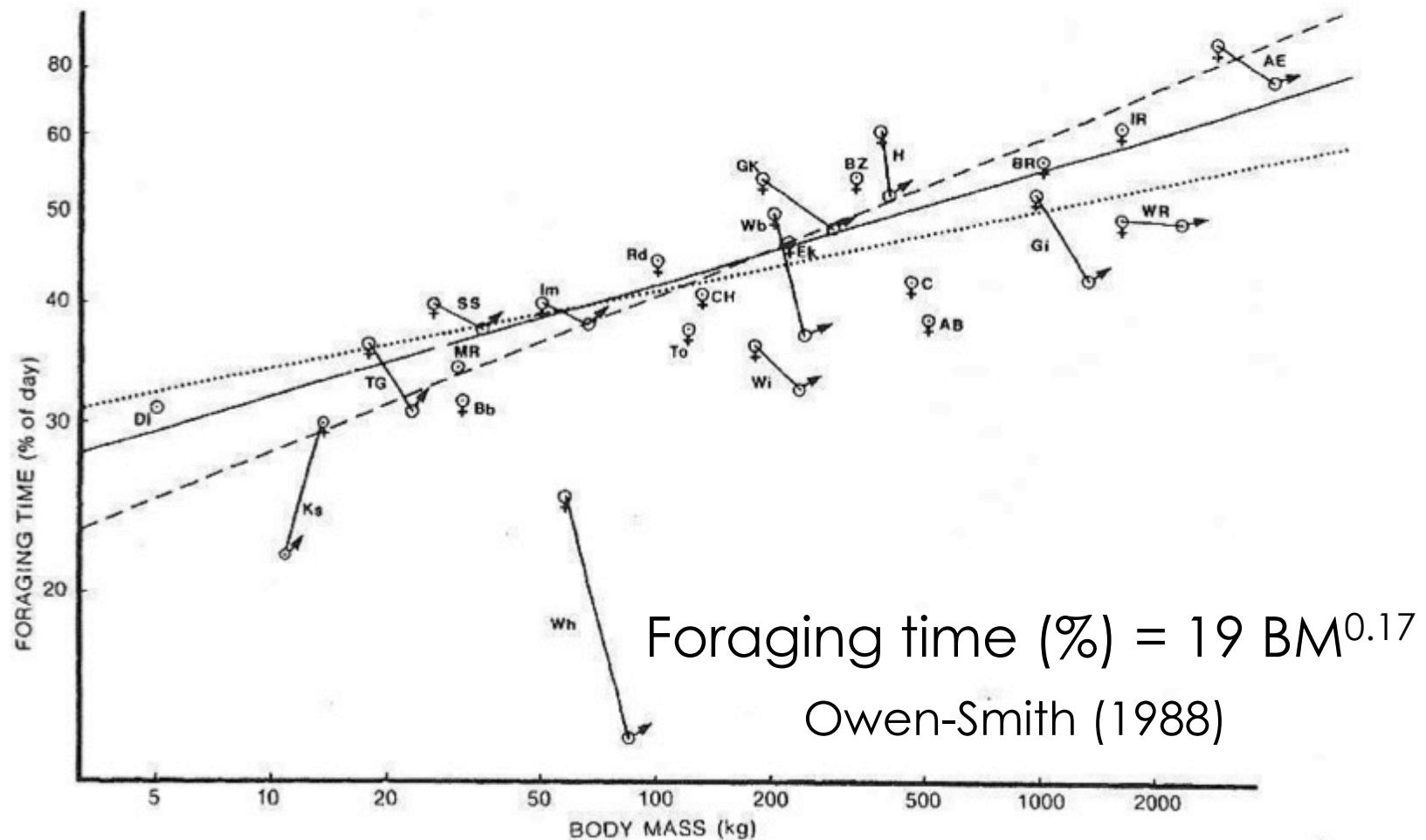
## General allometric considerations

At a certain body mass, ingesta particle size will only depend on plant morphology





# Foraging time and body size



Foraging: Sum of searching, cropping and chewing



## **Chewing limits body size**

*Chewing constrains the time available for feeding and therefore ultimately limits the body size of chewers.*

$$\text{Feeding time (in \% day)} = 19 \text{ Body mass}^{0.17}$$

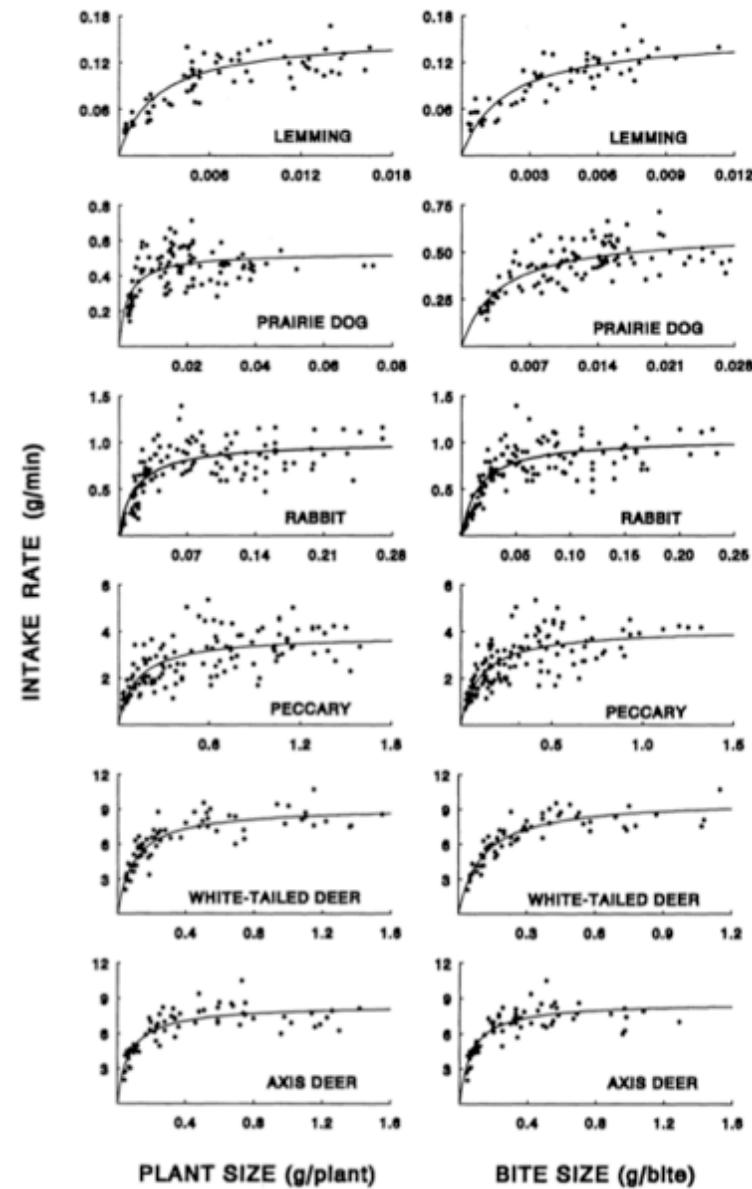
*from app. 18 tons onwards, herbivores would have to feed more than 24 hours per day!*



# The “Functional Response”

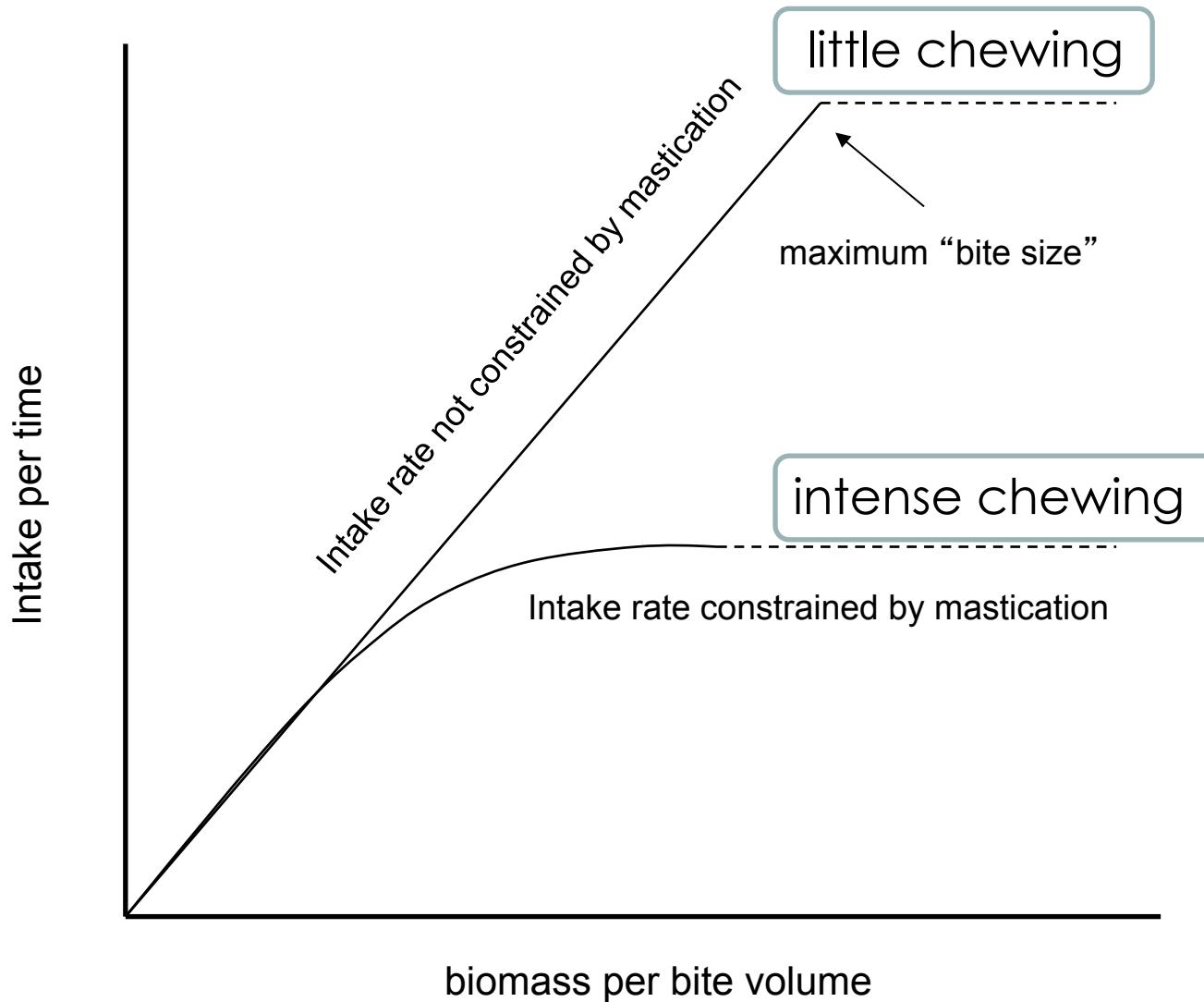
Chewing = food processing is a rate-limiting step  
=> at a certain amount of food on offer, intake rate cannot increase due to chewing

from Gross et al. (1993)



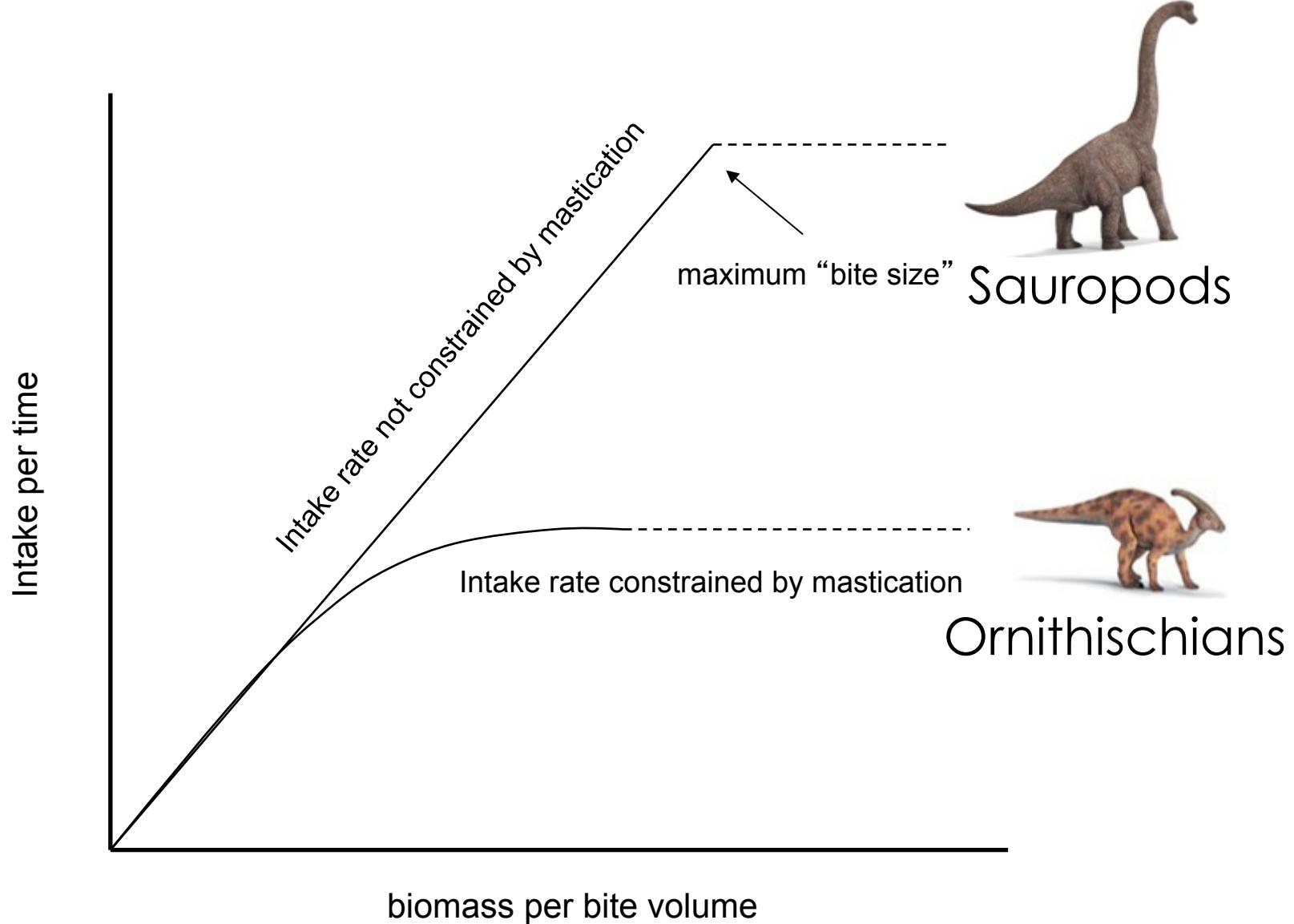


# Feeding time and body size



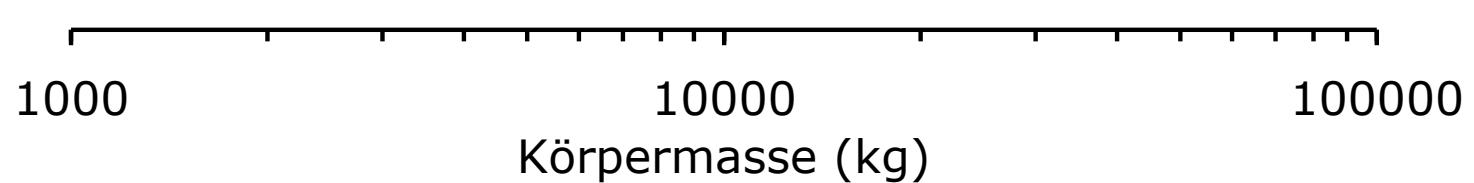


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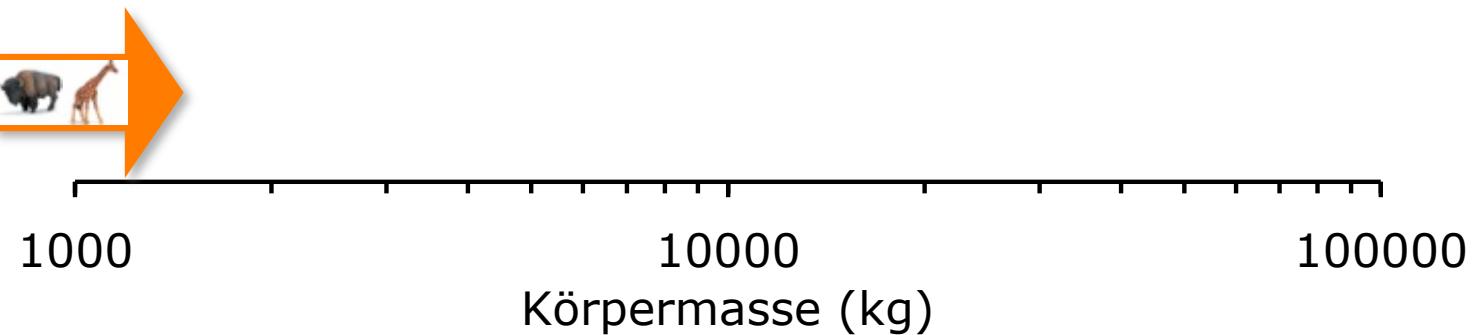


# Sizing up herbivores



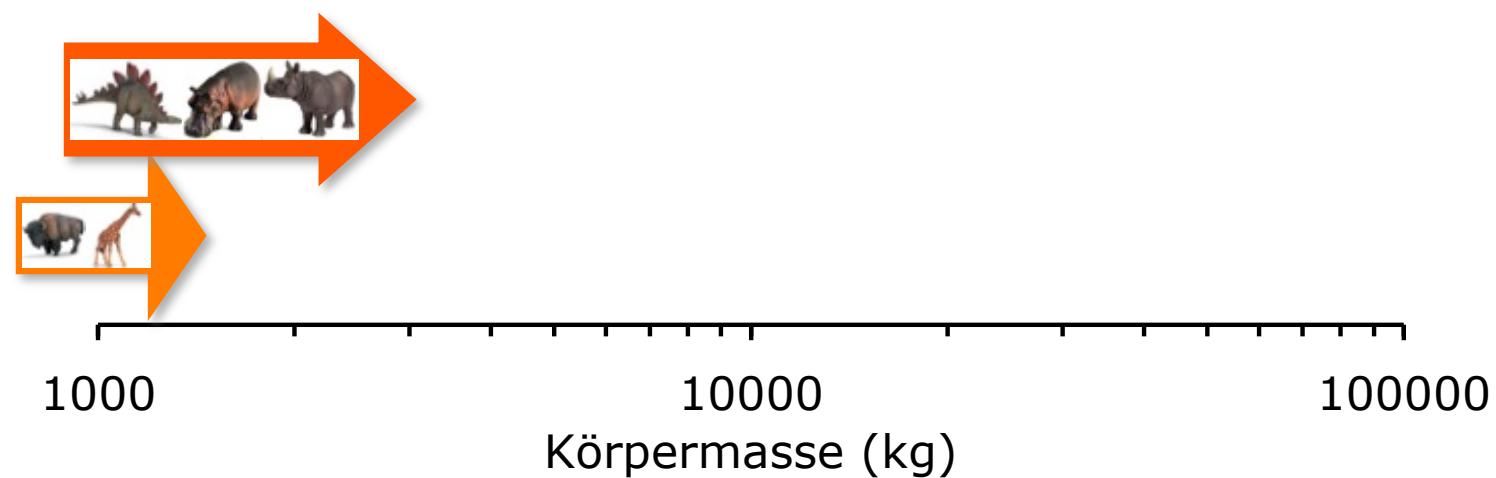


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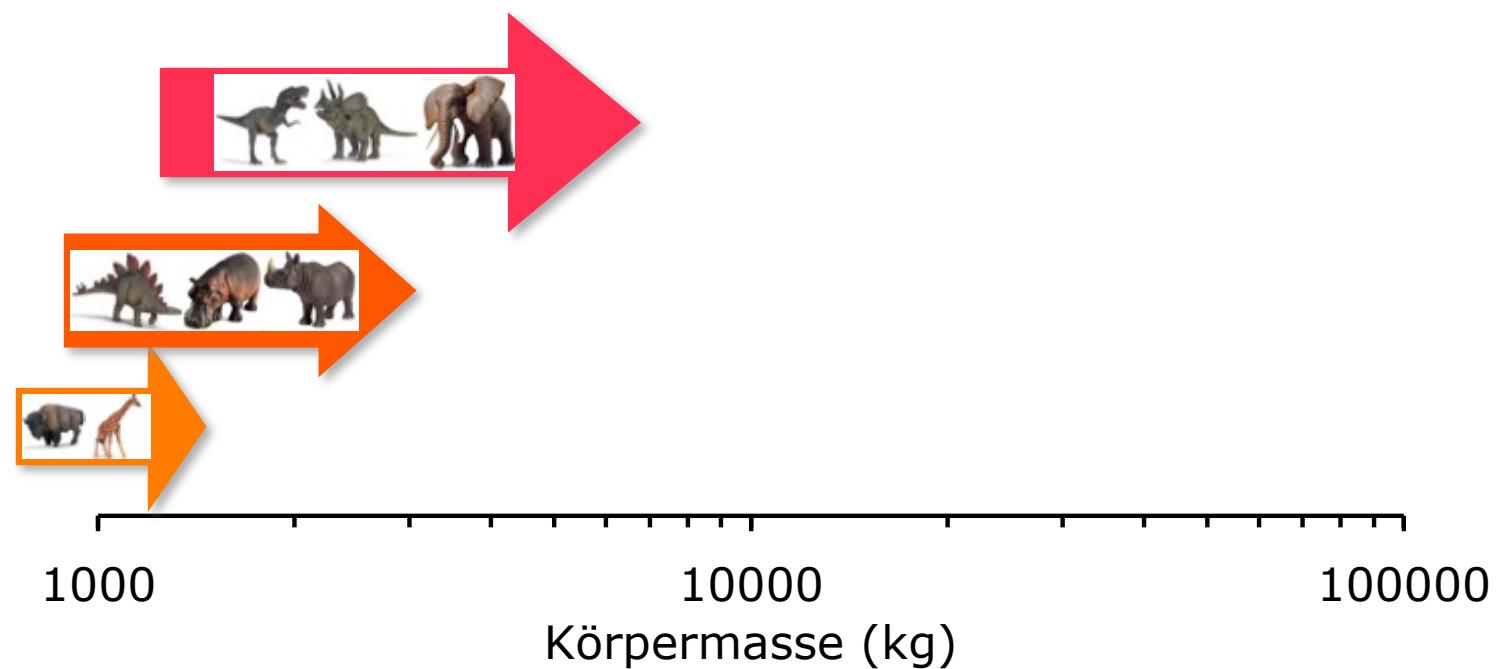


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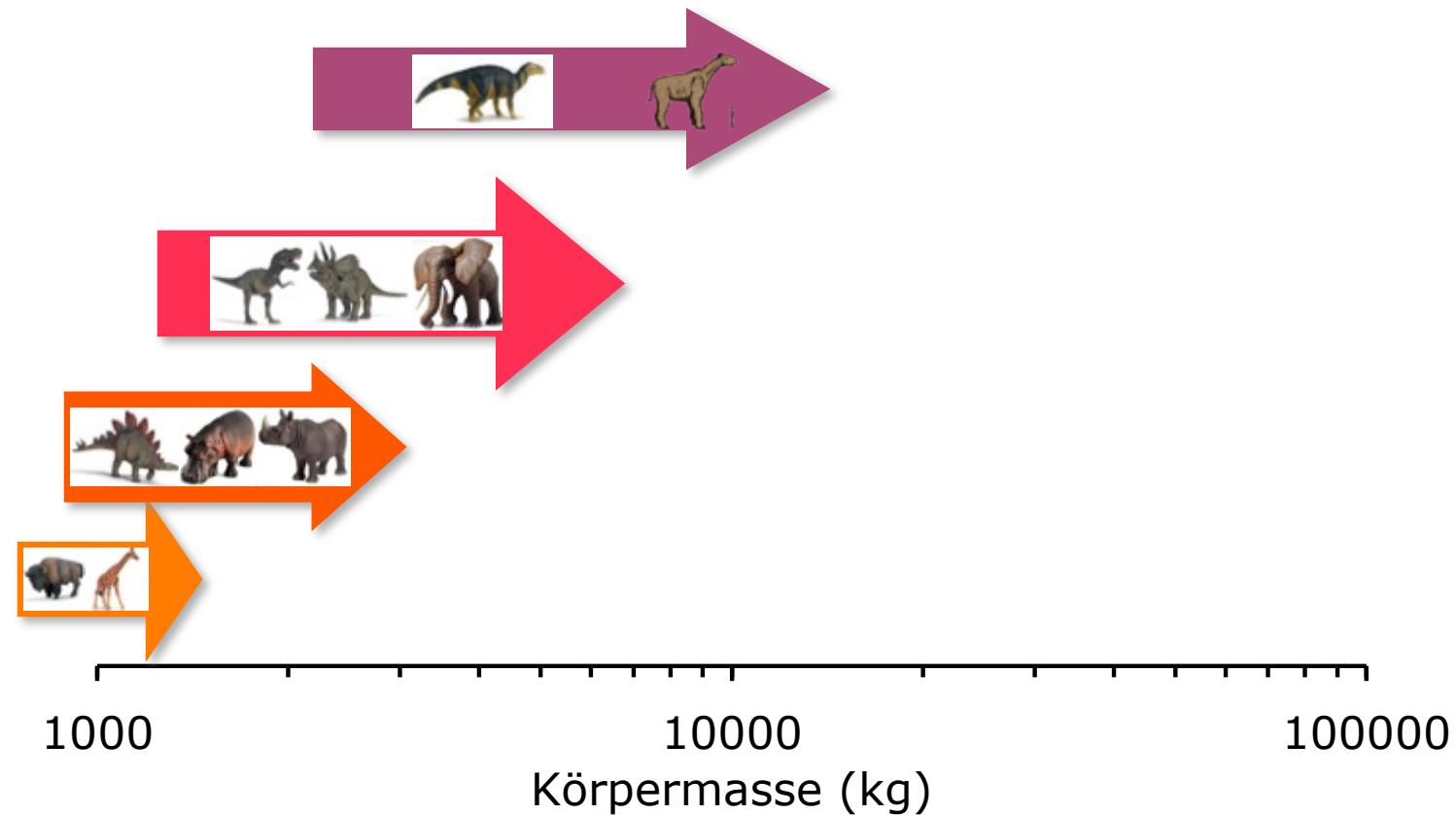


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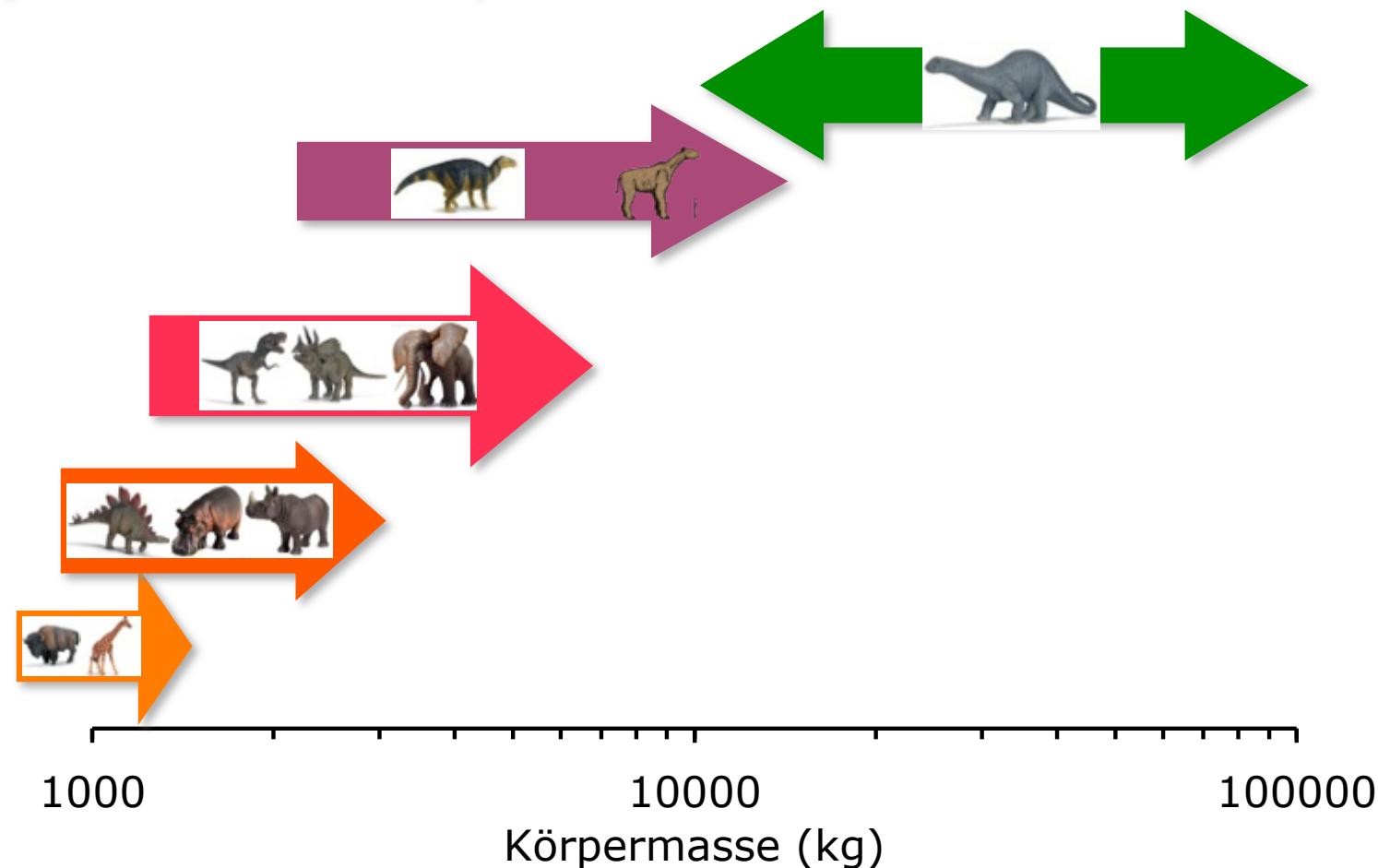
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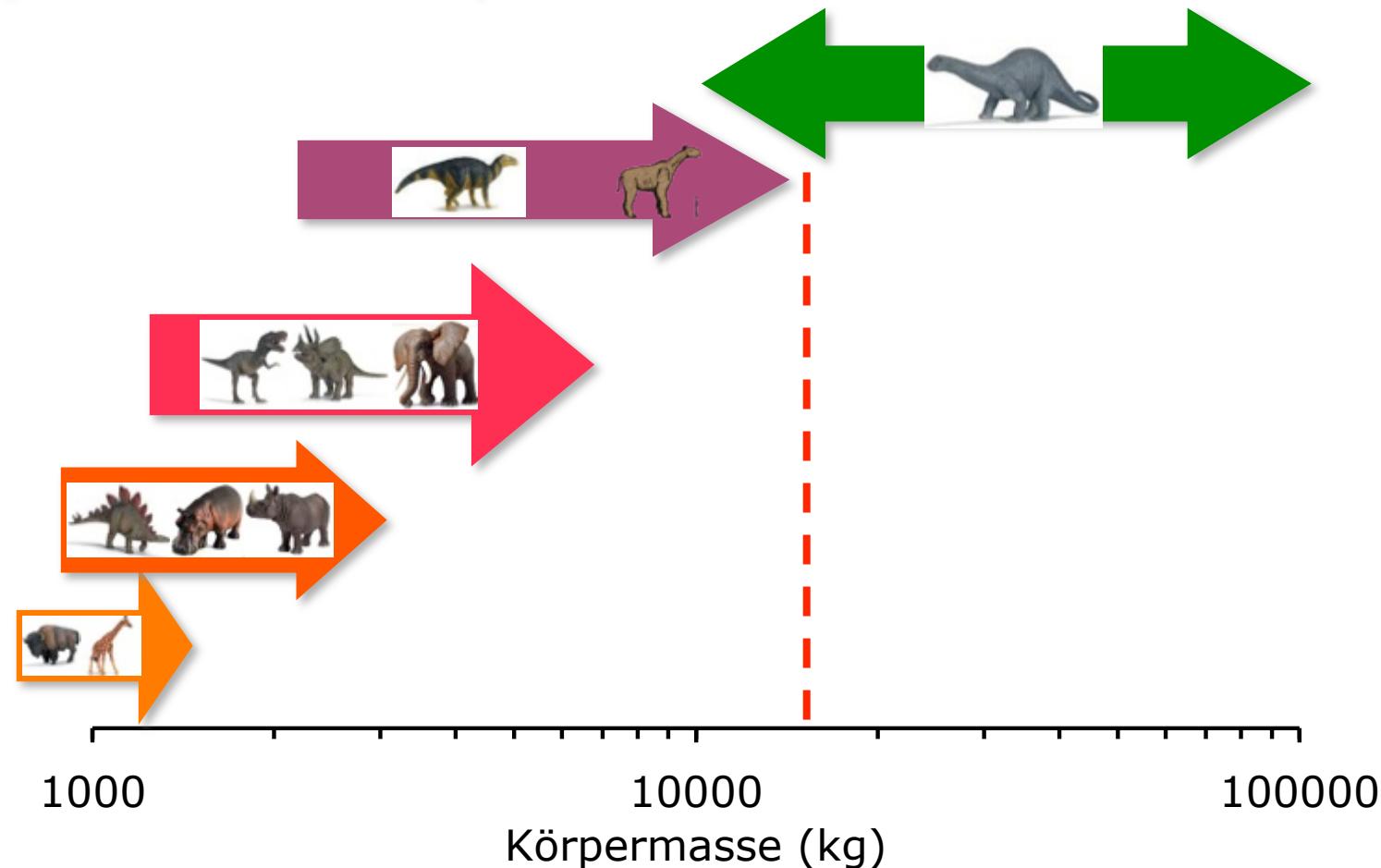
- Sauropods were the largest terrestrial animals (and herbivores) ever





## Sizing up herbivores

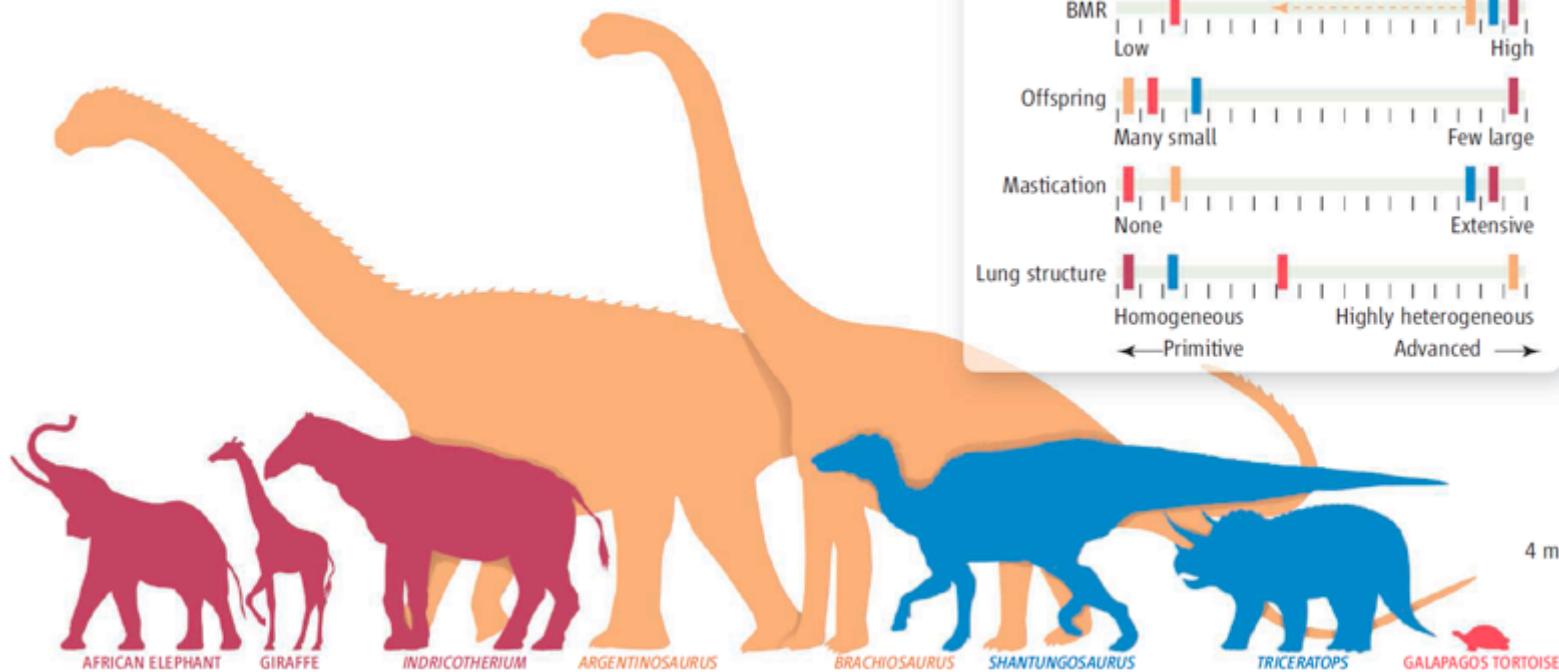
- Sauropods were the largest terrestrial animals (and herbivores) ever





# Sauropods

Absence of mastication is considered a “permissive factor” for sauropod gigantism



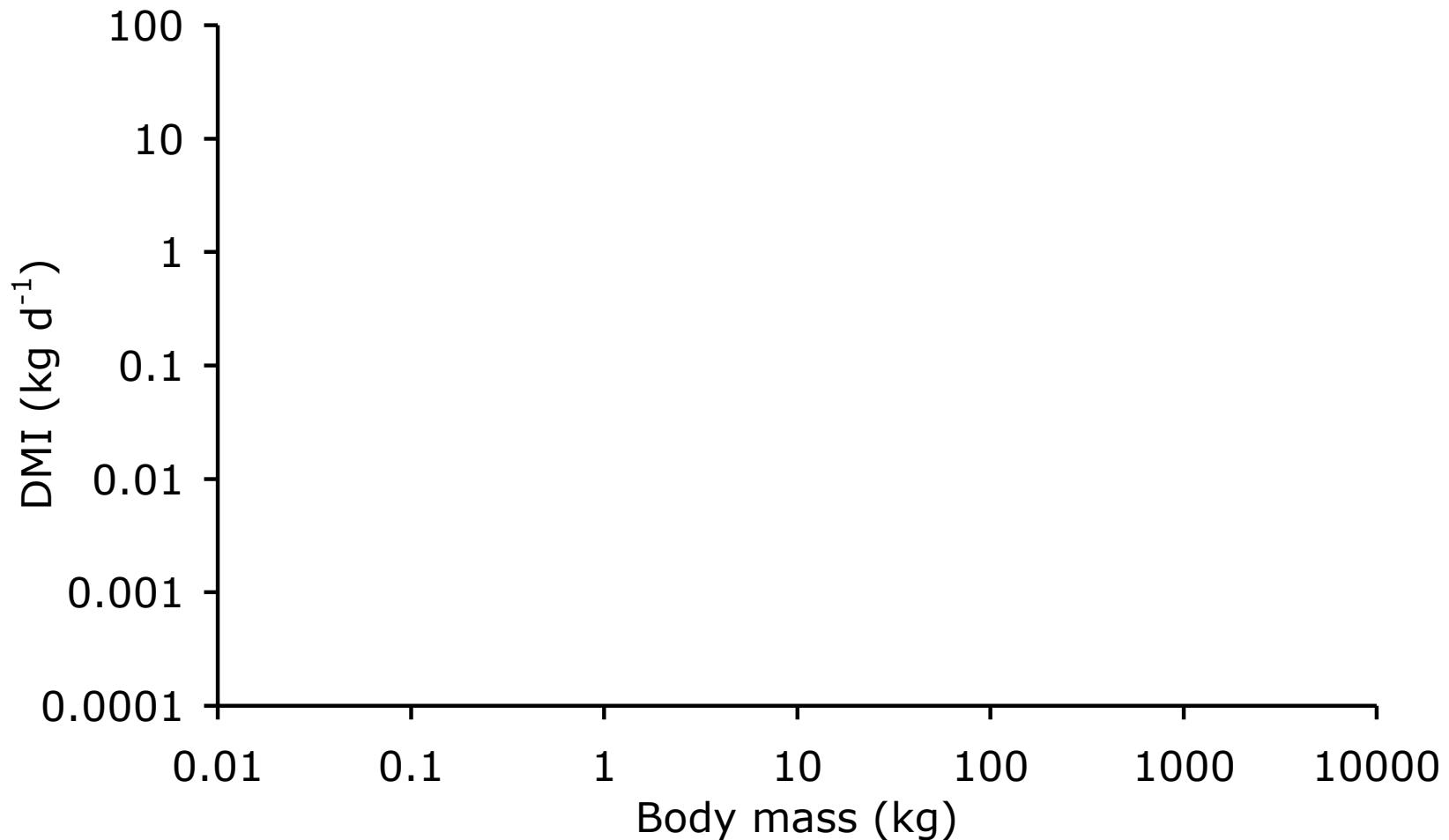
from Sander & Clauss (2008)



# Food intake



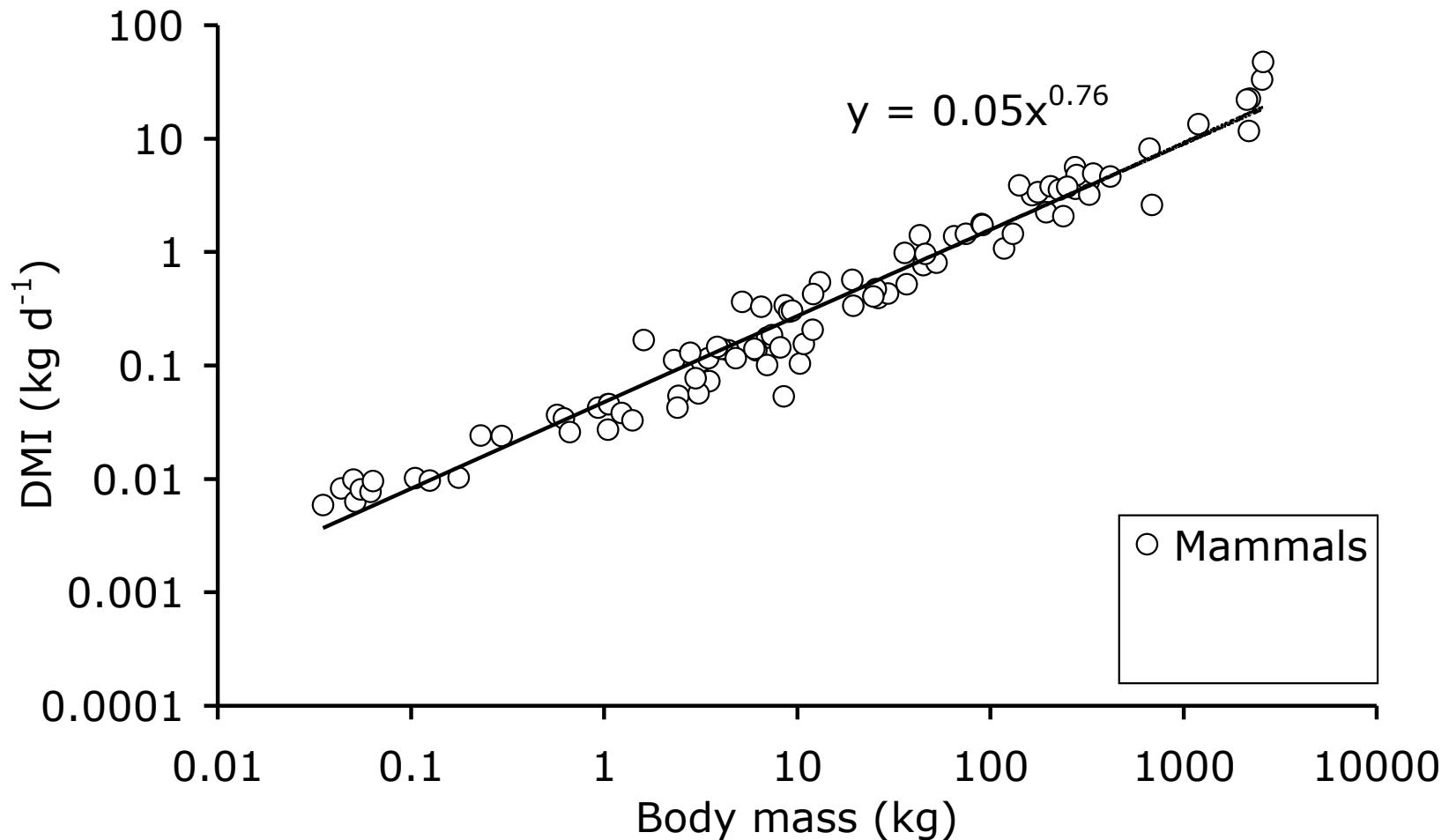
# Food intake



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



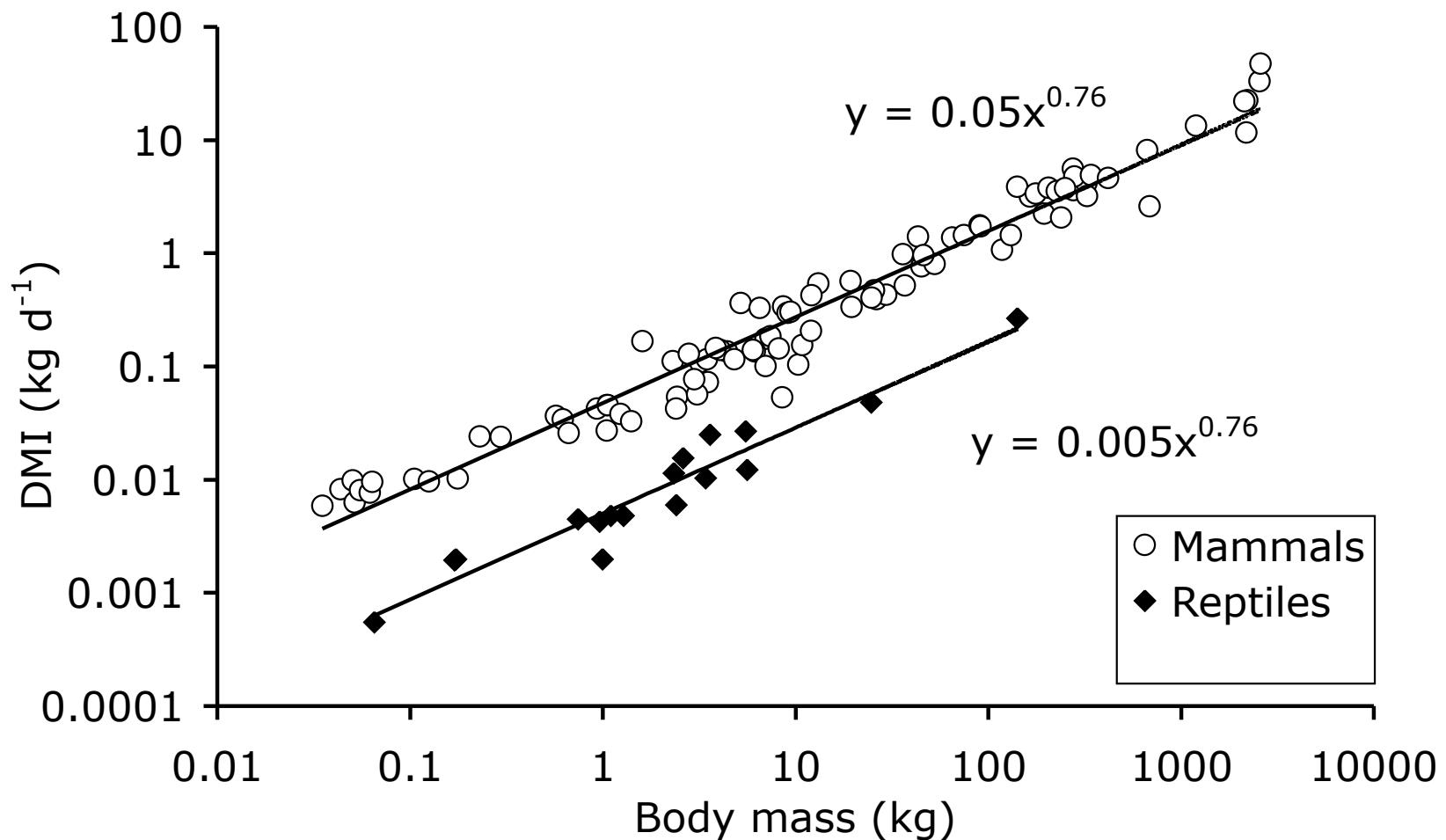
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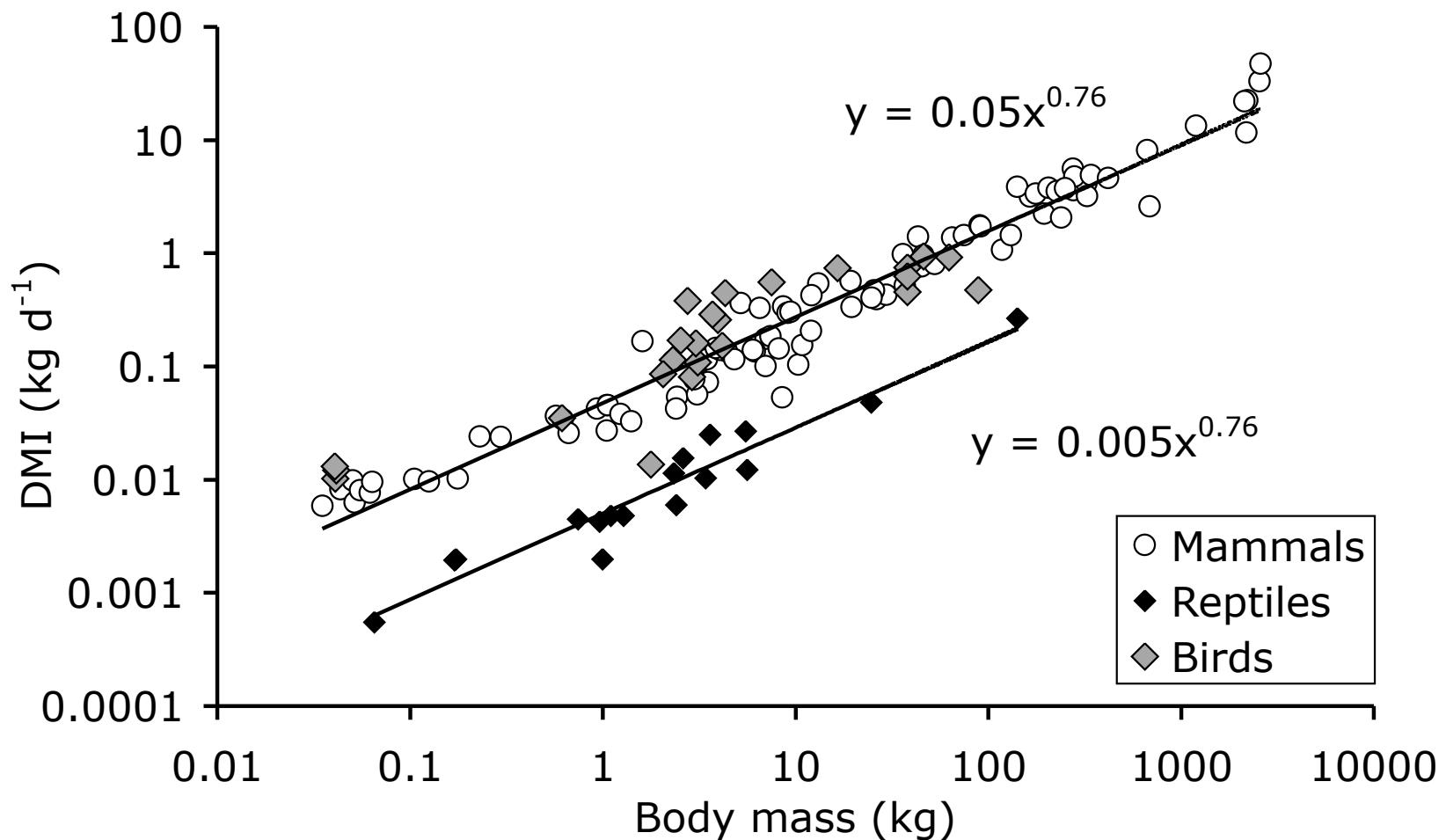
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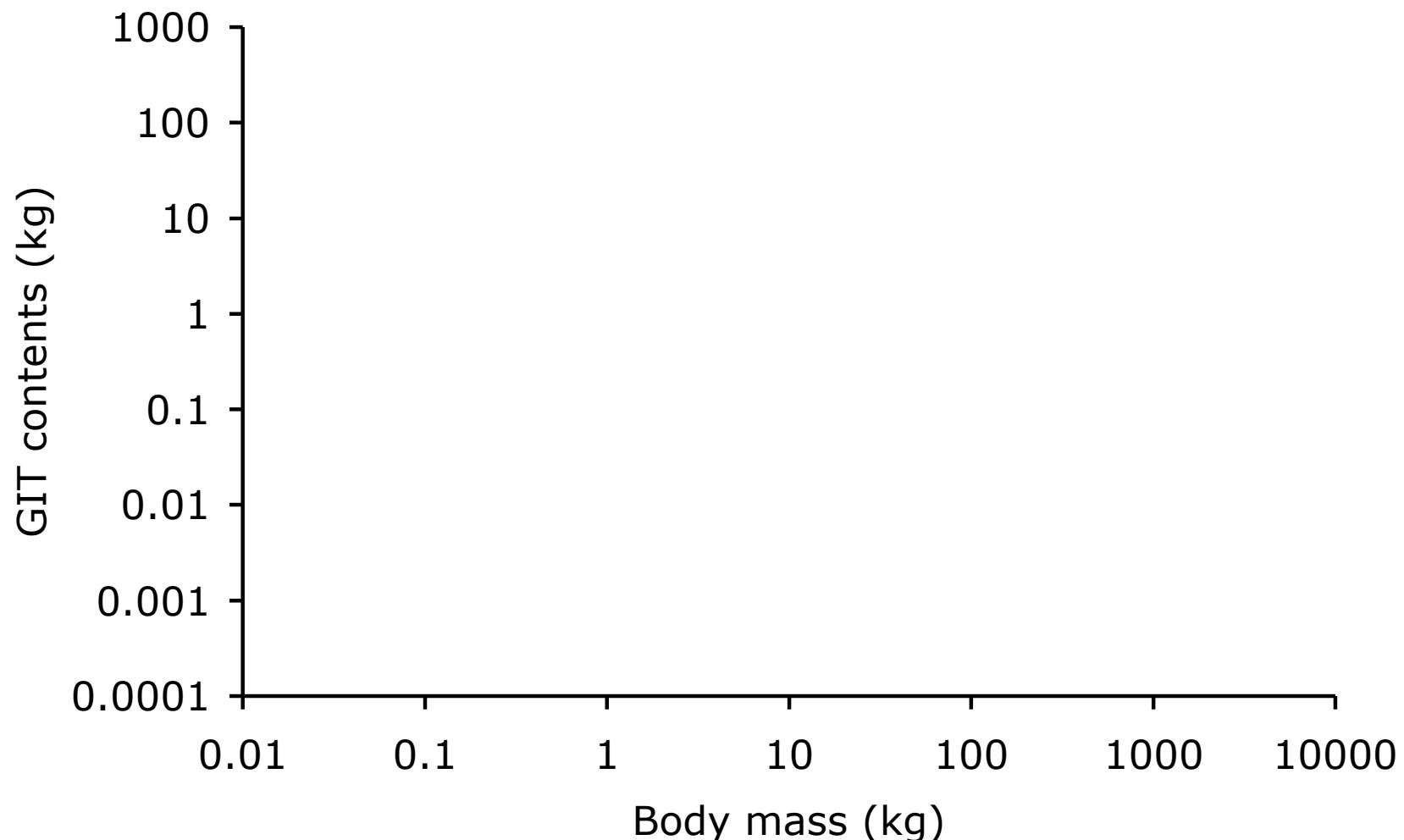


# Gut capacity



# Wet gut content mass

(measured by slaughtering)

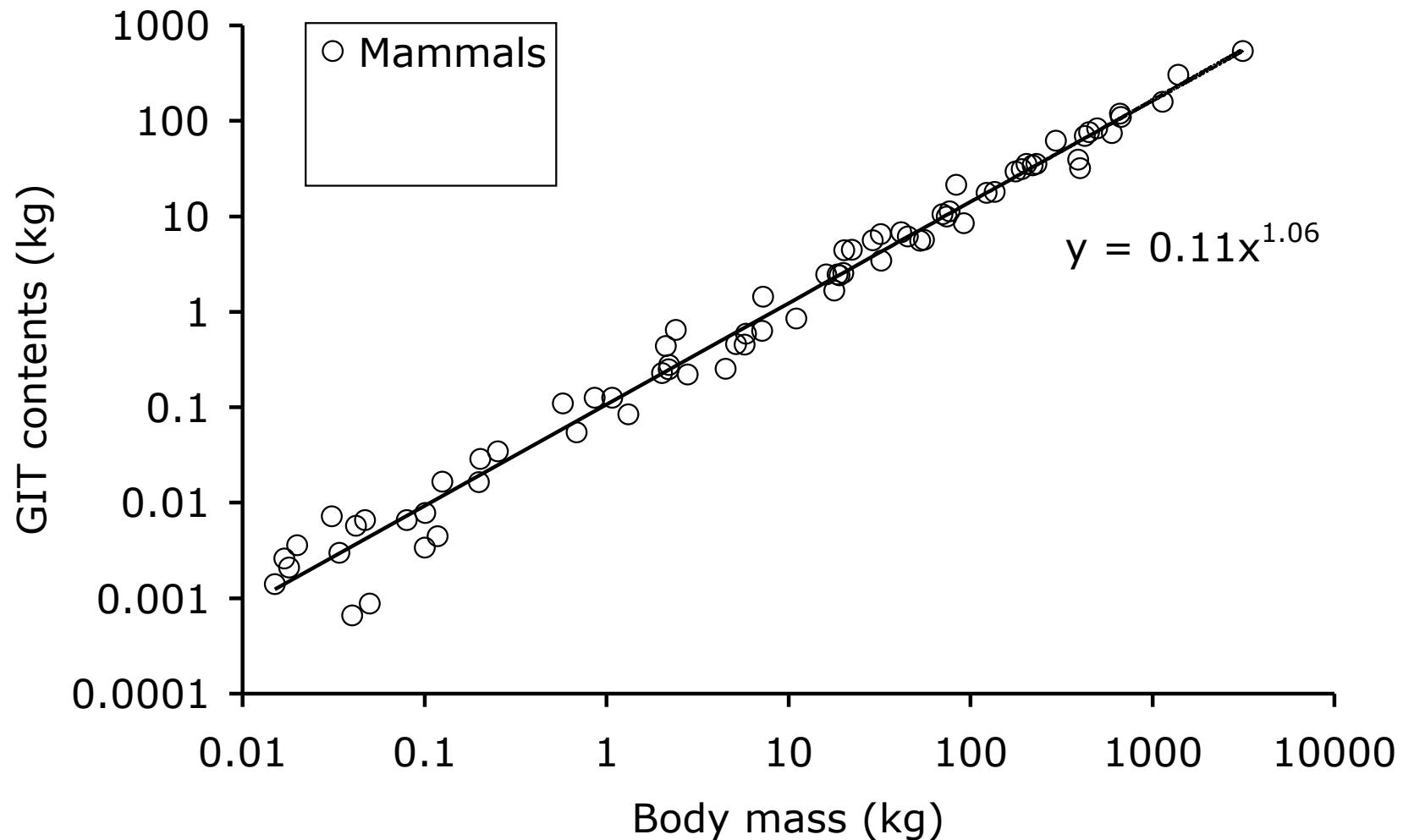


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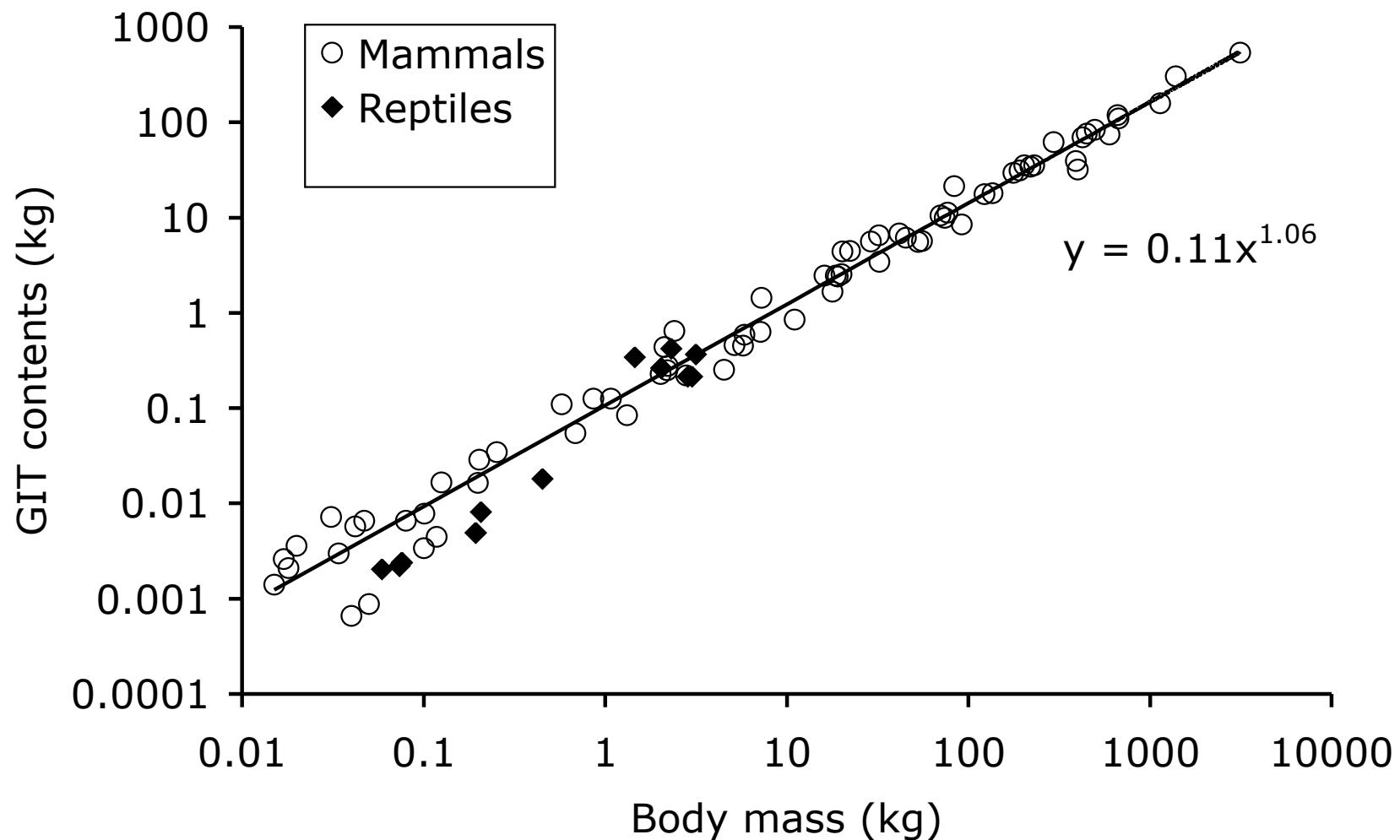


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(measured by slaughtering)

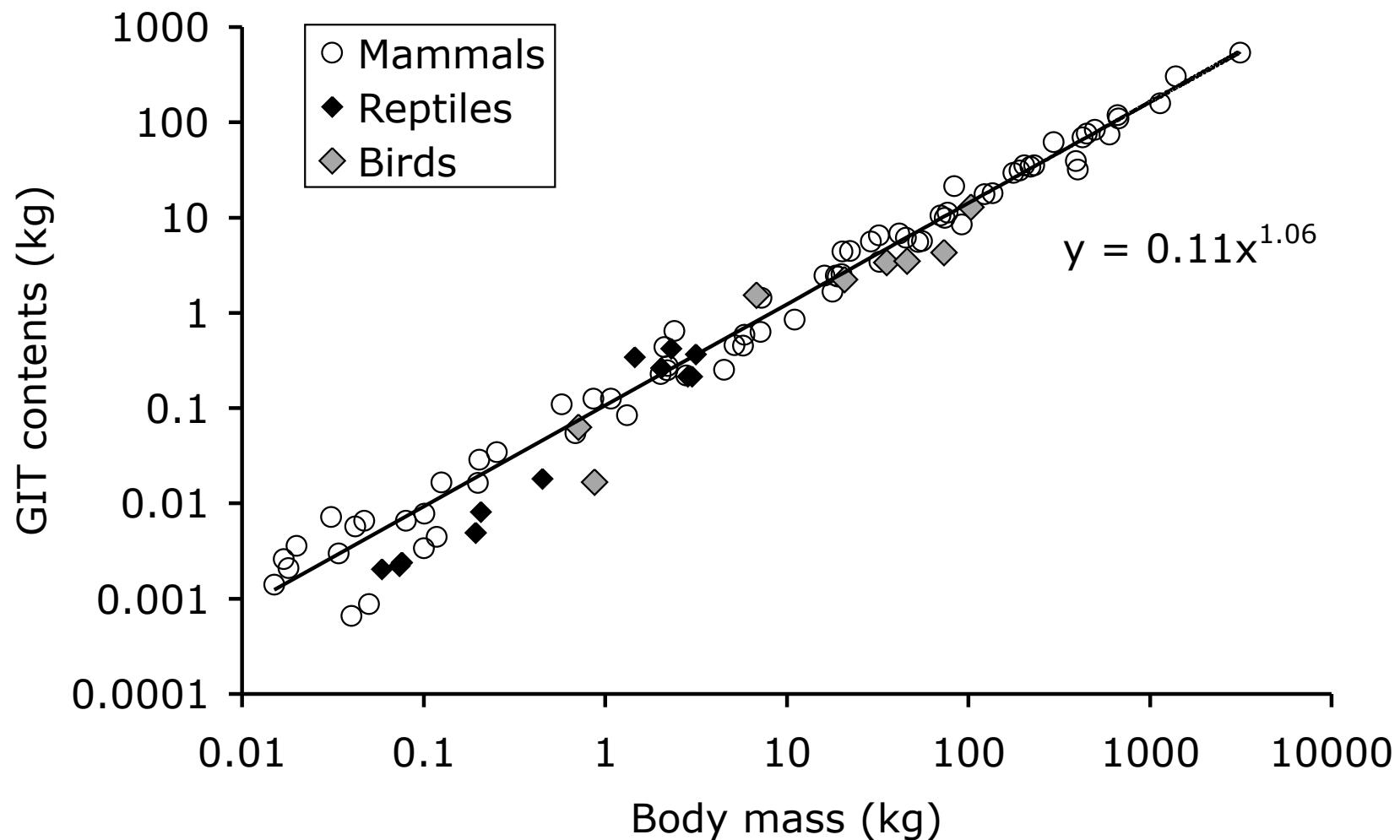


mammal data collection Clauss et al. (2007), reptile from Franz et al. (2009), bird from Fritz et al. (subm.)



# Wet gut content mass

(measured by slaughtering)



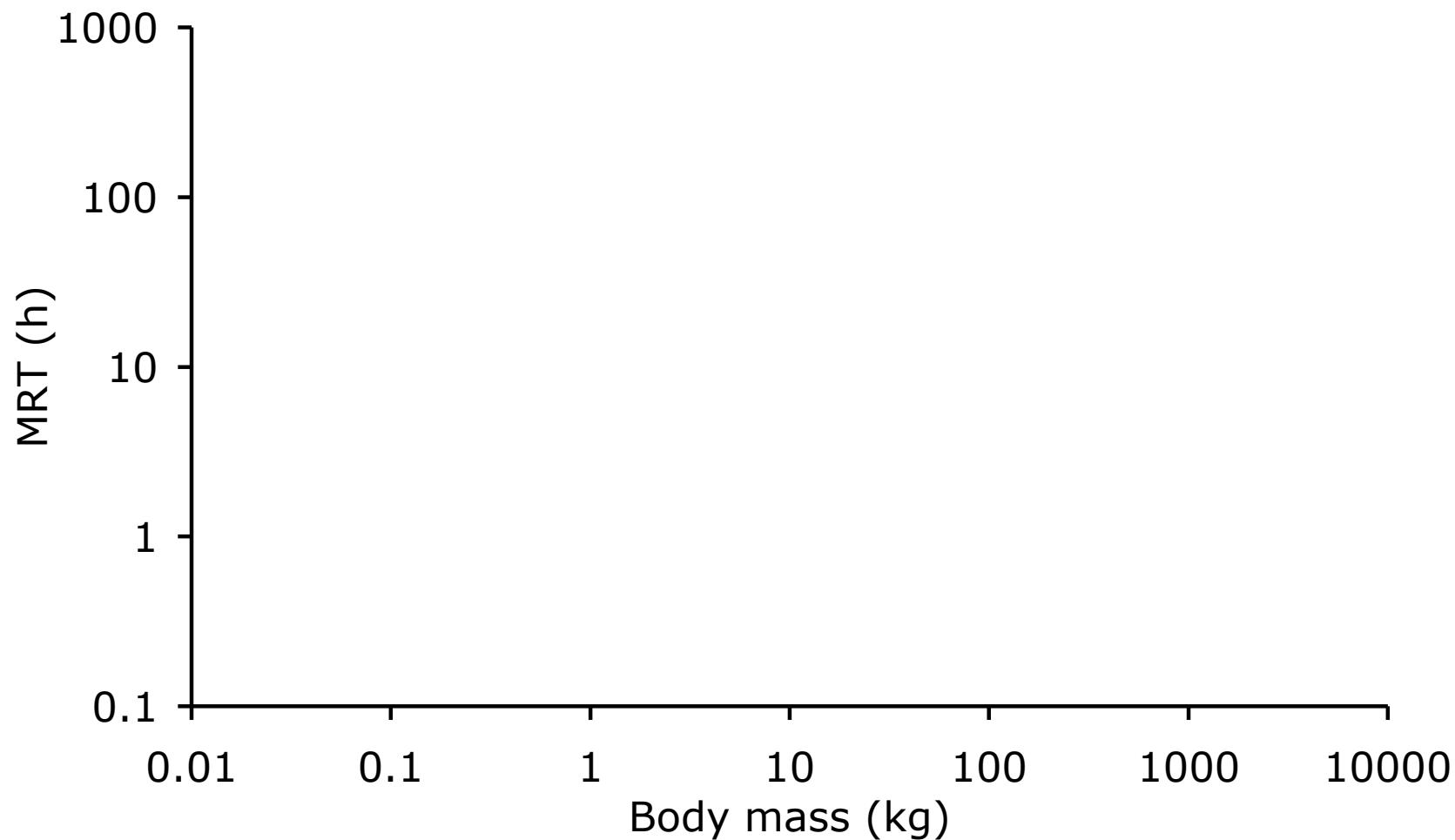
mammal data collection Clauss et al. (2007), reptile from Franz et al. (2009), bird from Fritz et al. (subm.)



# Digesta retention



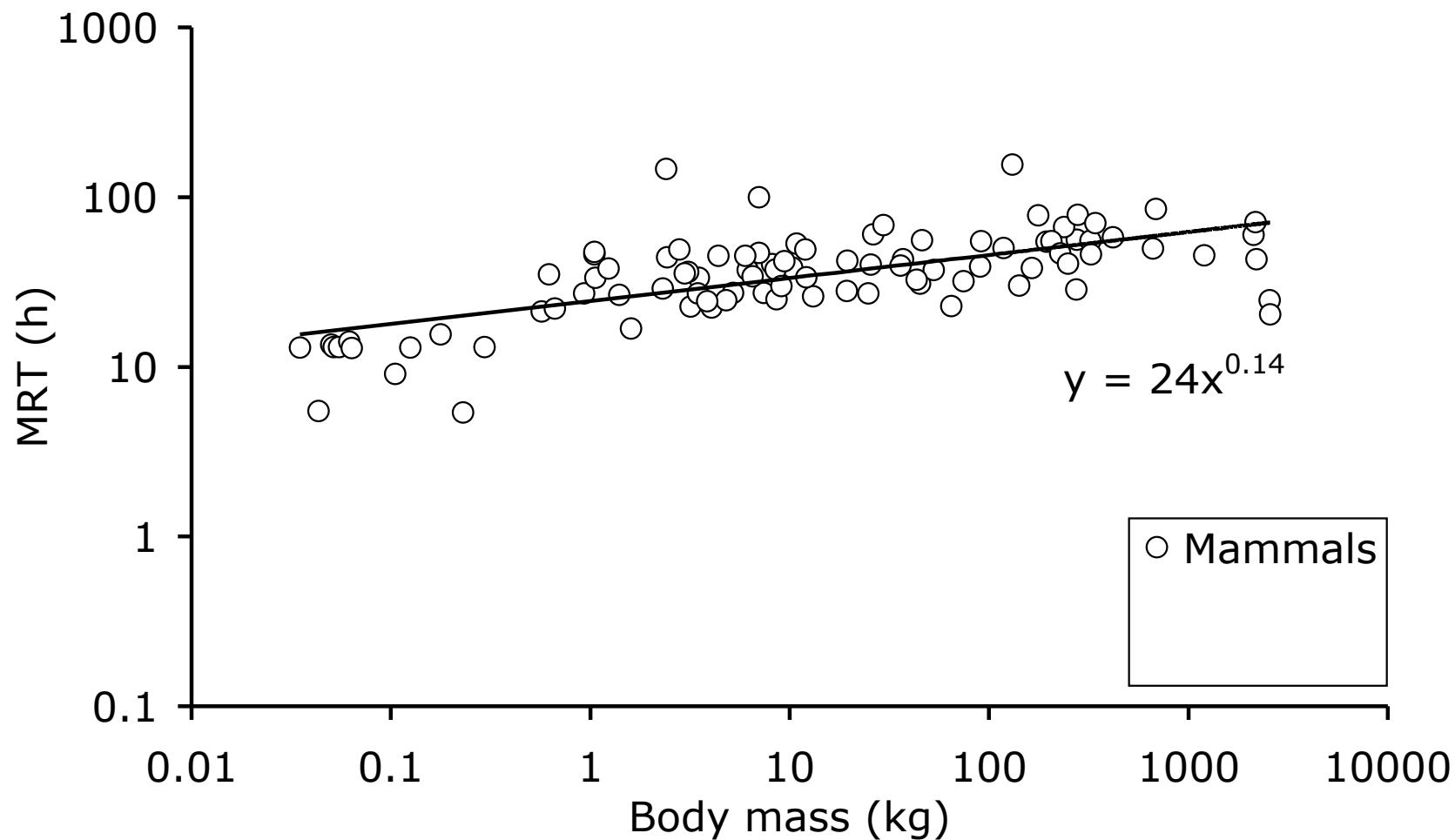
# Mean retention time



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



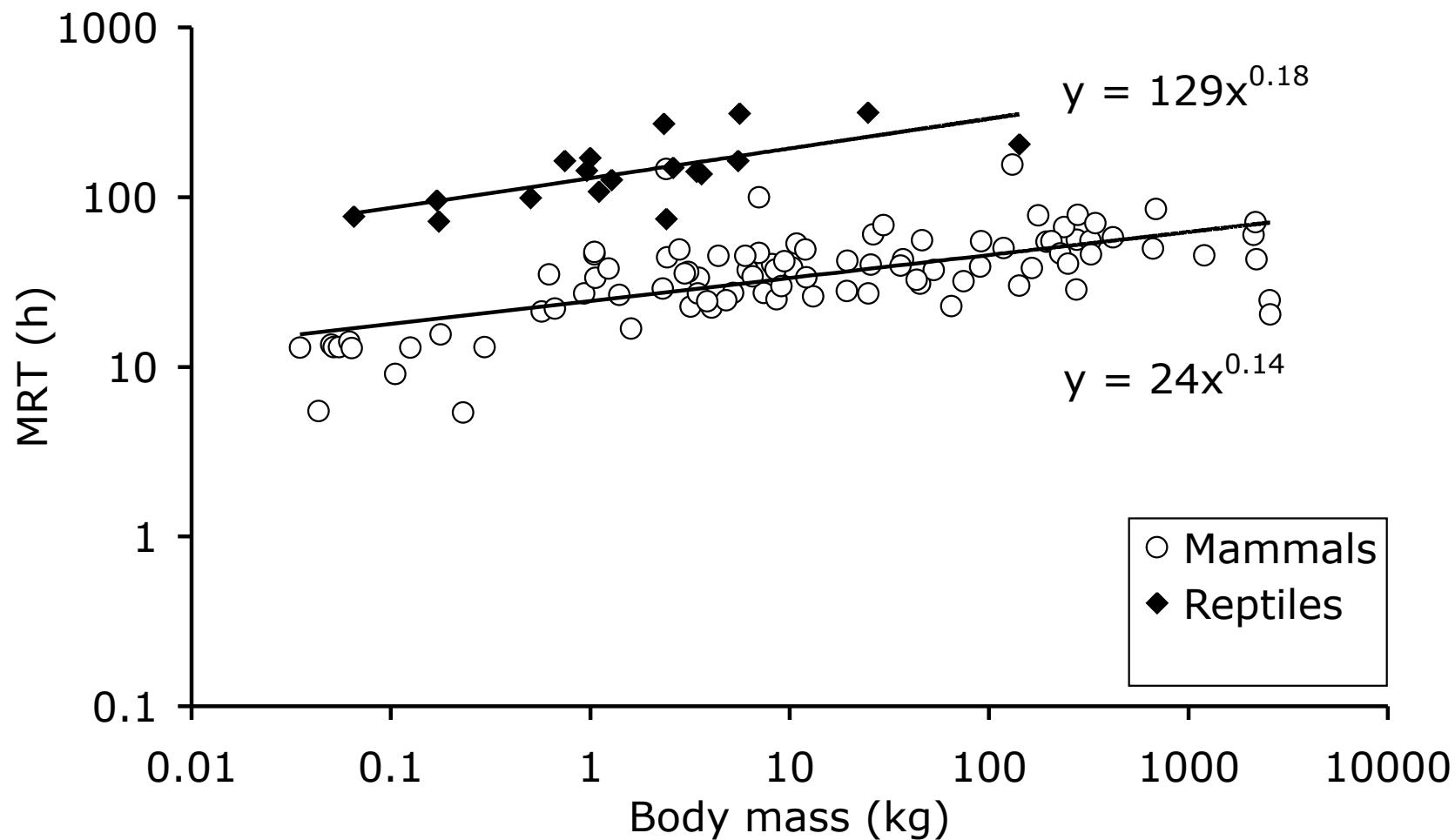
# Mean retention time



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



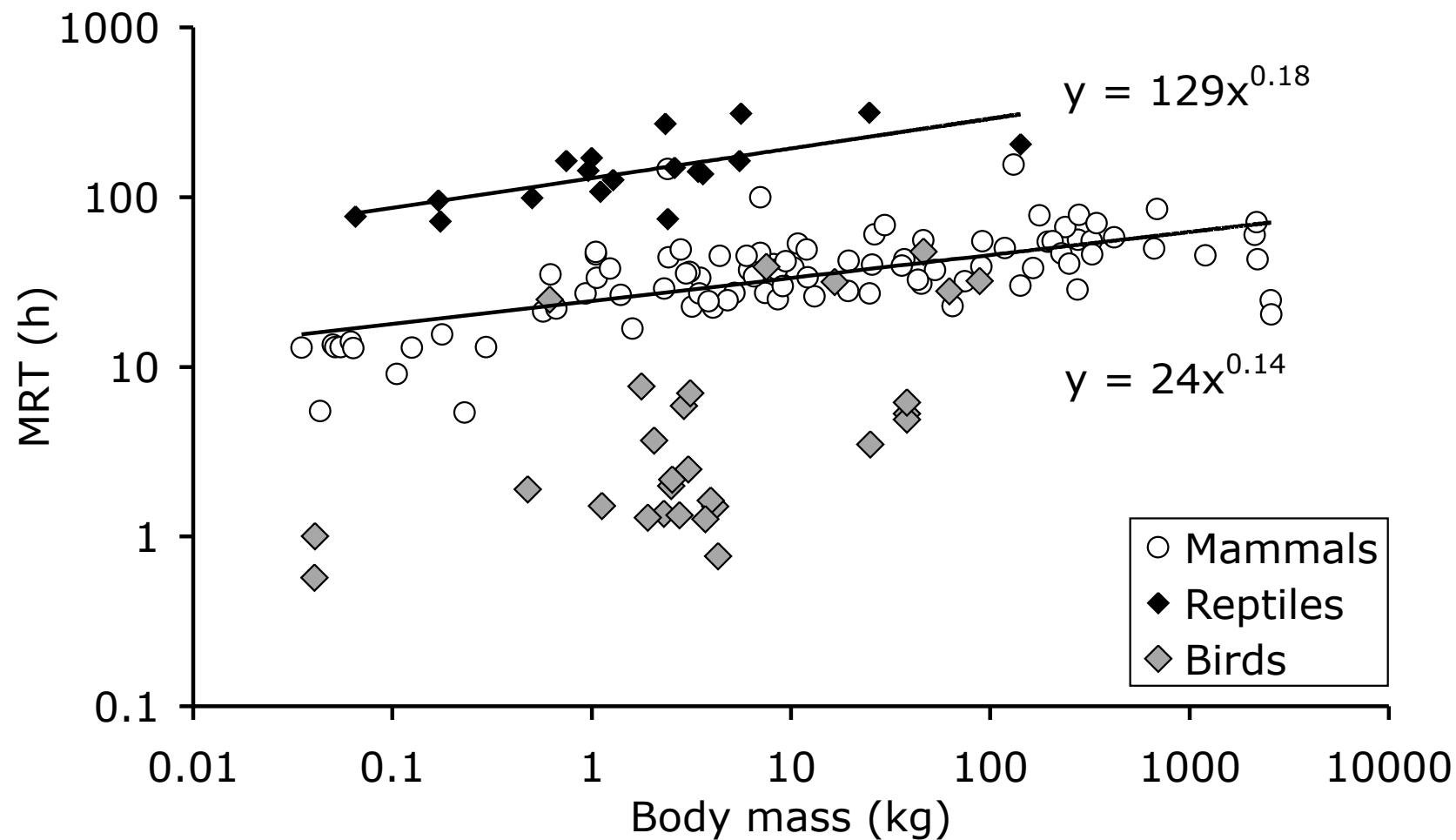
# Mean retention time



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



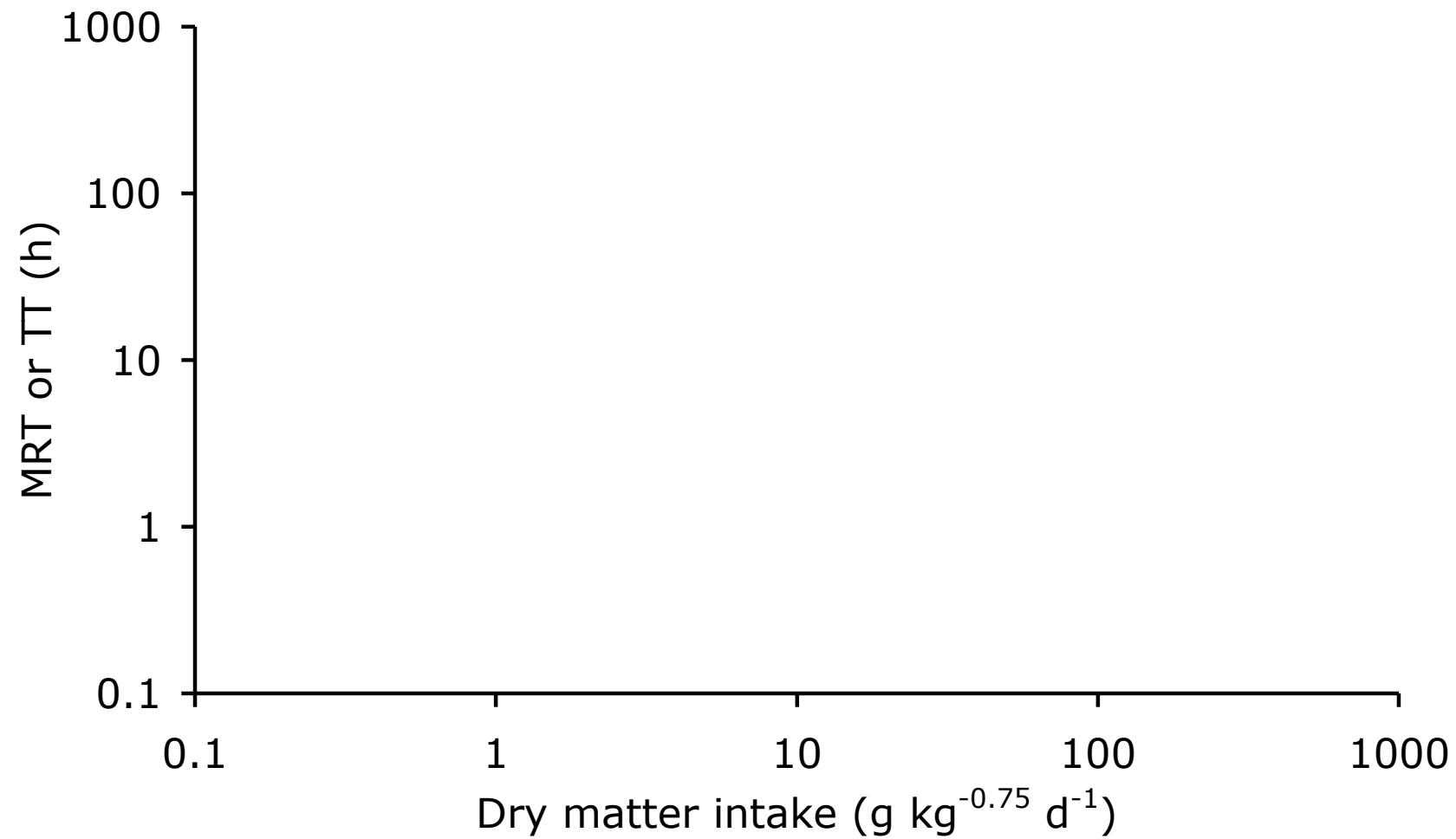
# Mean retention time



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



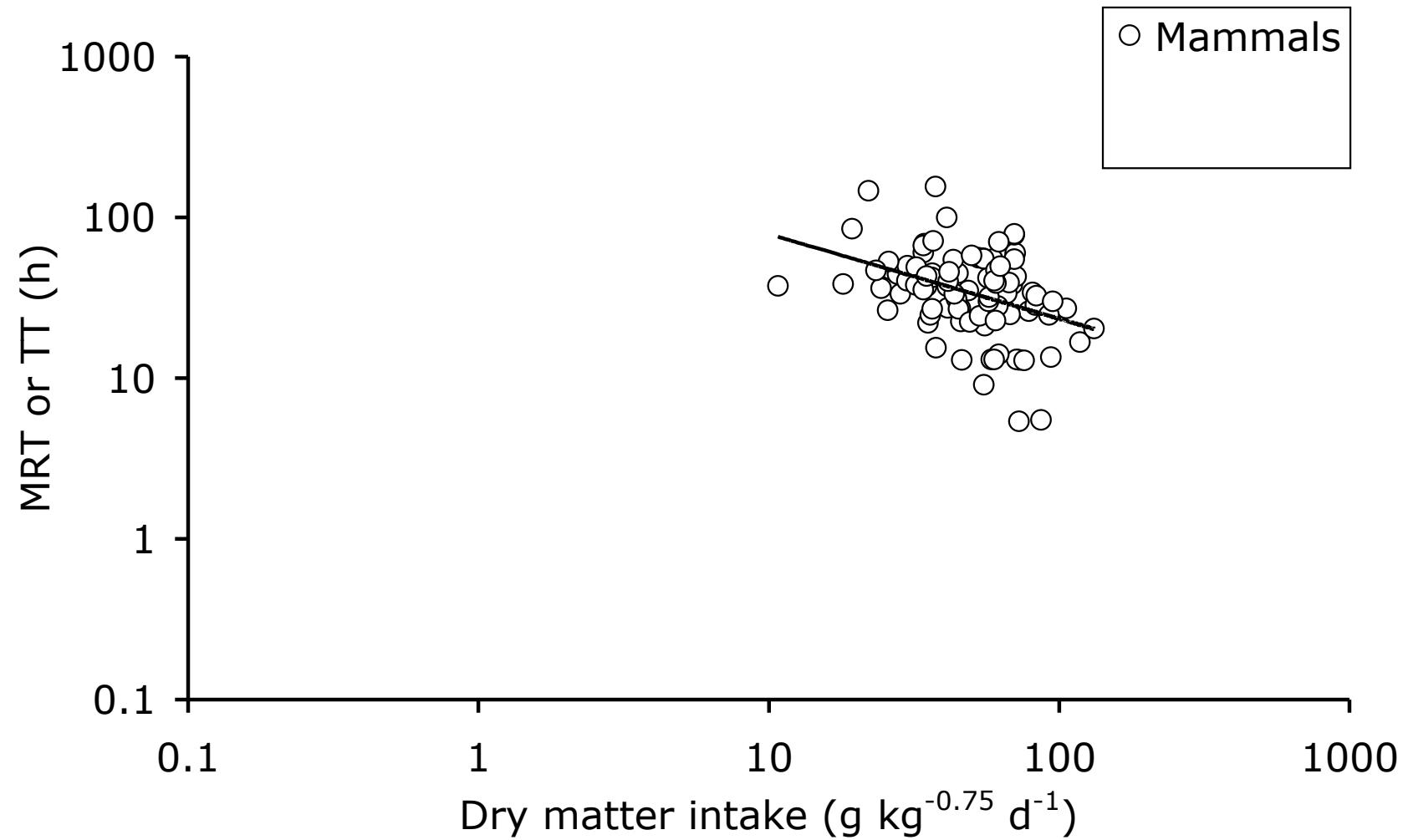
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mammal data collection Clauss et al. (2007), reptile from Franz et al. (2009), bird from Fritz et al. (subm.)



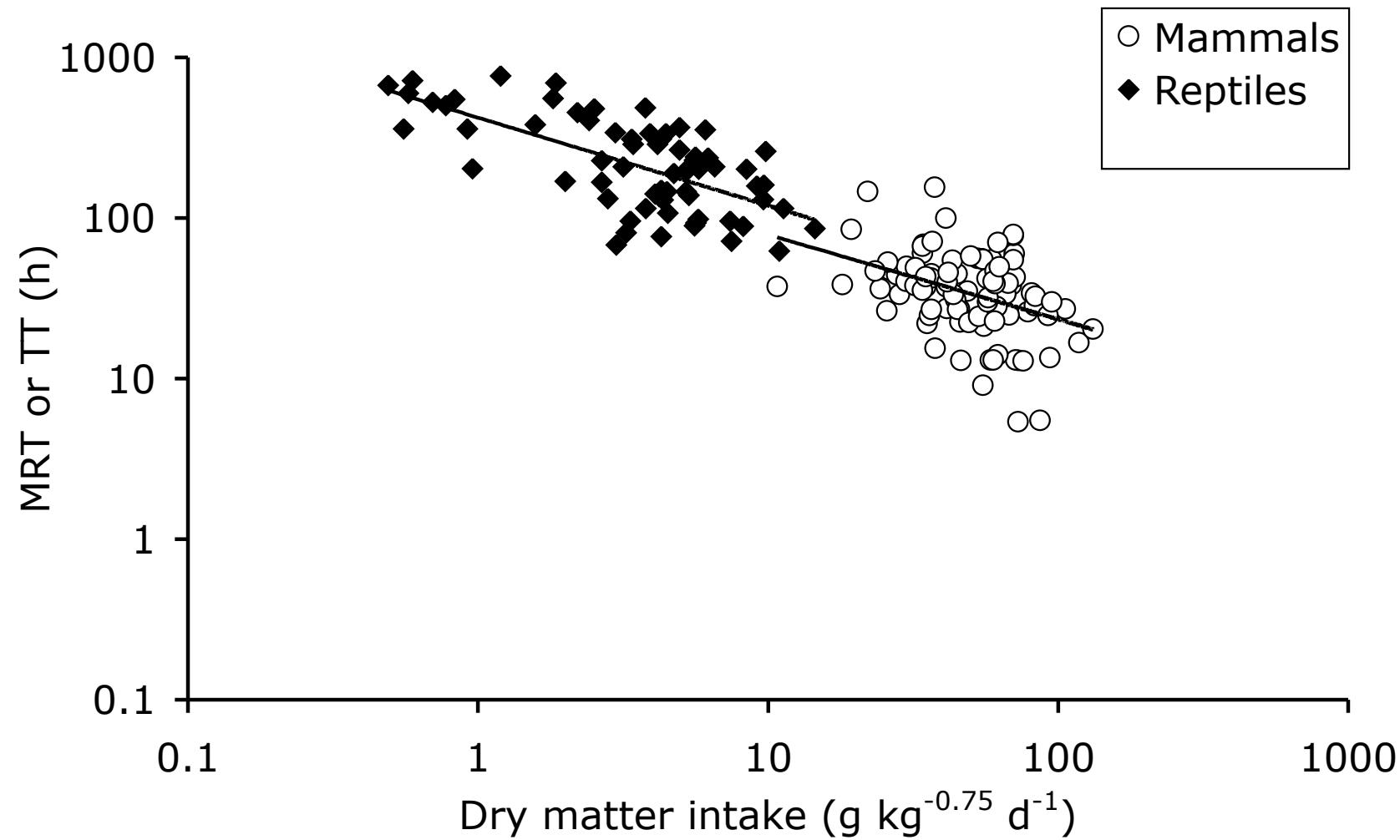
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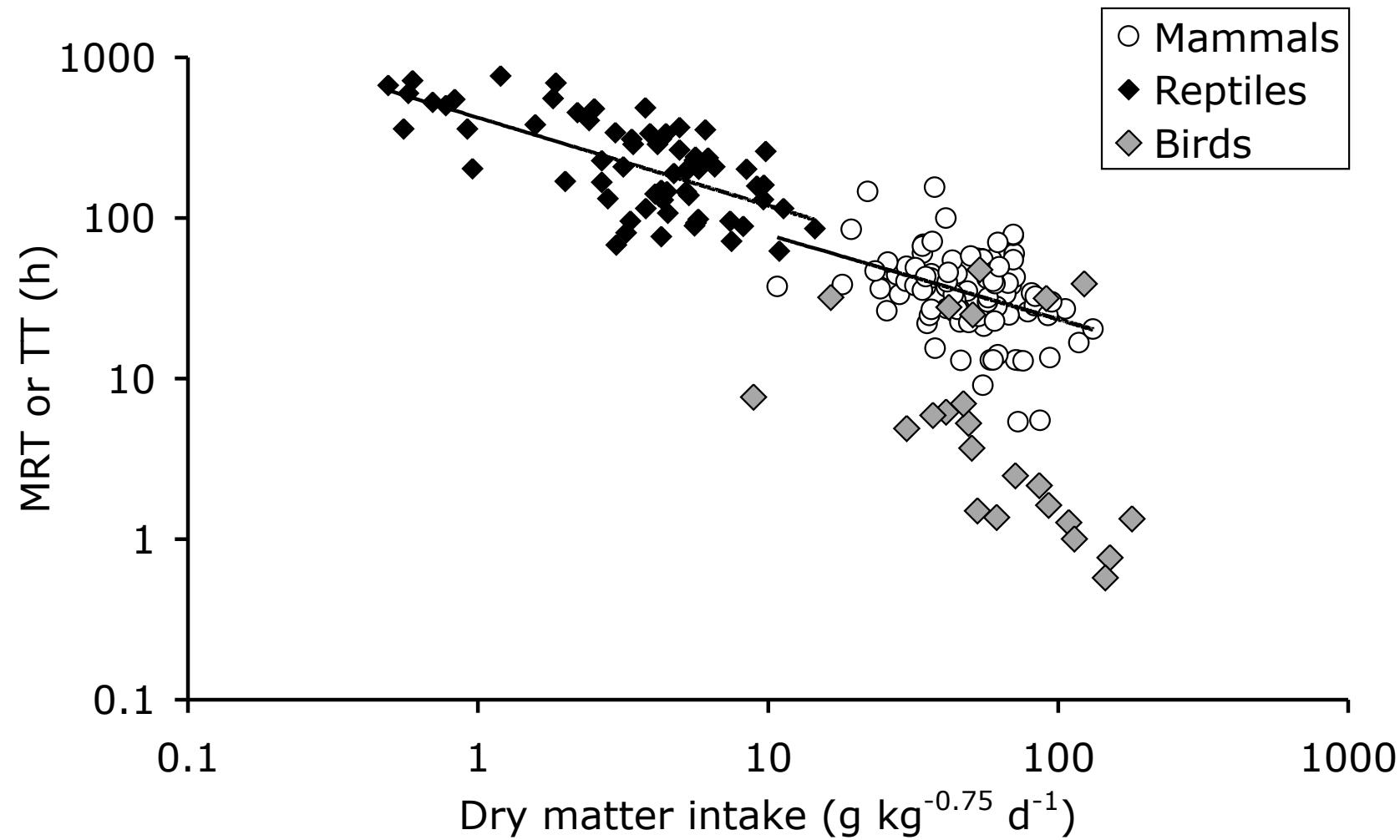
# Mean retention time



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



# Mean retention time



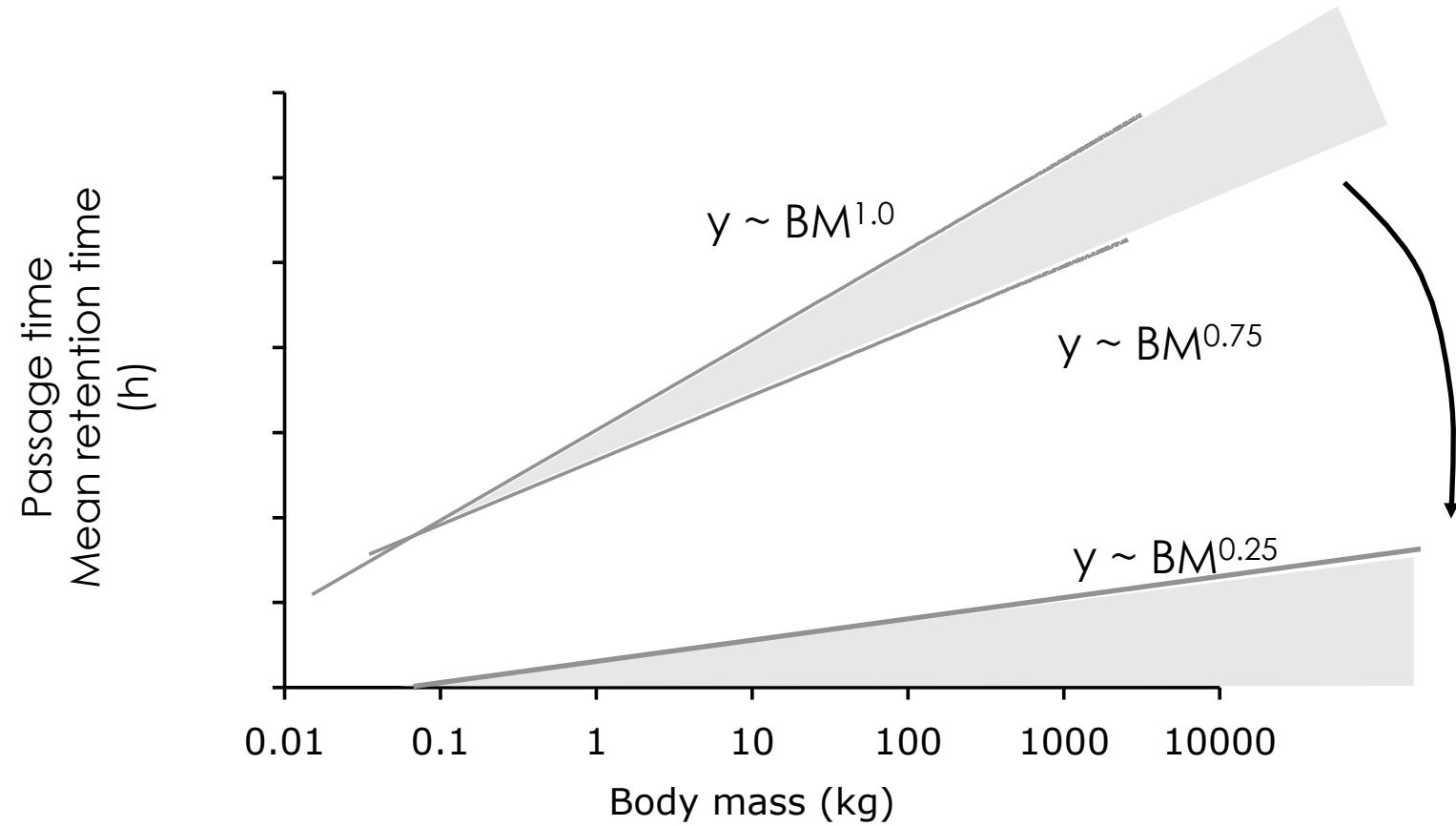
mammal data collection Clauss et al. (2007), reptile from Franz et al. (2009), bird from Fritz et al. (subm.)



# So what now?



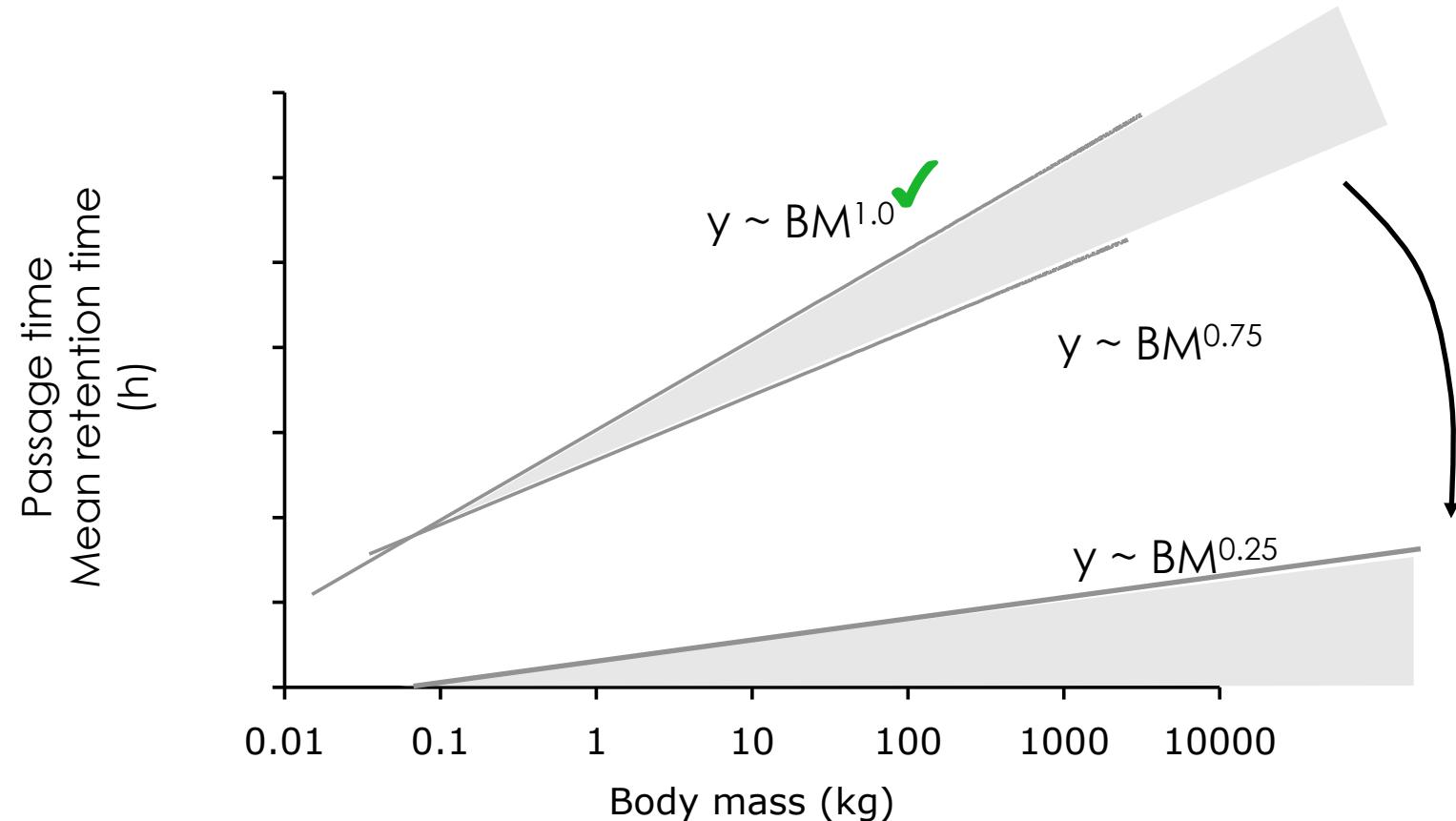
# General allometric considerations



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



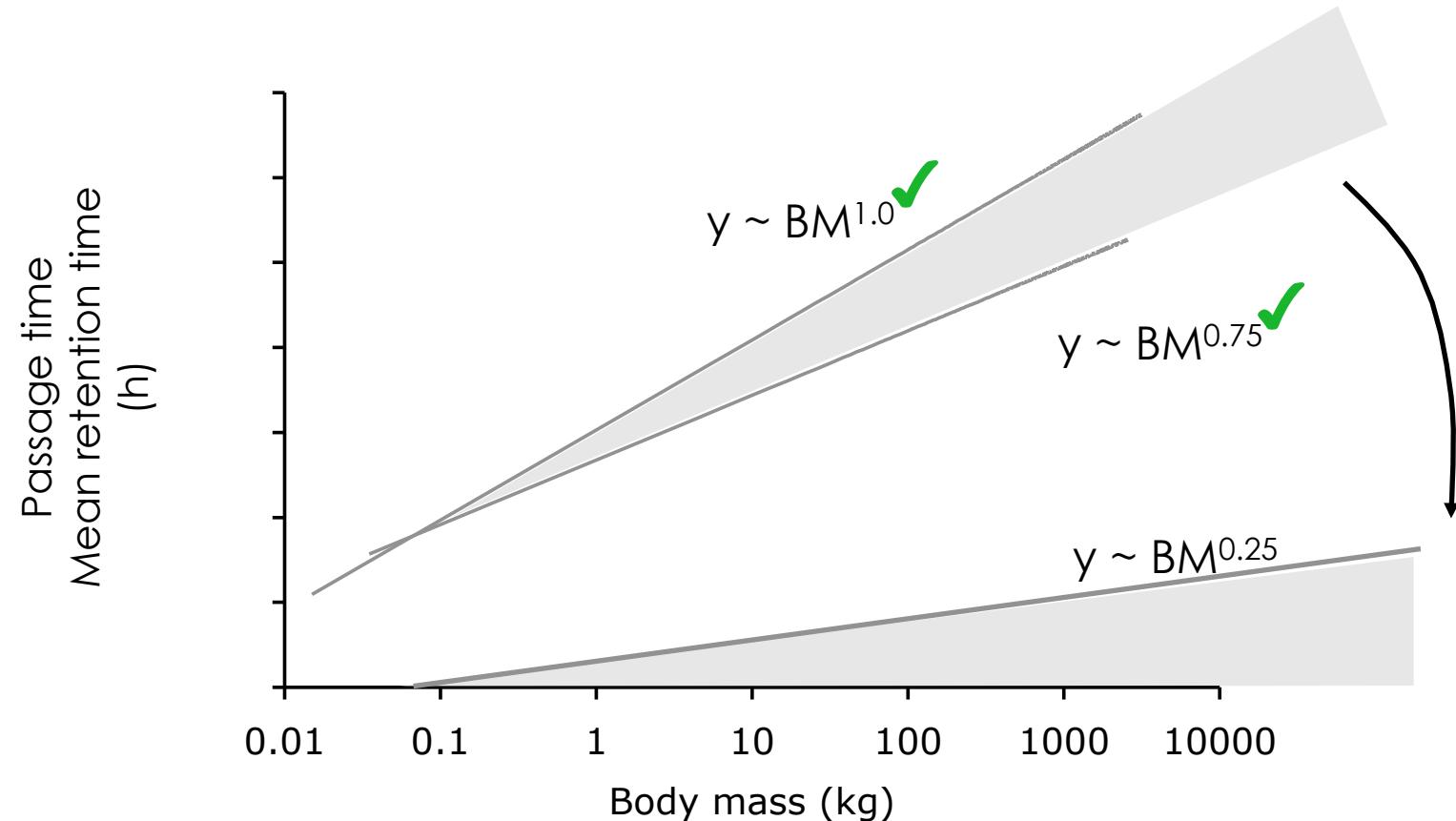
# General allometric considerations



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



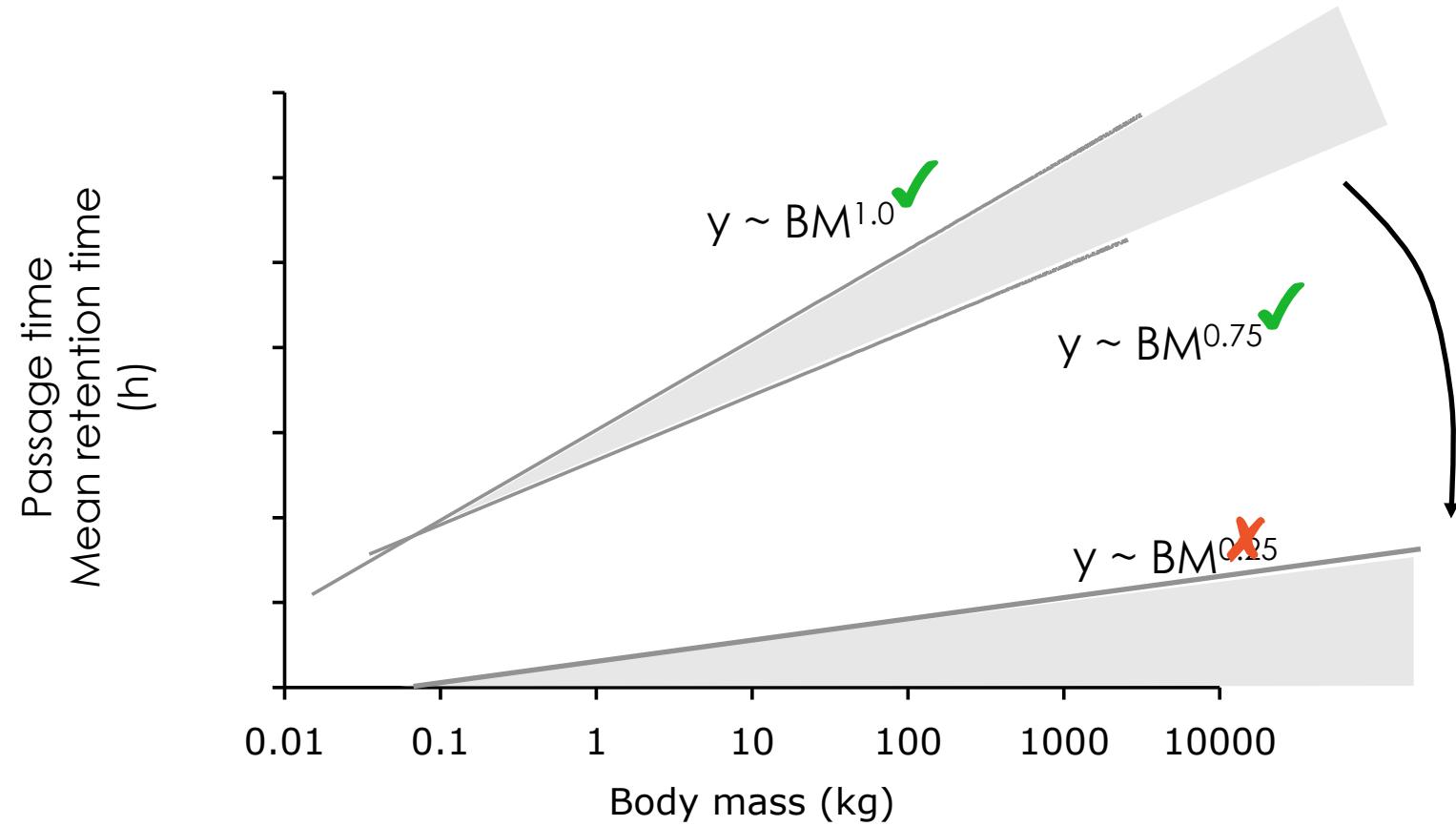
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# General allometric considerations



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



## A serious conceptual 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 there a logical flaw in the concept?
- 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?



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

Digesta retention then scales to  $BM^d = BM^{(a-b+c)}$

If  $a = 1.0$  and  $b = 0.75$  but  $d < 0.25$ , this implies that  $c < 0$ , i.e. a negative scaling of digestibility with  $BM$  in the dataset.



## 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)

---



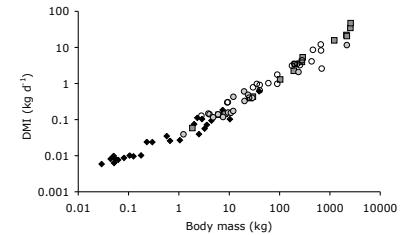
# Using a single dataset

Measurement

Scaling (95%CI)

Dry matter intake

0.76 (0.73-0.79)





# Using a single dataset

Measurement

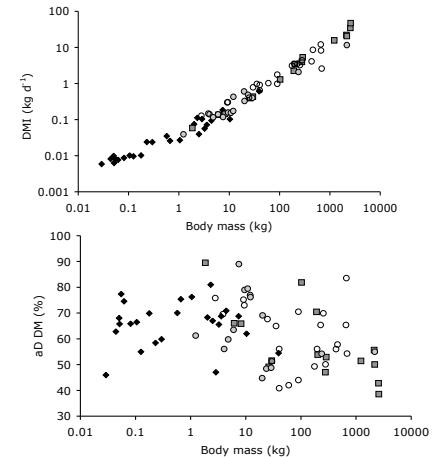
Scaling (95%CI)

Dry matter intake

0.76 (0.73-0.79)

Digestibility

-0.03 (-0.04--0.01)





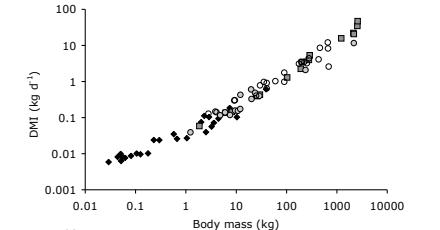
# Using a single dataset

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Scaling (95%CI)

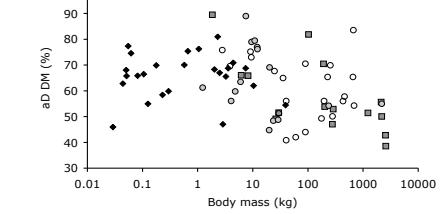
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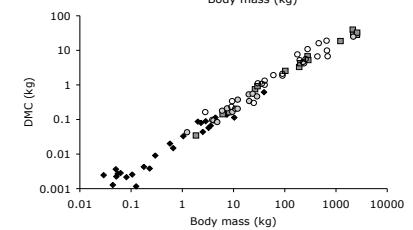
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Dry matter gut fill

0.93 (0.90-0.96)





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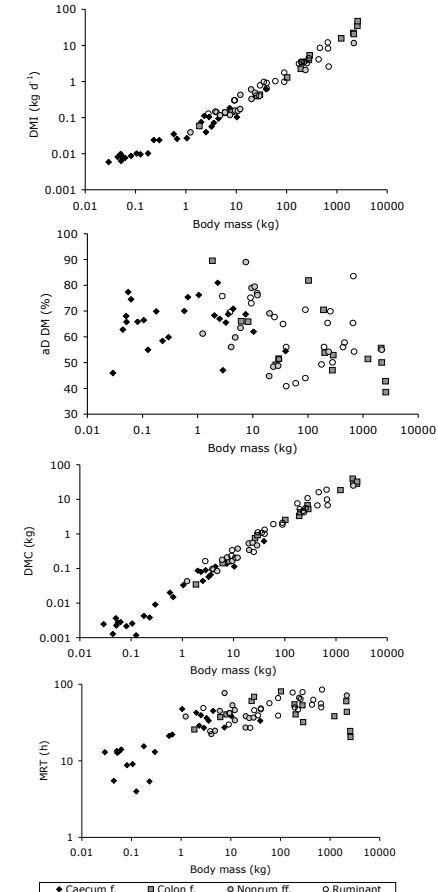
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Dry matter gut fill

0.93 (0.90-0.96)

Particle retention time

0.16 (0.12-0.19)





# The *really real* exponents

Measurement

Scaling (95%CI)

Dry matter intake

0.76 (0.73-0.79)

Digestibility

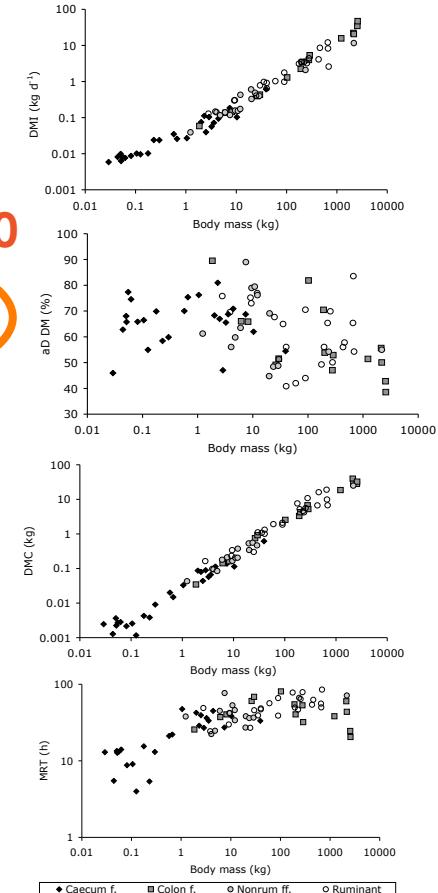
-0.03 (-0.04--0.01)  
*not 0*

Dry matter gut fill

0.93 (0.90-0.96)

Particle retention time

0.16 (0.12-0.19)





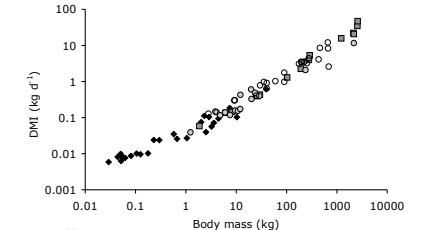
# The *really real* exponents

Measurement

Scaling (95%CI)

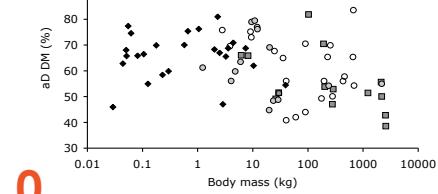
Dry matter intake

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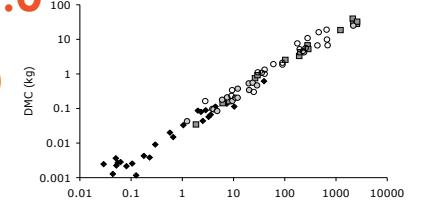
Digestibility

-0.03 (-0.04--0.01)



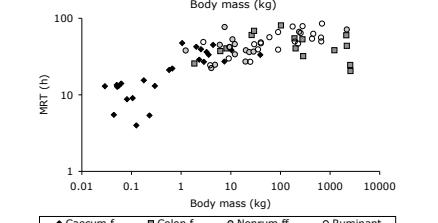
Dry matter gut fill

0.93 (0.90-0.96)  
**not 1.0**



Particle retention time

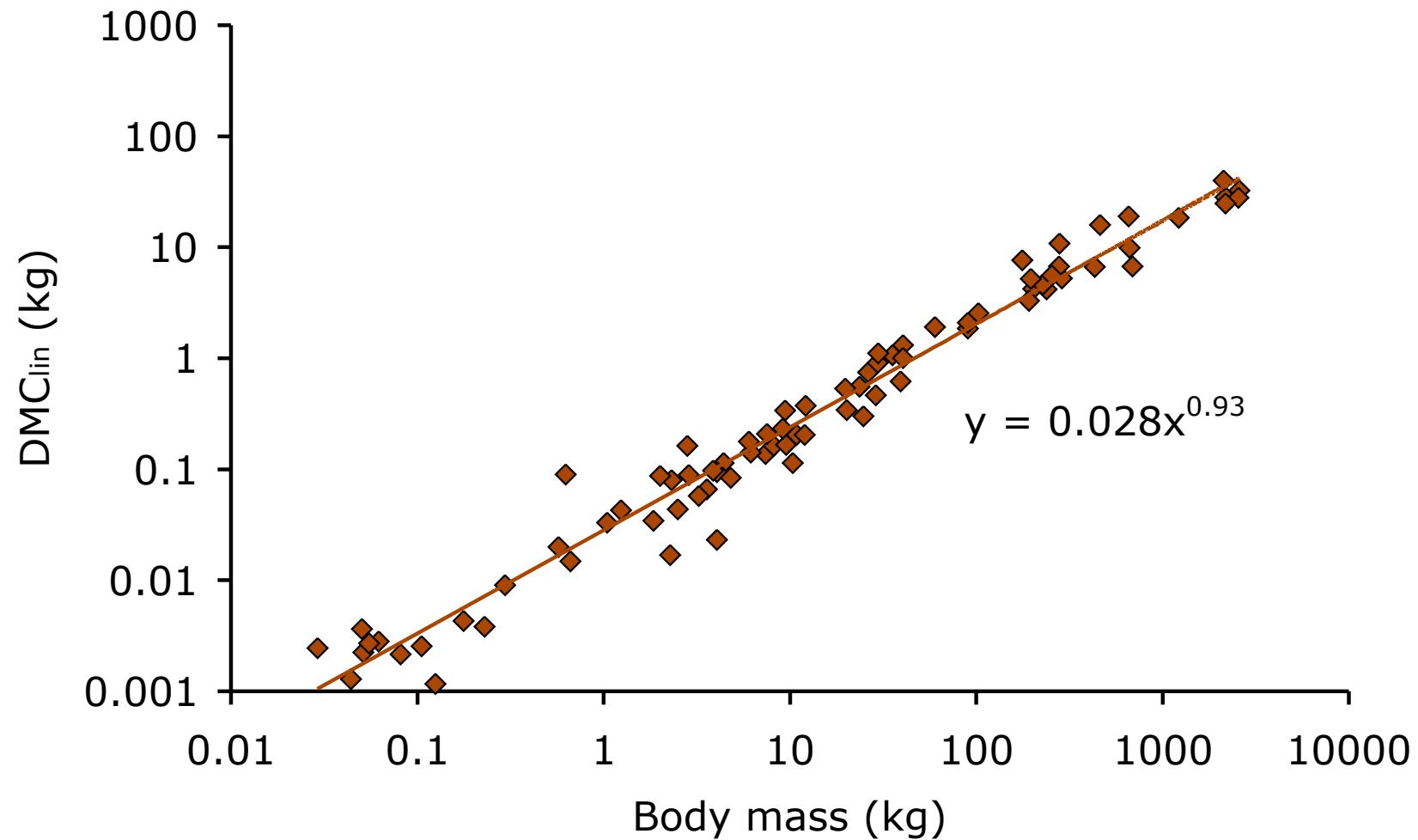
0.16 (0.12-0.19)



◆ Caecum f.    ■ Colon f.    ○ Nonrum ff.    □ Ruminant



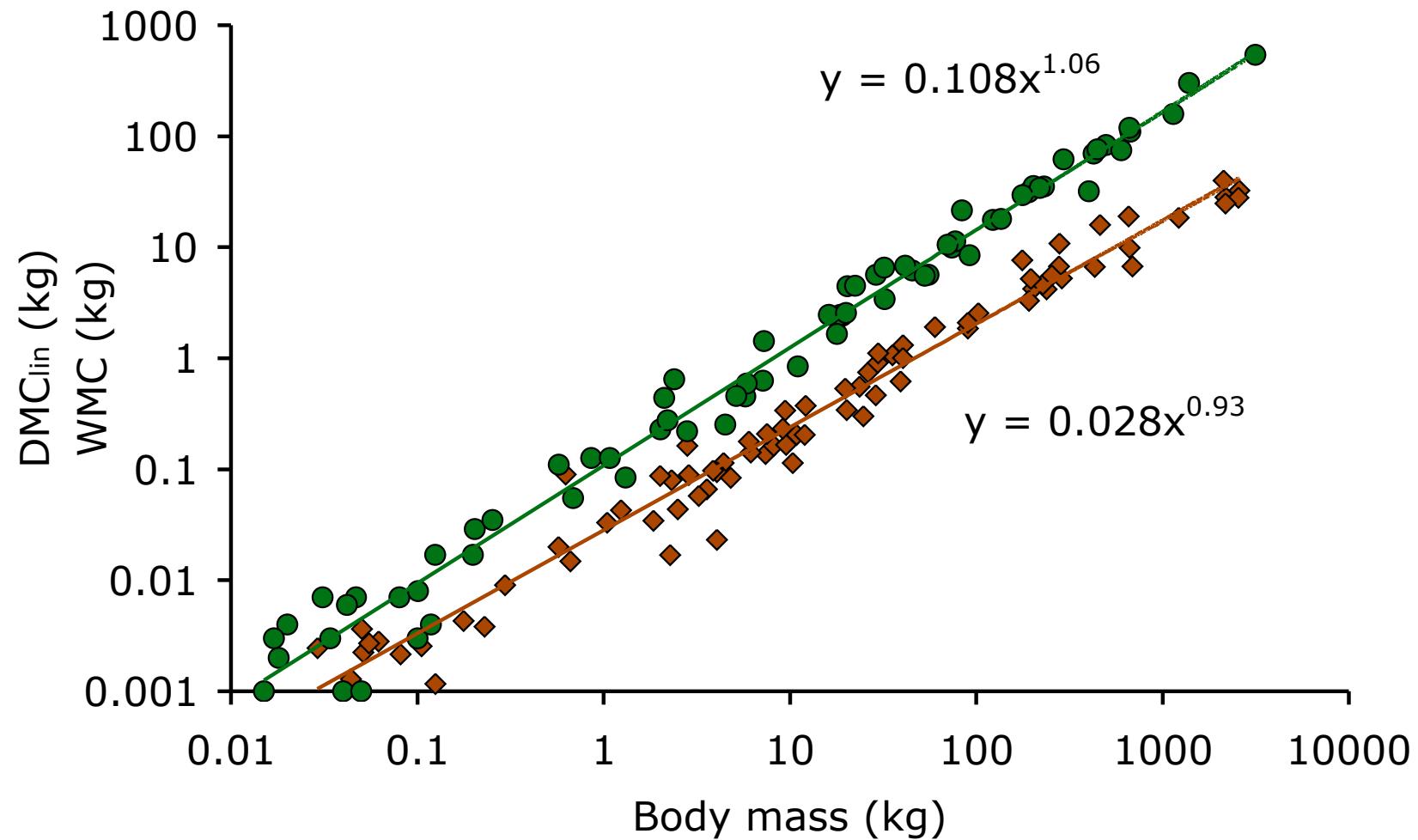
# Gut moisture content



from Müller et al. (subm.)



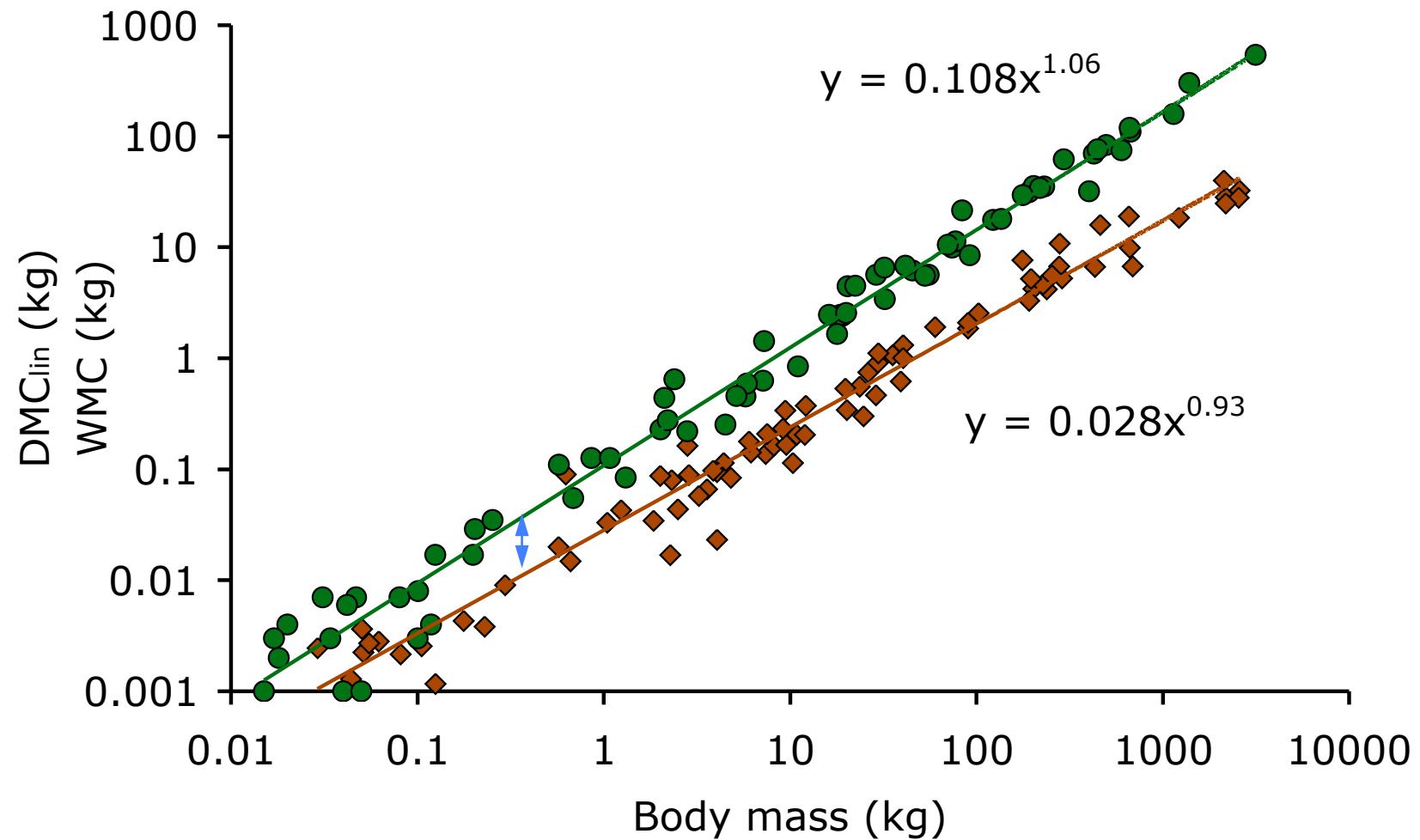
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from Müller et al. (subm.)



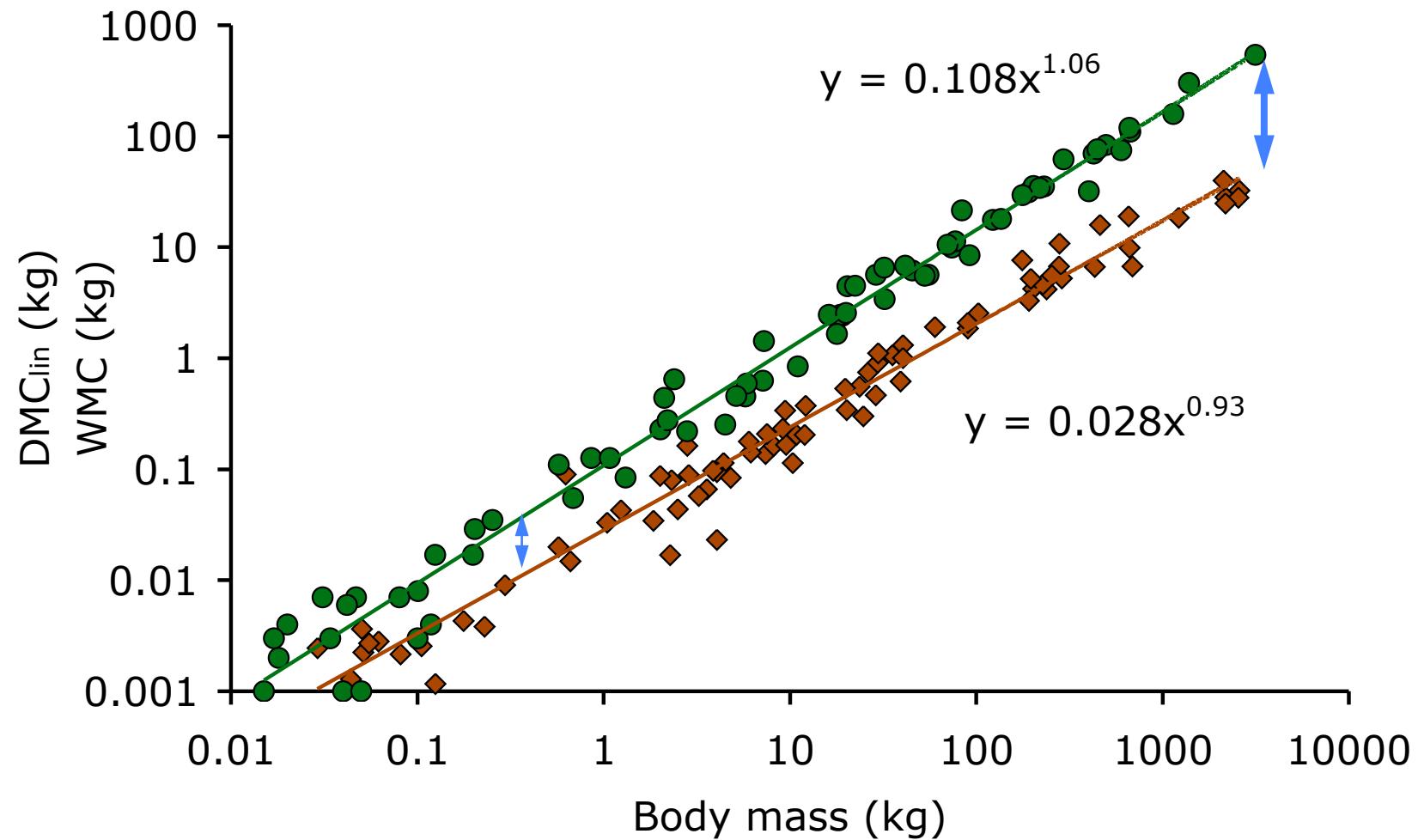
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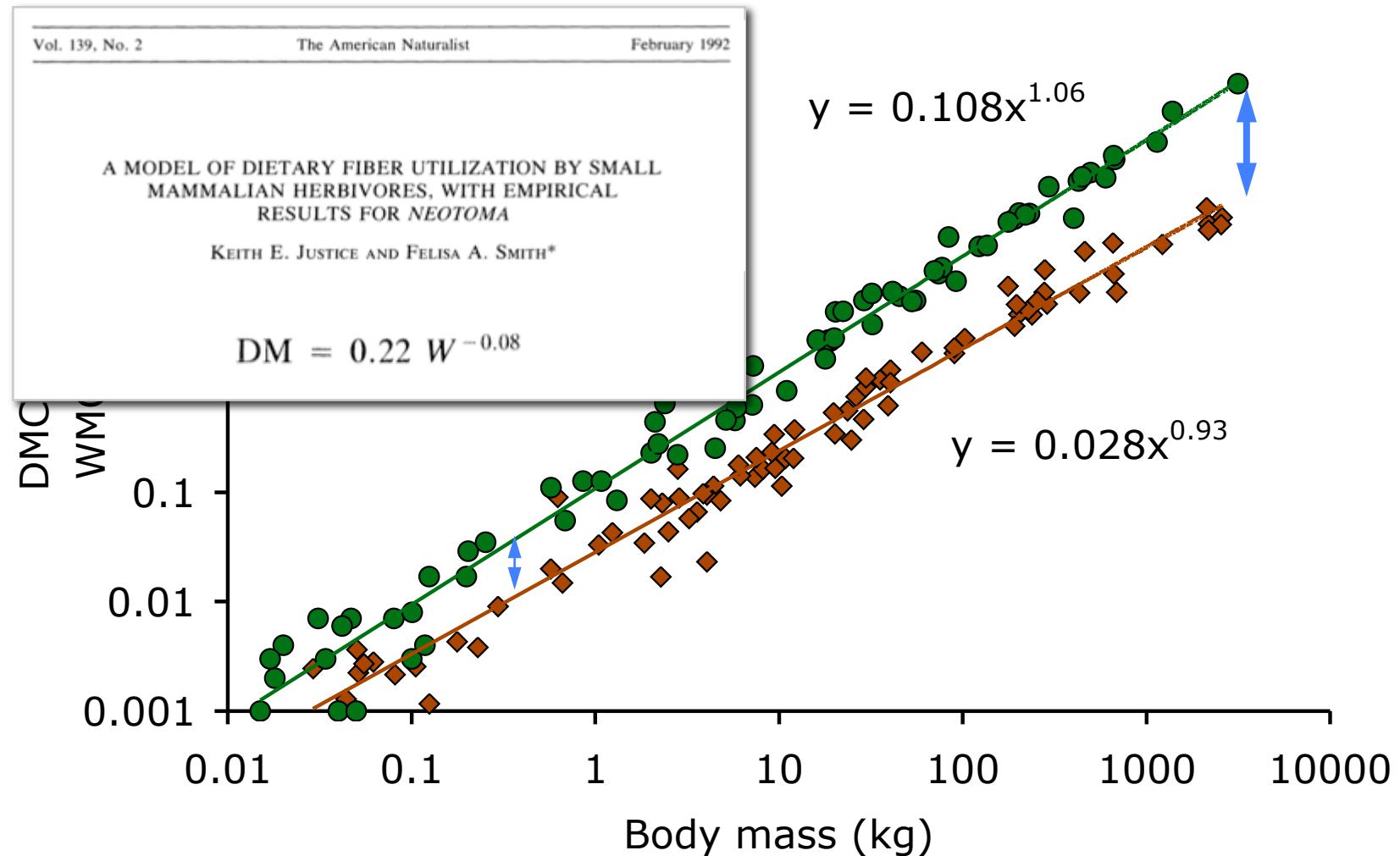
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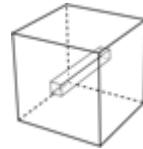
# Gut moisture content



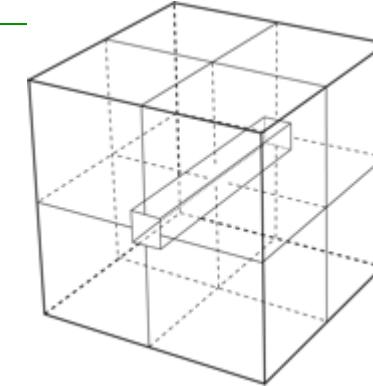
from Müller et al. (subm.)



# Surface/volume geometry



**6:1**

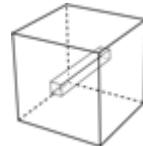


**24:8=3:1**

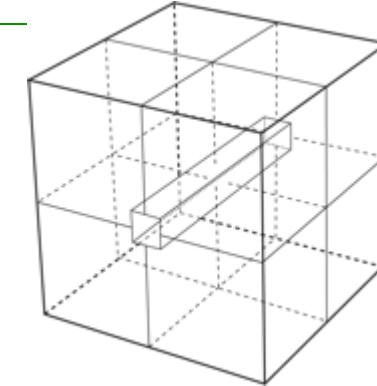
*... affects all surface-related processes*



# Surface/volume geometry

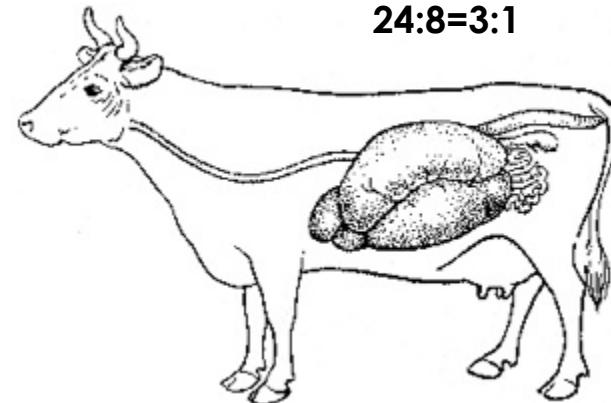
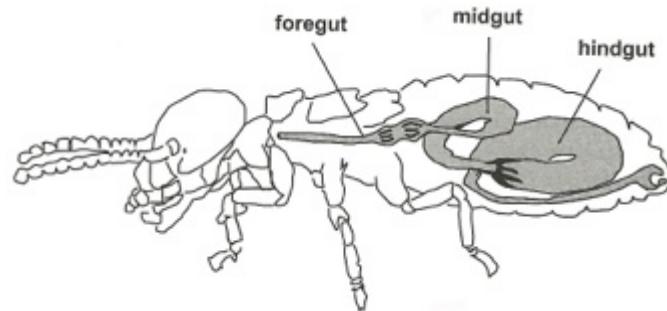


**6:1**



... affects all surface-related processes

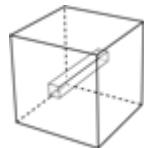
**24:8=3:1**



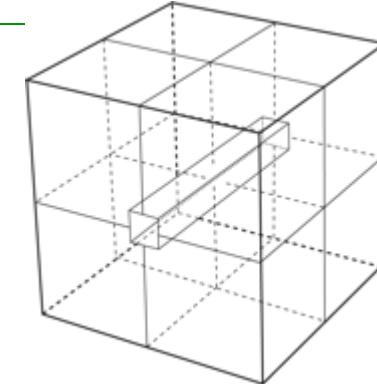
from Karasov & Martinez del Rio (2007)



# Surface/volume geometry

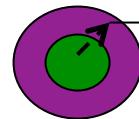
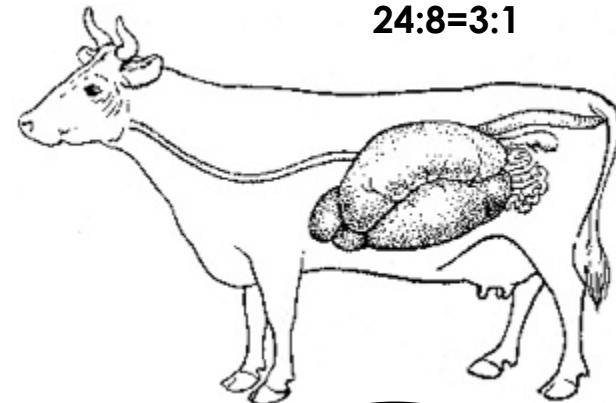
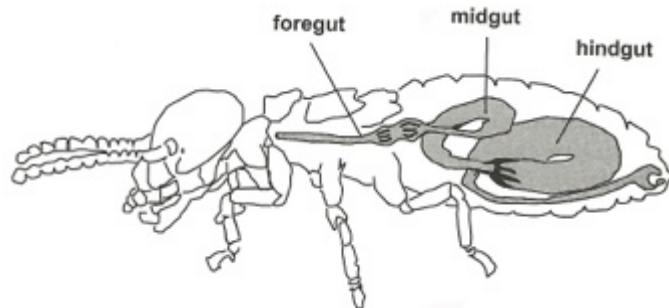


6:1



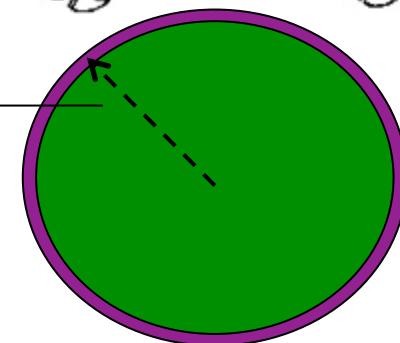
... affects all surface-related processes

24:8=3:1



short  
long

diffusion ways



from Karasov & Martinez del Rio (2007)



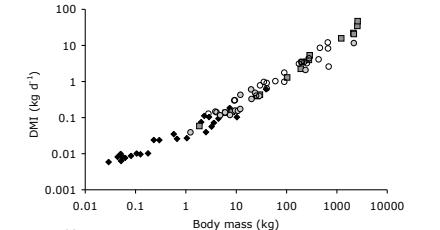
# The *really real* exponents

Measurement

Scaling (95%CI)

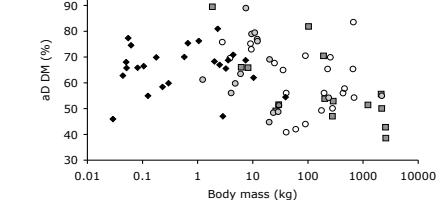
Dry matter intake

0.76 (0.73-0.79)



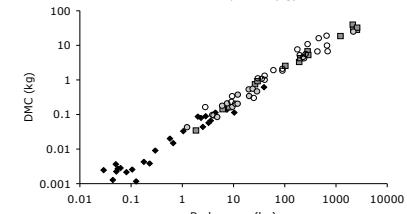
Digestibility

-0.03 (-0.04--0.01)



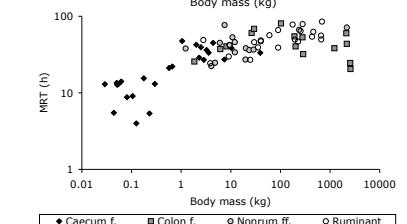
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Particle retention time

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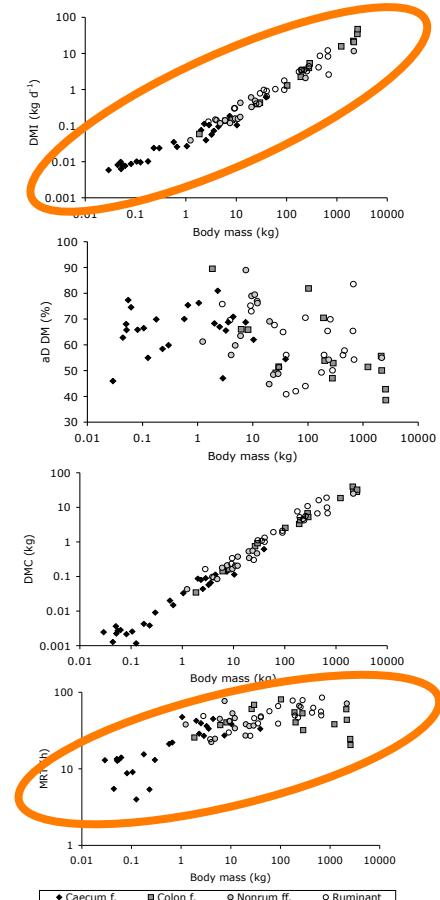
Dry matter gut

**Is this really linear  
scaling in log-log  
space ...**

0.93 (0.90-0.96)

Particle retention time

0.16 (0.12-0.19)





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Dry matter intake

Digestibility

Dry matter gut

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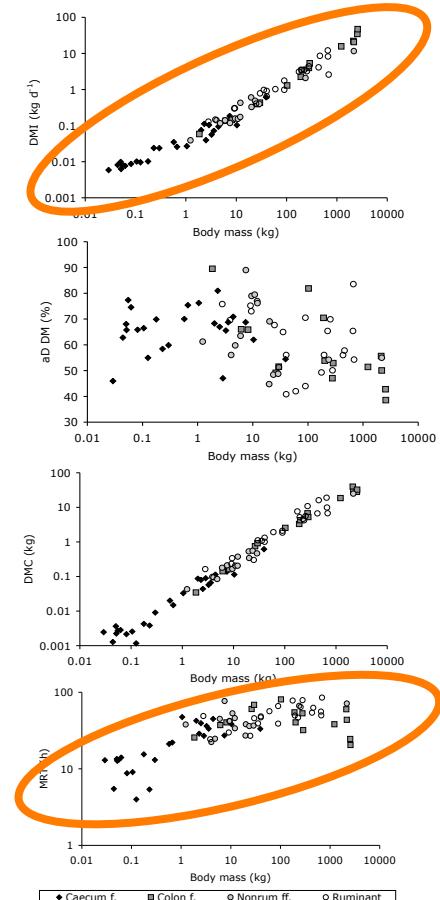
-0.03 (-0.04--0.01)

0.93 (0.90-0.96)

0.16 (0.11-0.19)

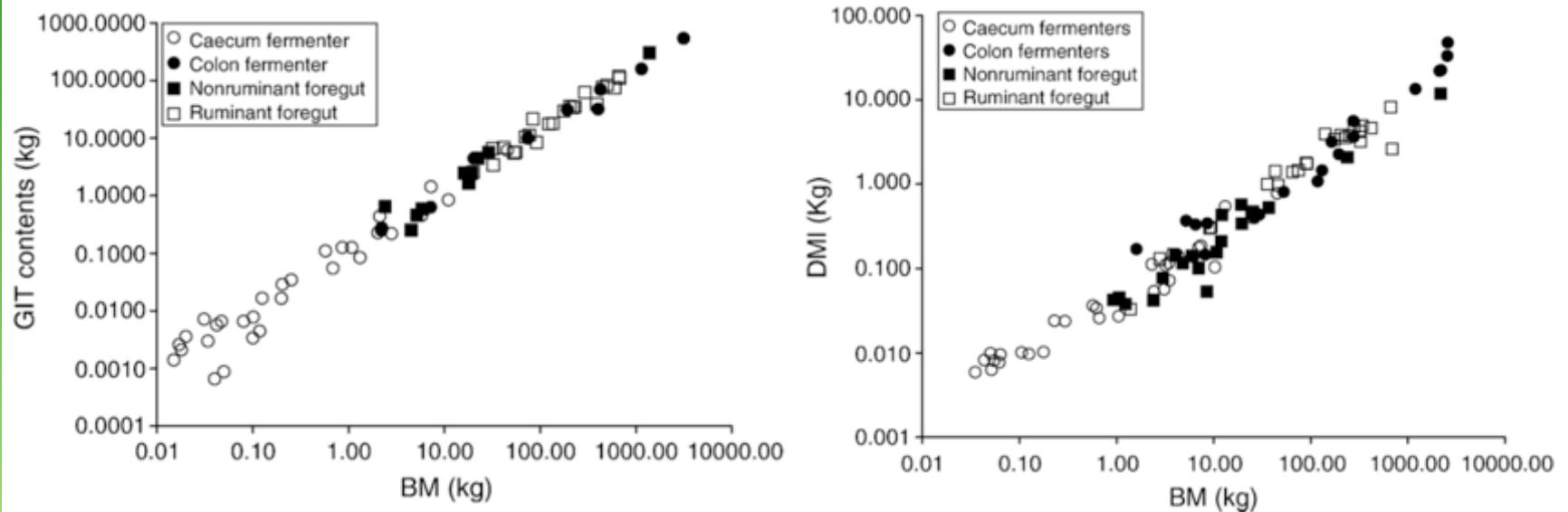
**Is this really linear  
scaling in log-log  
space ...**

**... or a curvature?**





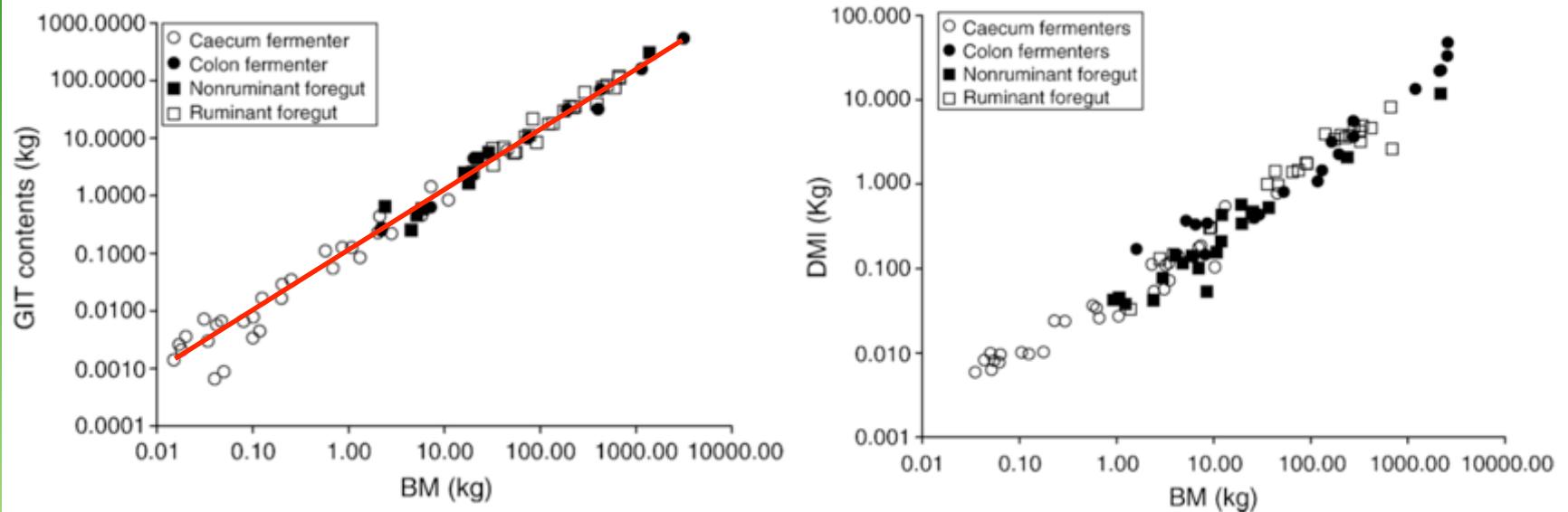
# Straight line ... ?



from Clauss et al. (2007)



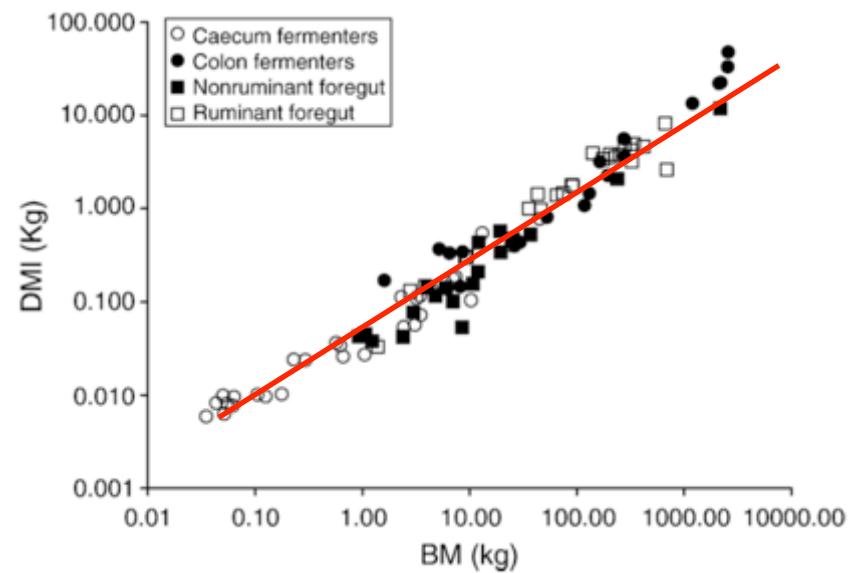
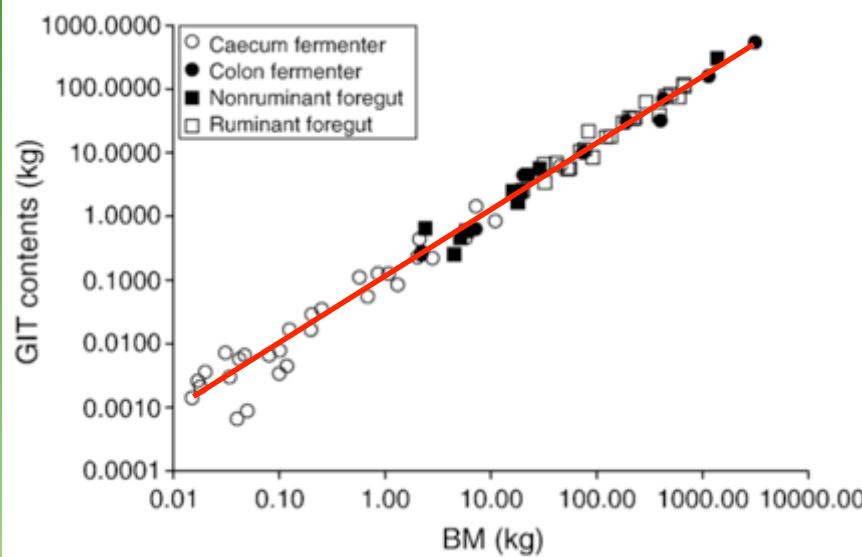
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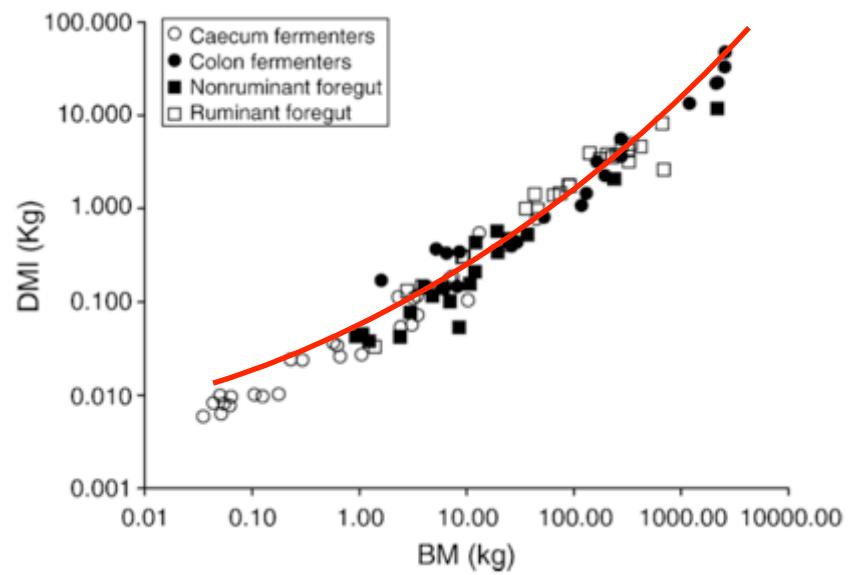
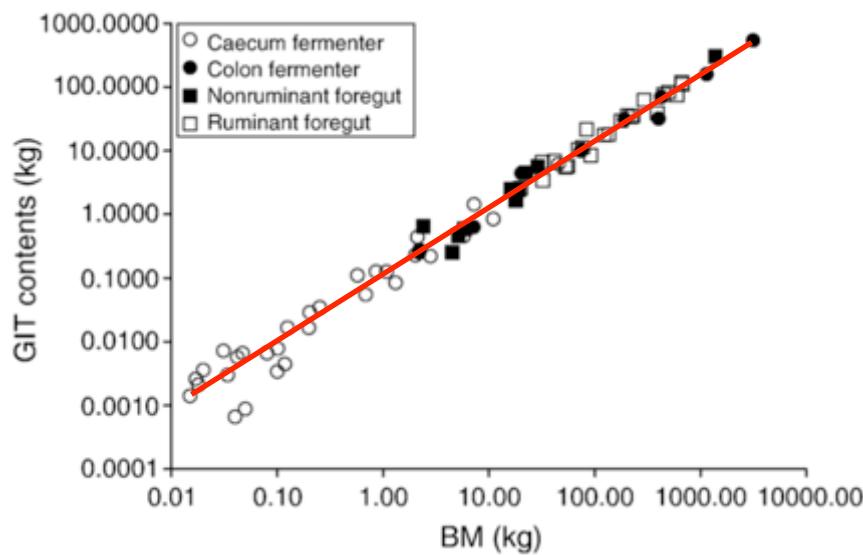
# Straight line ... ?



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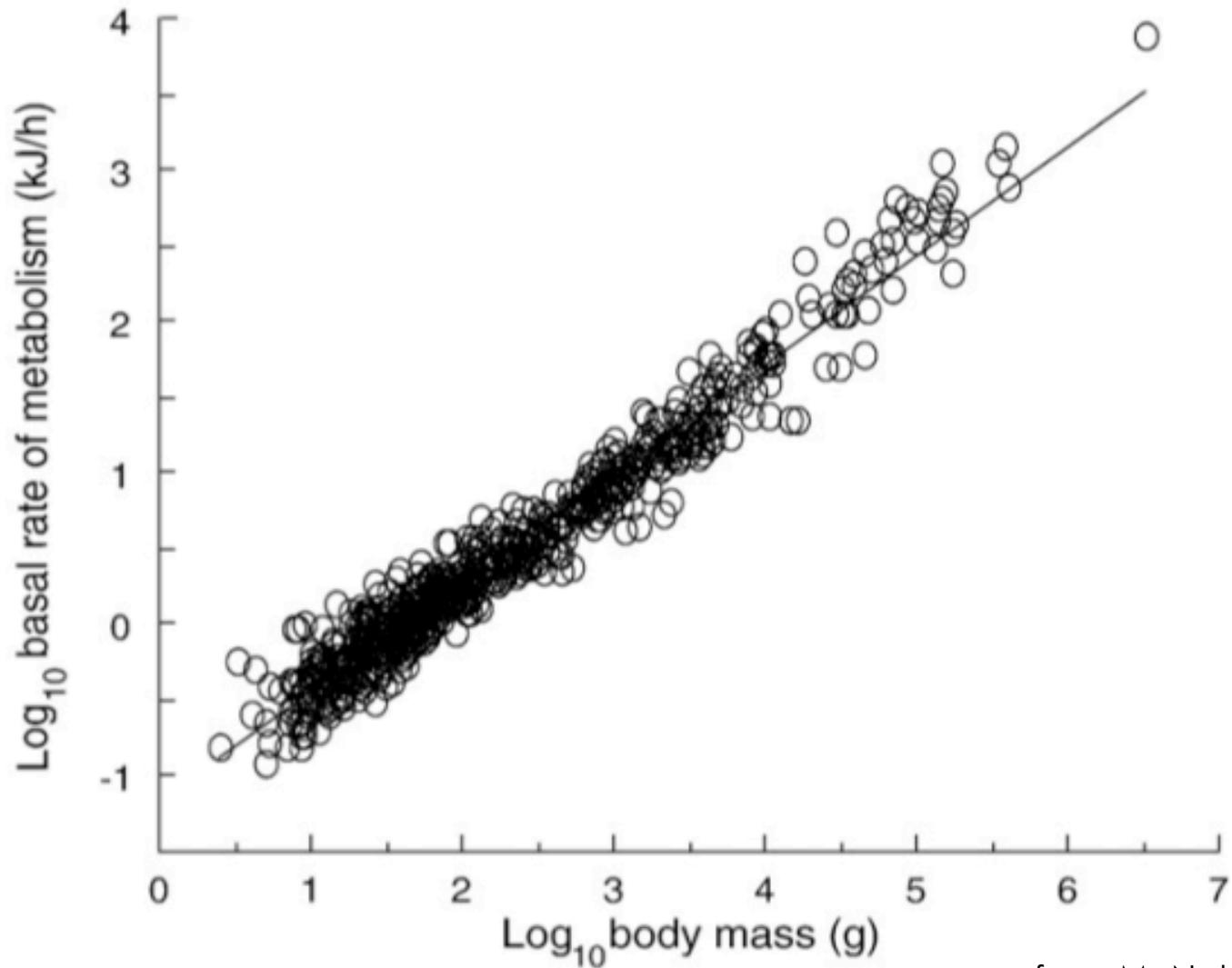
# Straight line ... or curvature?



from Clauss et al. (2007)



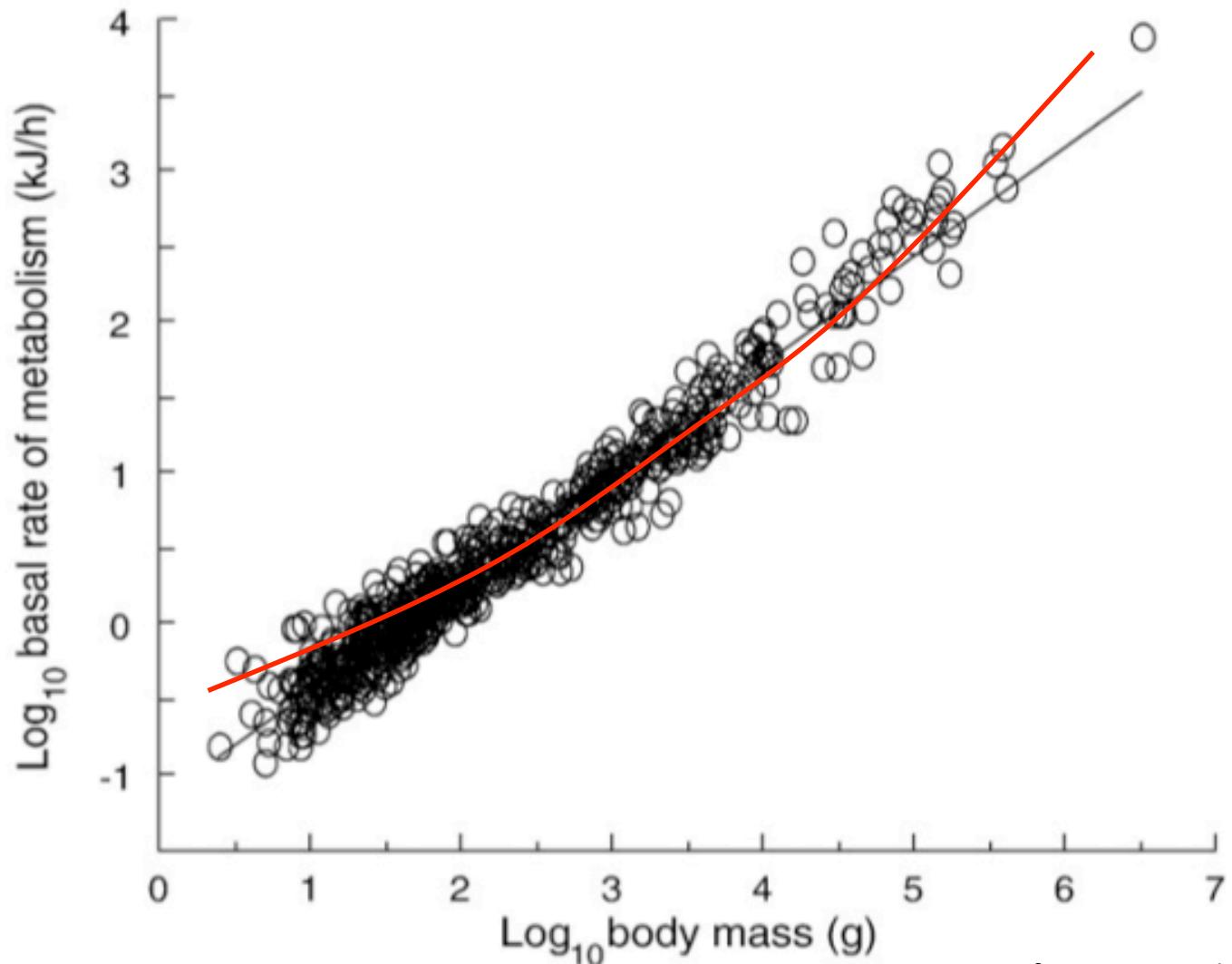
## Straight line ... or curvature?



from McNab (2008)



## Straight line ... or curvature?



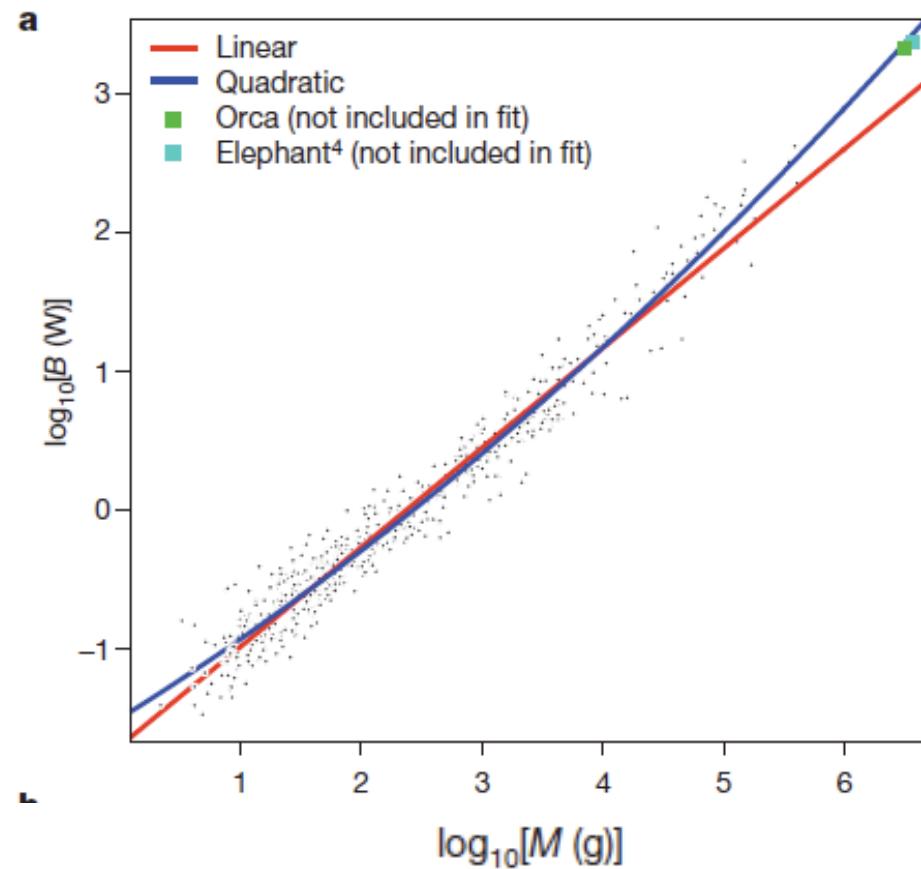
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# LETTERS

## Curvature in metabolic scaling

Tom Kolokotrones<sup>1</sup>, Van Savage<sup>2</sup>, Eric J. Deeds<sup>1</sup> & Walter Fontana<sup>1</sup>





# *Why the curvature?*



# Why the curvature?

Vol 464 | 1 April 2010 | doi:10.1038/nature08920

nature

## LETTERS

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### Curvature in metabolic scaling

Tom Kolokotrones<sup>1</sup>, Van Savage<sup>2</sup>, Eric J. Deeds<sup>1</sup> & Walter Fontana<sup>1</sup>

These modifications demonstrate that the WBE model can, in principle, be brought into agreement with the observed curvature, while still preserving core assumptions, such as the primacy of resource distribution networks.



## *Why the curvature?*

- Or is curvature an artefact due to the inclusion of different individual scaling relationships in the mammal clade?



## *Why the curvature?*

- Or is curvature an artefact due to the inclusion of different individual scaling relationships in the mammal clade?
- “shooting in the dark”: checking for patterns that might resemble the BMR pattern

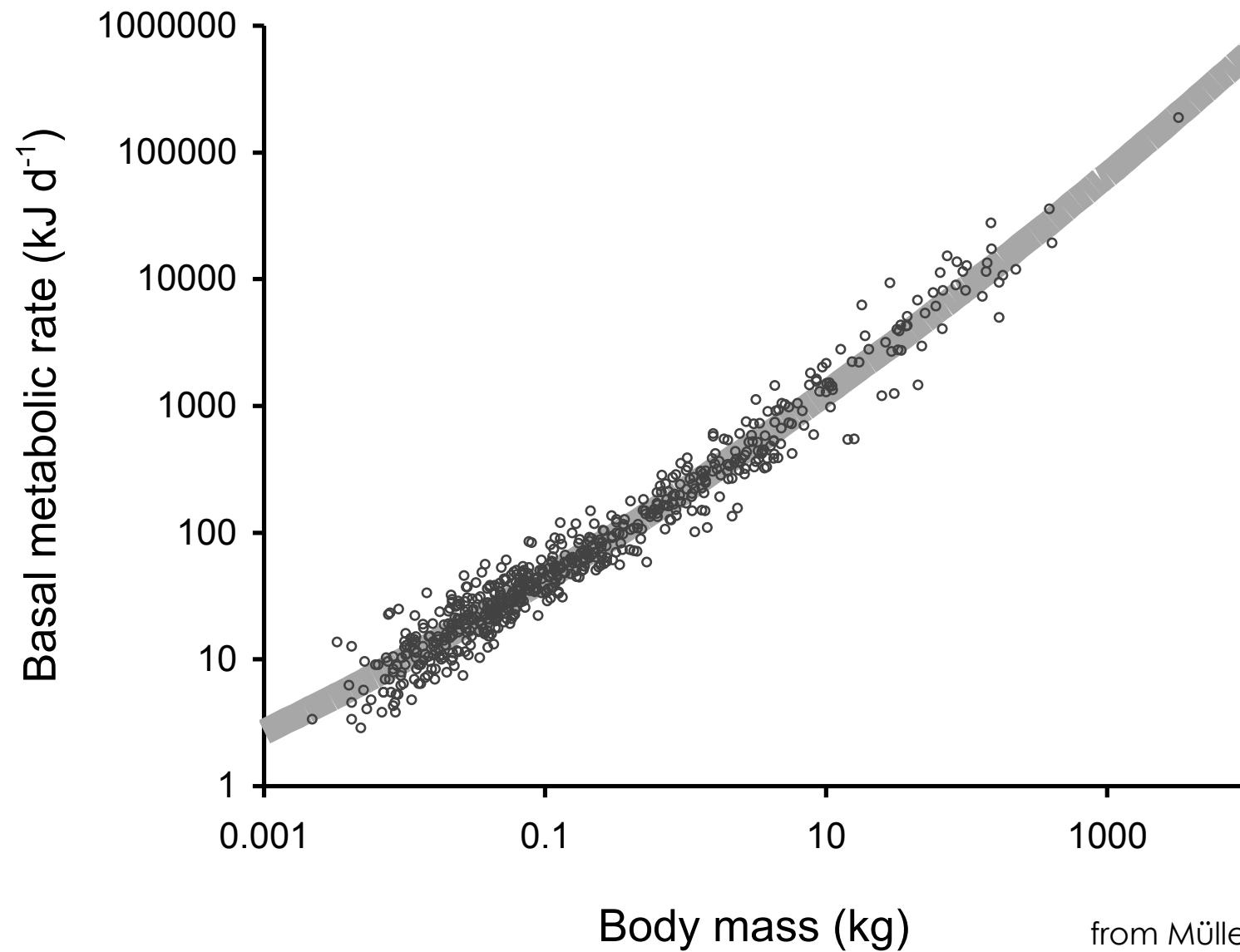


## *Why the curvature?*

- Or is curvature an artefact due to the inclusion of different individual scaling relationships in the mammal clade?
- “shooting in the dark”: checking for patterns that might resemble the BMR pattern
- Mode of reproduction

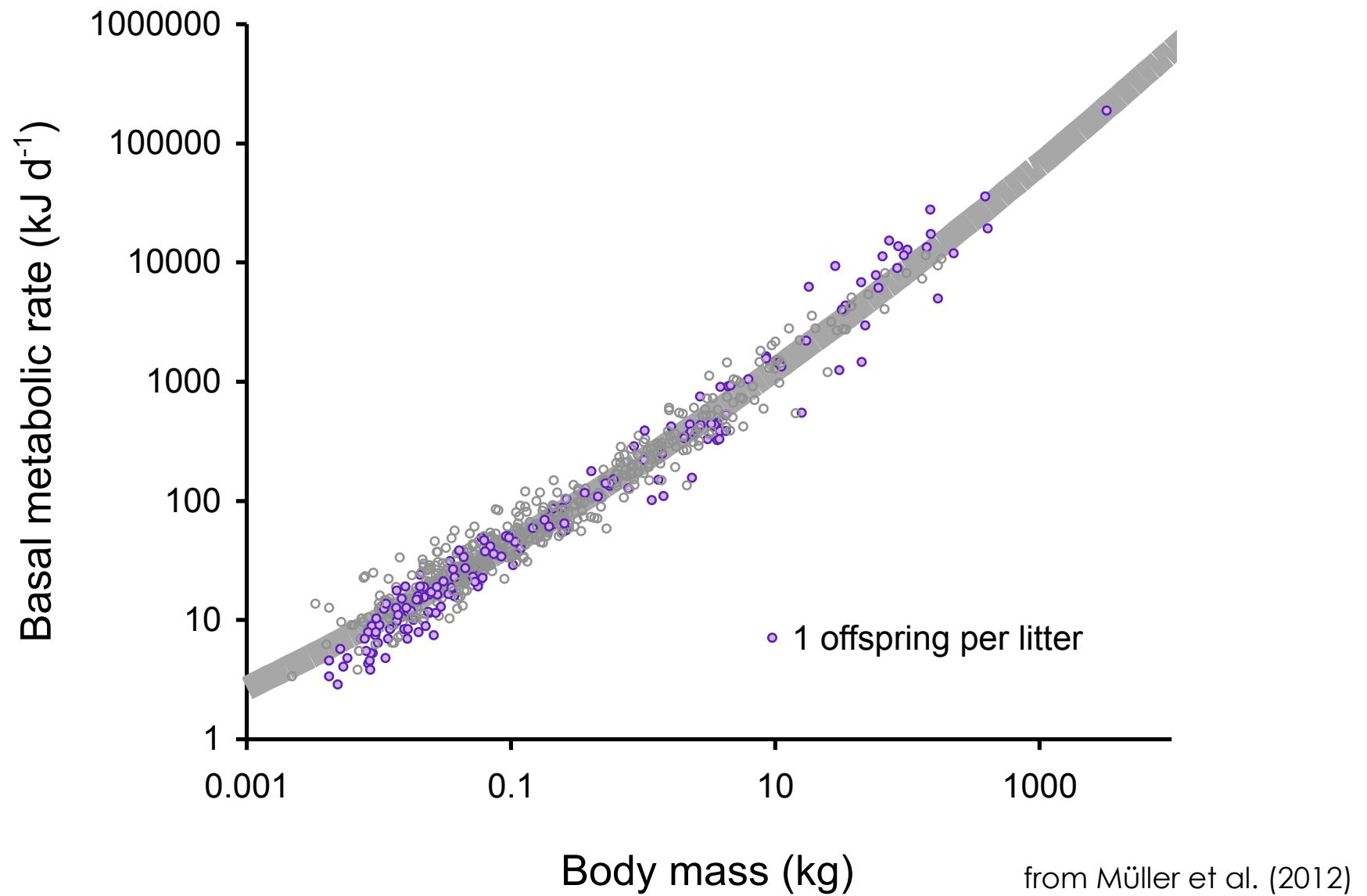


## *Mode of reproduction?*



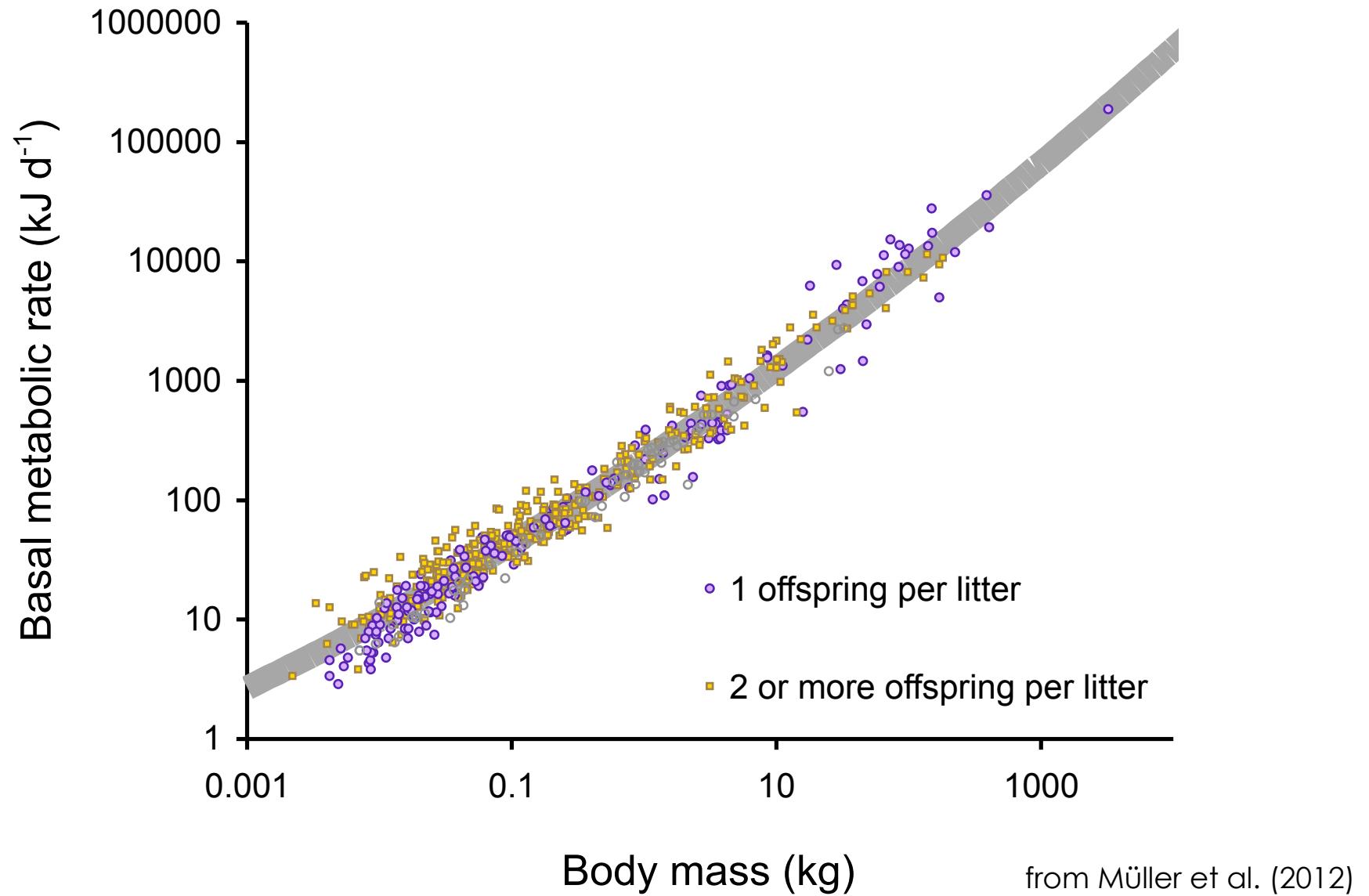


## *Mode of reproduction?*



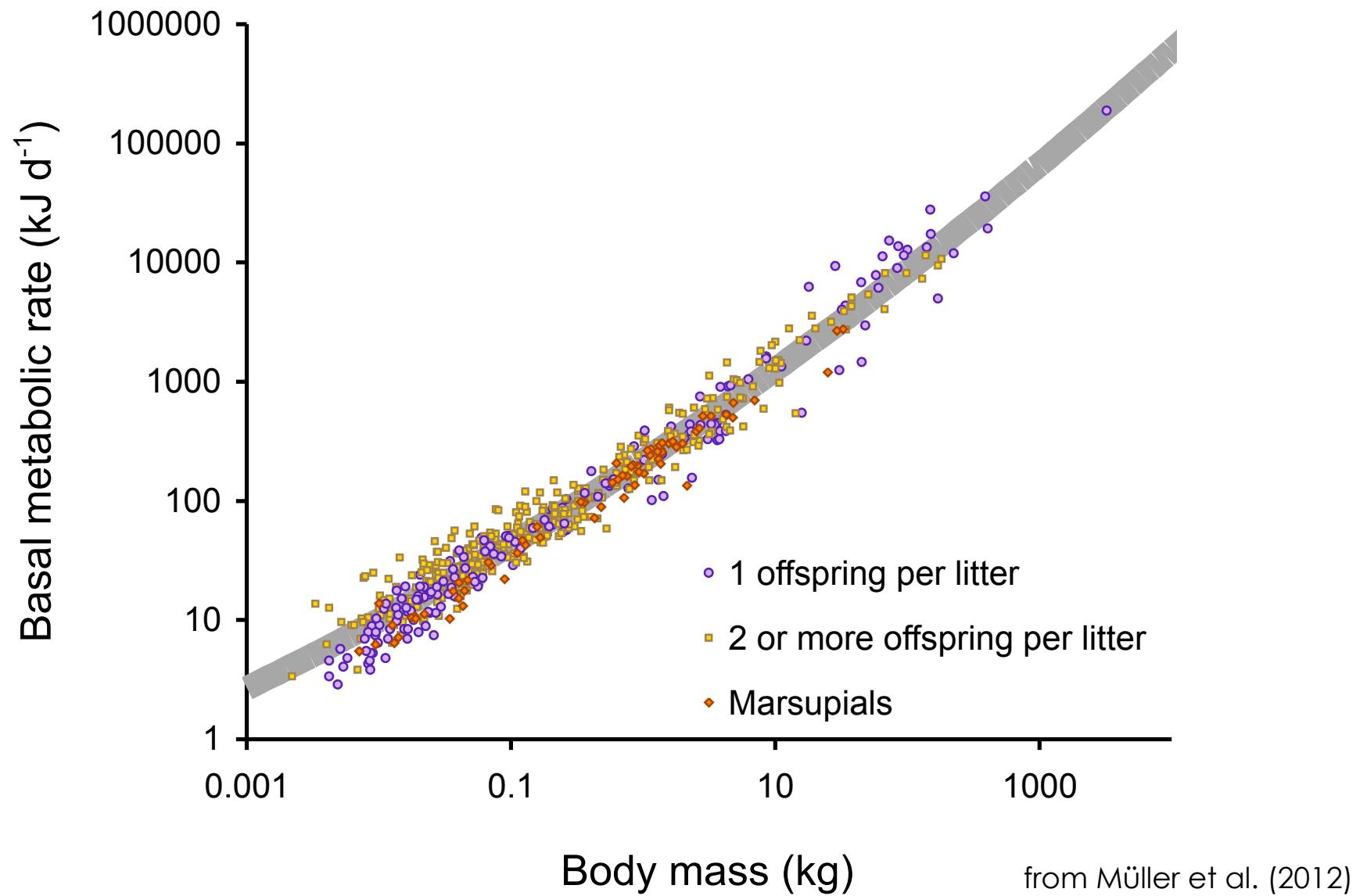


## *Mode of reproduction?*



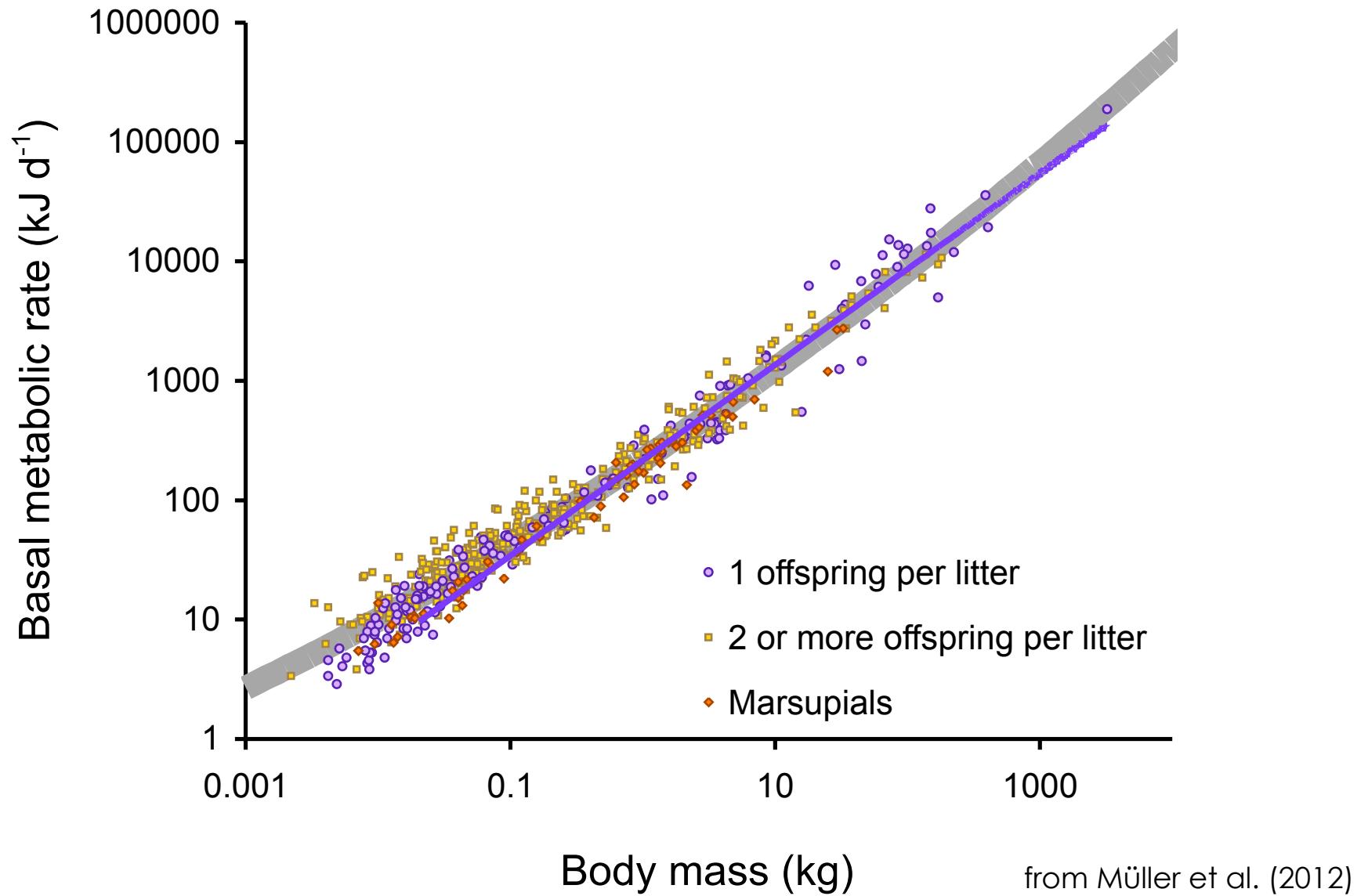


## *Mode of reproduction?*



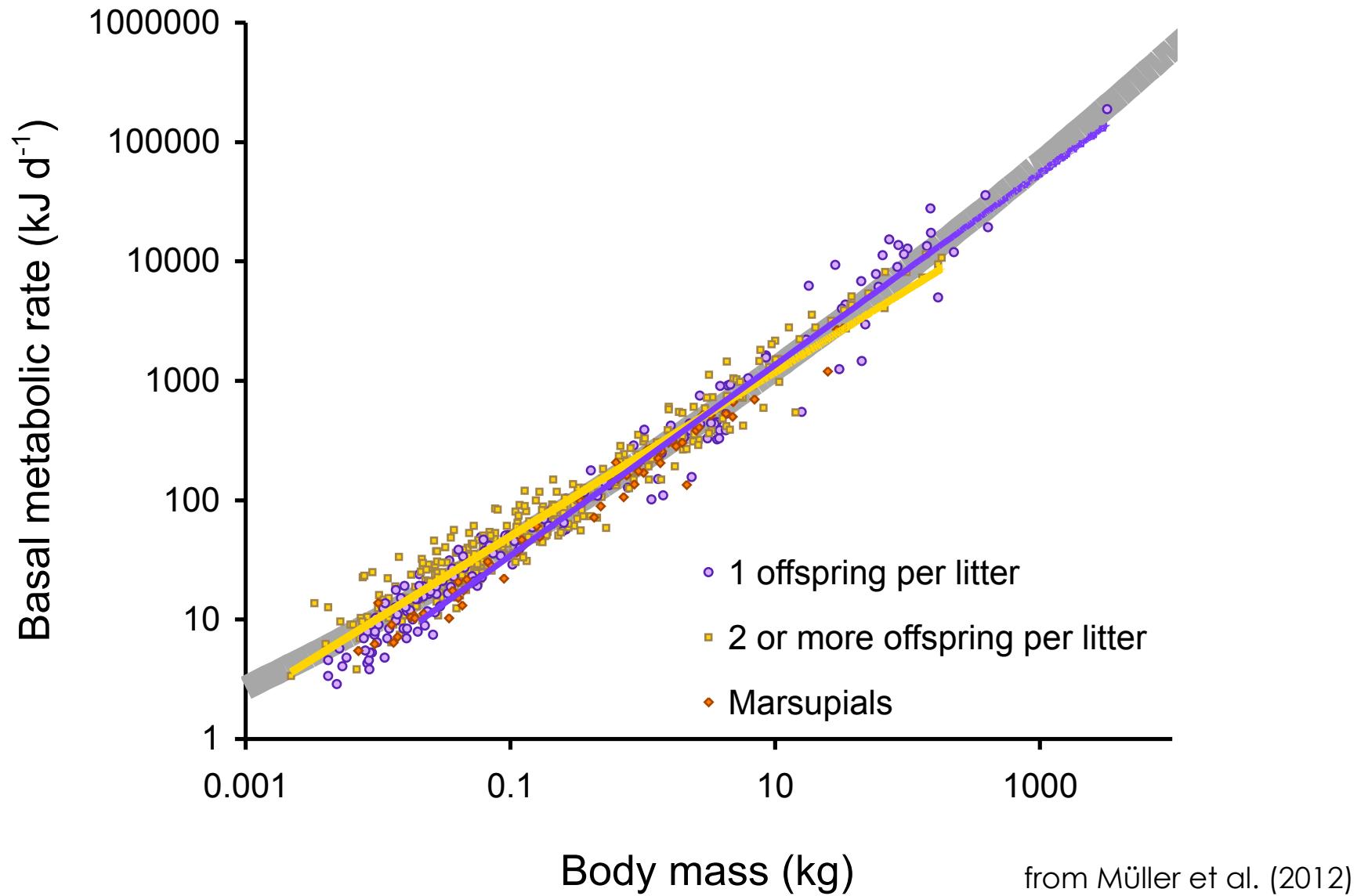


## *Mode of reproduction?*



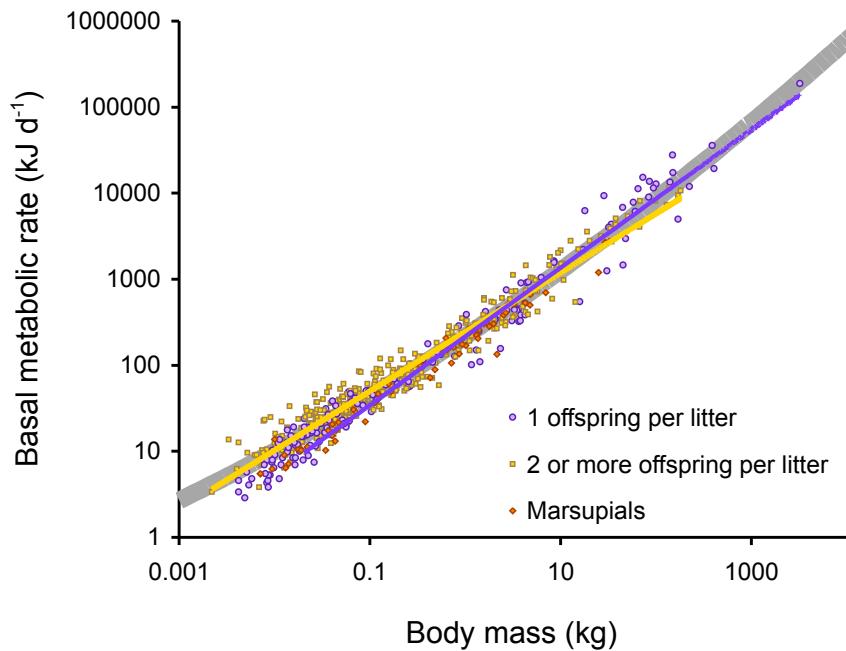


## *Mode of reproduction?*





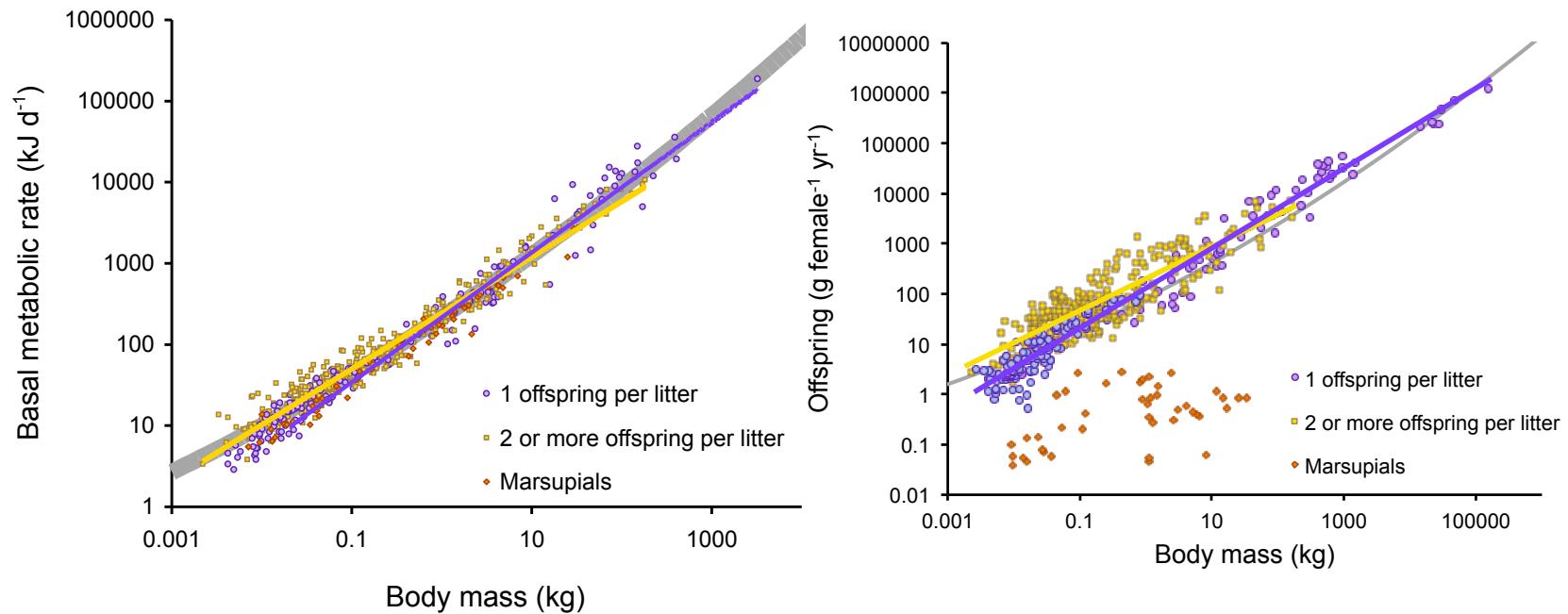
# *Mode of reproduction?*



from Müller et al. (2012)



# Mode of reproduction?



from Müller et al. (2012)



# Why the curvature?

Oikos 121: 102–115, 2012

doi: 10.1111/j.1600-0706.2011.19505.x

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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](mailto:mclauss@vetclinics.uzh.ch)), Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, Univ. of Zurich, Winterthurerstr. 260, CH-8057 Zurich, Switzerland. – J. Werner and E. Maria Griebeler, Inst. of Zoology, Dept of Ecology, Johannes Gutenberg-Univ. of Mainz, DE-55099 Mainz, Germany. – J. Fritz, Chair of Animal Nutrition and Dietetics, Dept of Veterinary Sciences, Schönleutnerstraße 8, DE-85764 Oberschleißheim, Germany. – J. Hummel, Inst. of Animal Science, Univ. of Bonn, Endenicher Allee 15, DE-53115 Bonn, Germany.



# The *really real* exponents

Measurement

Scaling (95%CI)

Dry matter intake

0.76 (0.73-0.79)

Digestibility

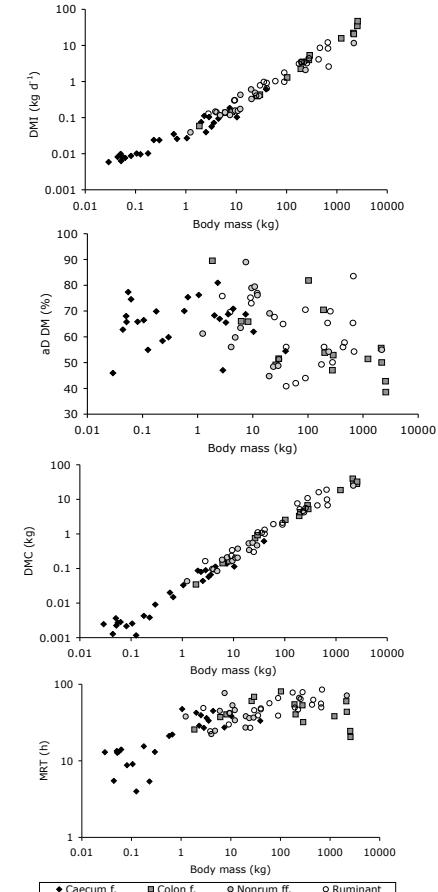
-0.03 (-0.04--0.01)

Dry matter gut fill

0.93 (0.90-0.96)

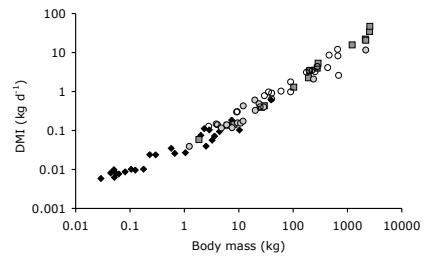
Particle retention time

0.16 (0.12-0.19)

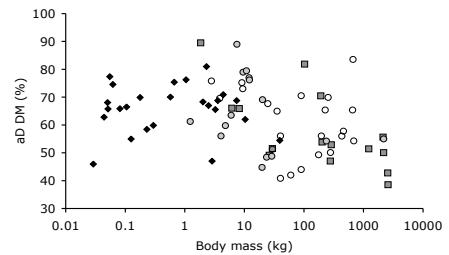




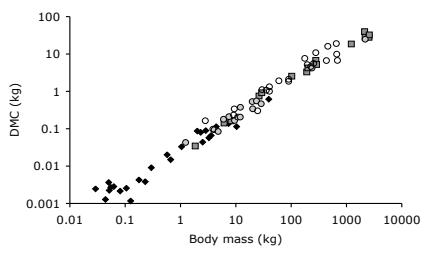
# The curvature in herbivore digestive physiology



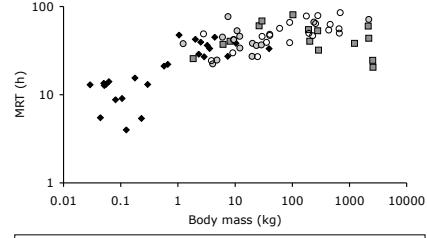
Dry matter intake



Digestibility



Dry matter gut content

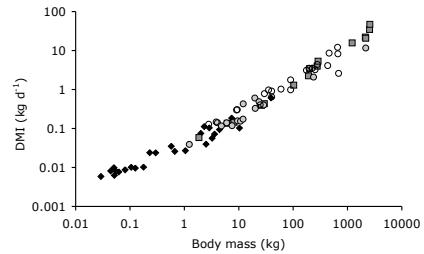


Particle retention time

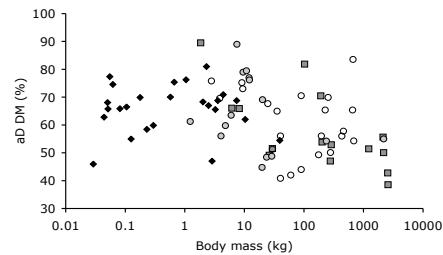
◆ Caecum f. ■ Colon f. ○ Nonrum ff. □ Ruminant



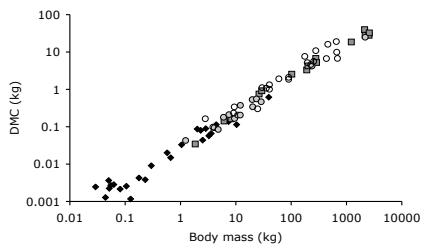
# The curvature in herbivore digestive physiology - plotting residuals



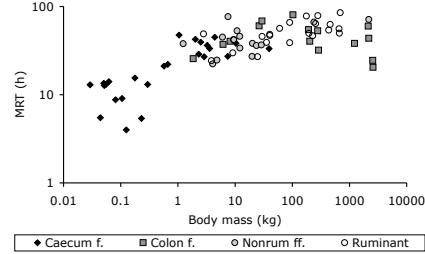
Dry matter intake



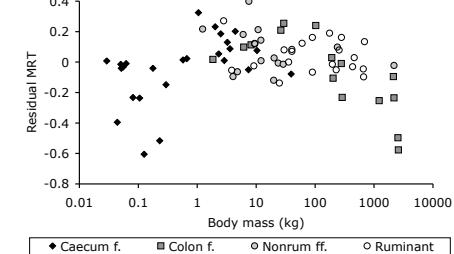
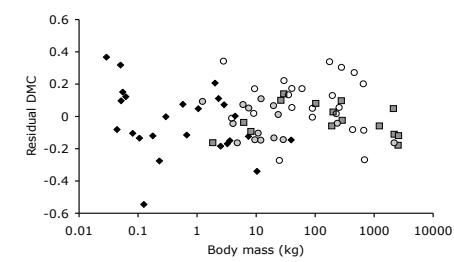
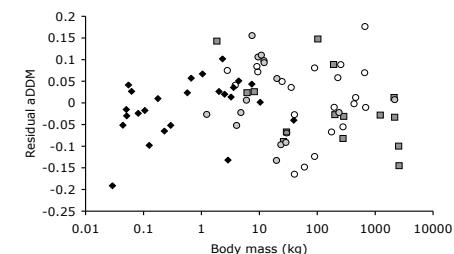
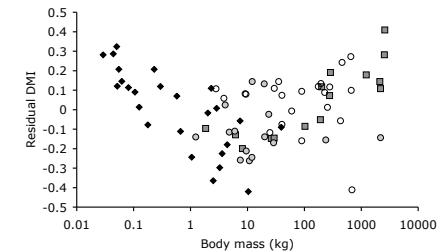
Digestibility



Dry matter gut content



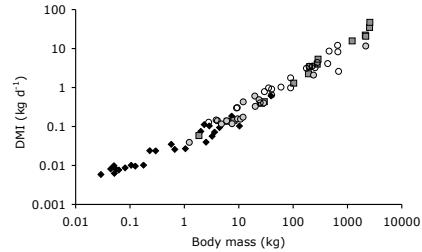
Particle retention time



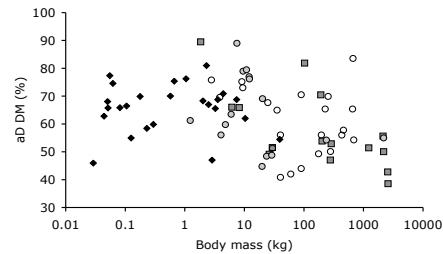
◆ Caecum f. ■ Colon f. ○ Nonrum ff. □ Ruminant



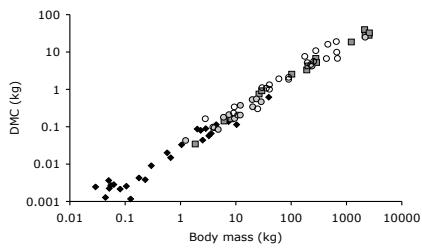
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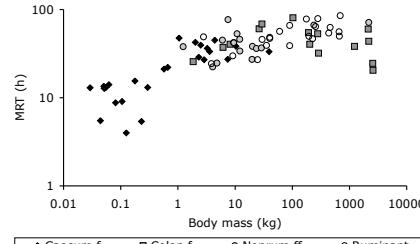
Dry matter intake



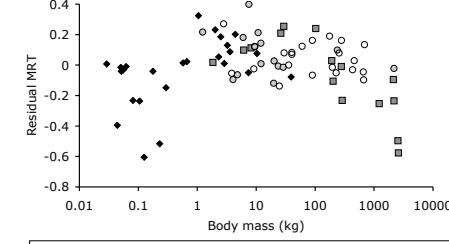
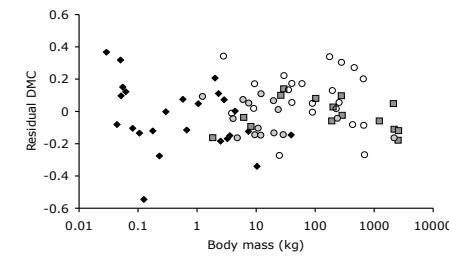
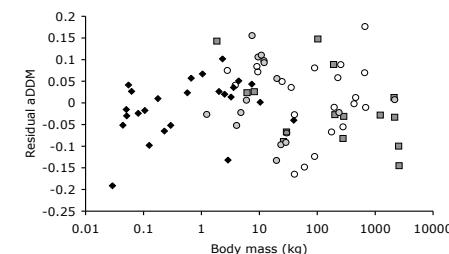
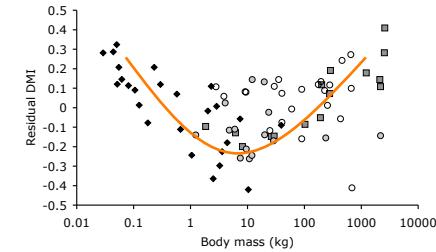
Digestibility



Dry matter gut content



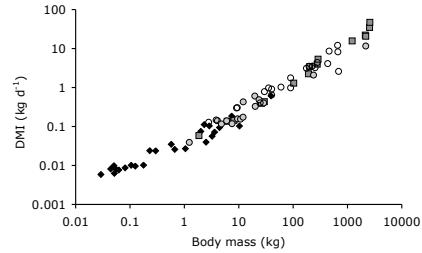
Particle retention time



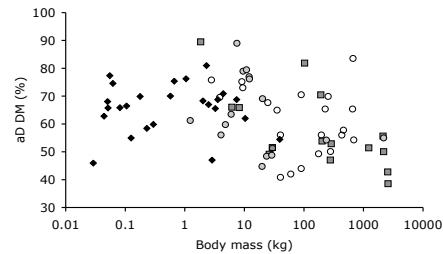
◆ Caecum f. ■ Colon f. ○ Nonrum ff. □ Ruminant



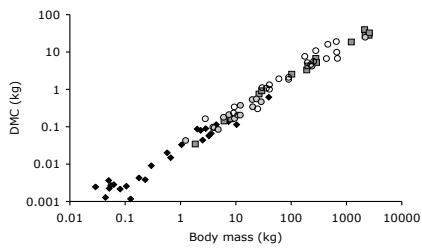
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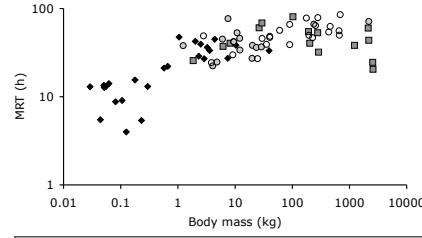
Dry matter intake



Digestibility

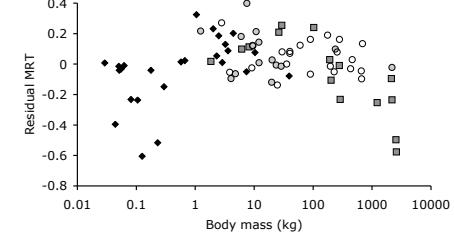
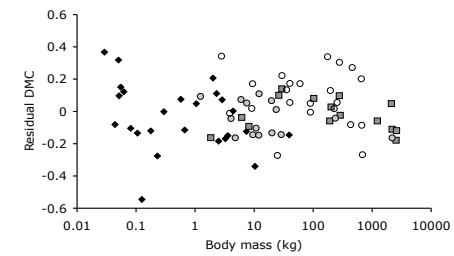
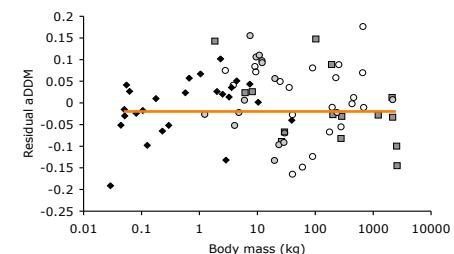
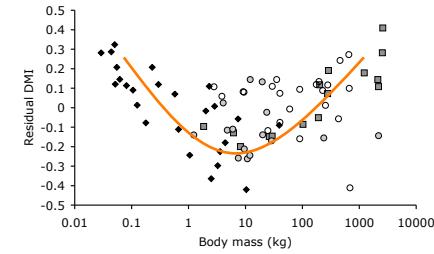


Dry matter gut content



Particle retention time

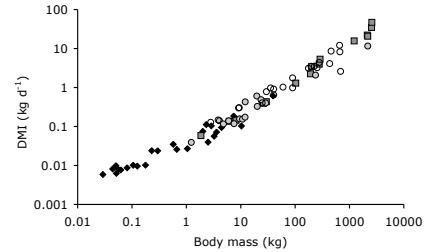
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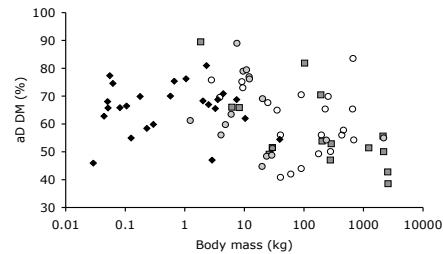
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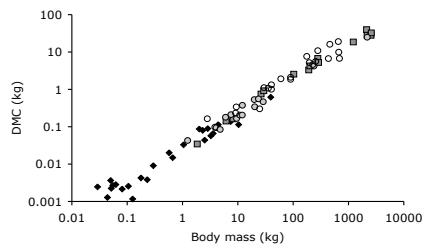
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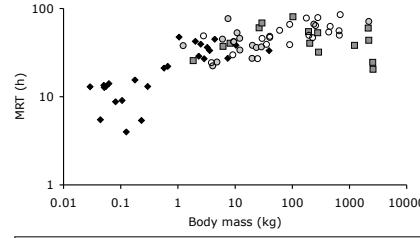
Dry matter intake



Digestibility

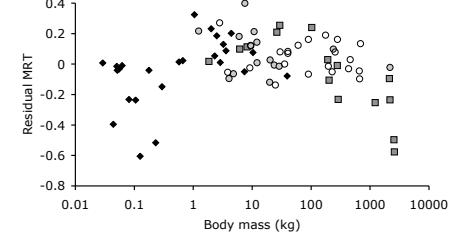
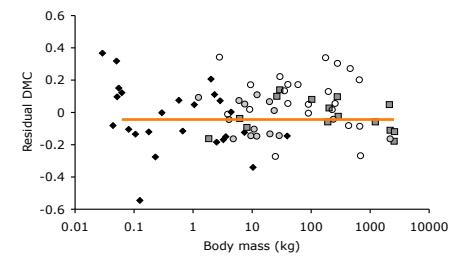
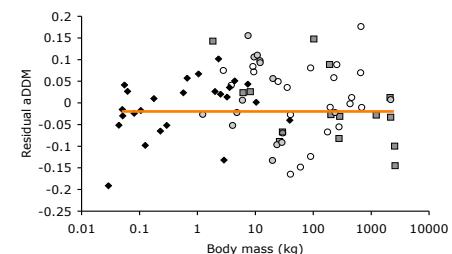
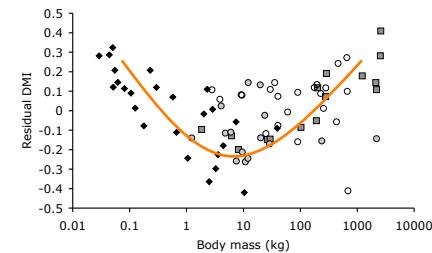


Dry matter gut content



Particle retention time

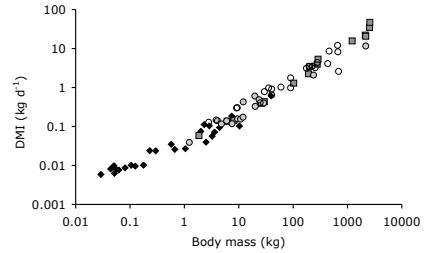
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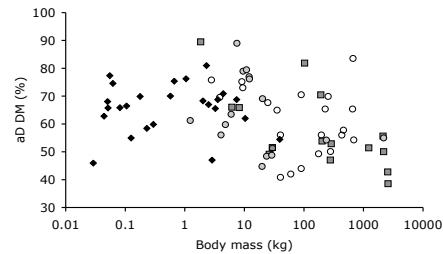
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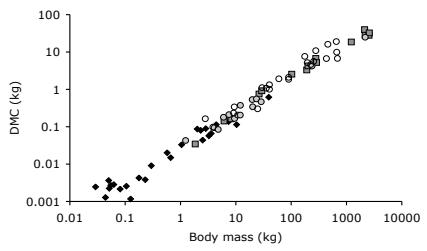
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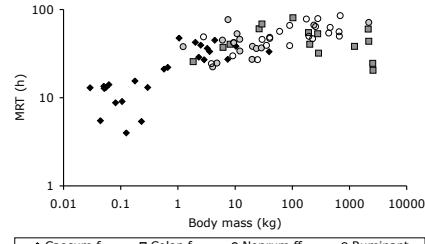
Dry matter intake



Digestibility

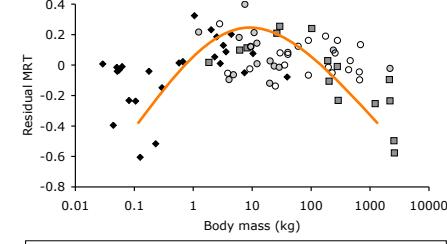
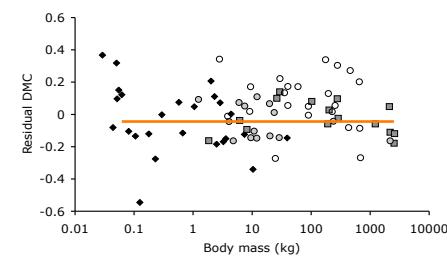
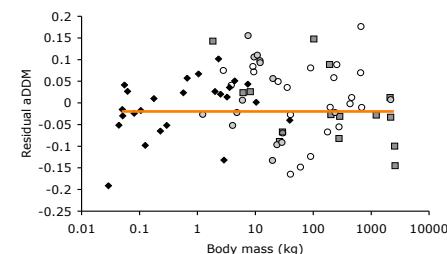
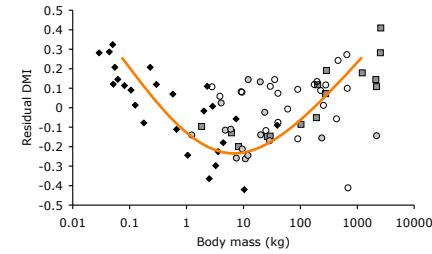


Dry matter gut content



Particle retention time

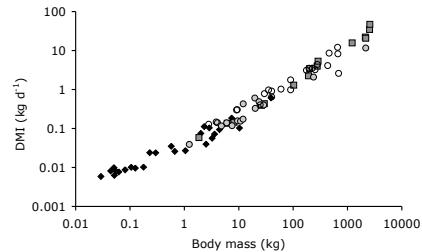
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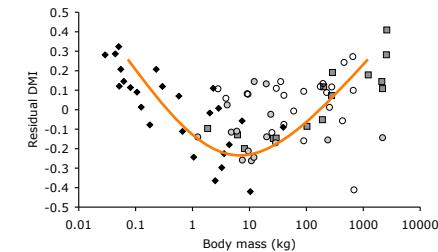
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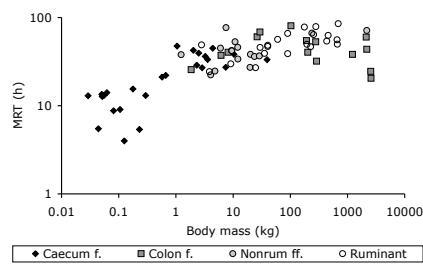
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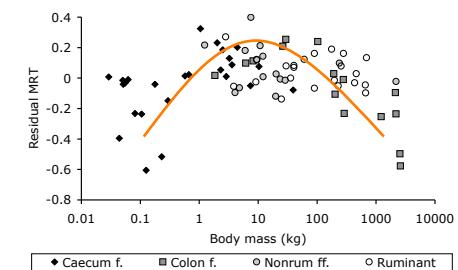
Dry matter intake



*corresponding  
inverse  
curvatures*



Particle retention time





## 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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# Conclusions

## Jarman-Bell-principle



Summary: little evidence for positive effect of increasing body size on digestive physiology



Gut contents

----- near-linear scaling -----  
Increase in moisture with BM ? ?

Food intake

----- near-metabolic scaling -----  
Higher scaling at high BM ? ?

Retention time

----- less-than-expected scaling -----  
except at low BM

Particle size

----- increase with body mass -----

Digestibility

----- no indication for increase with body mass -----

Methane production

----- linear scaling -----

Are birds different?



Summary: little evidence for positive effect of increasing body size on digestive physiology



Gut contents

Food intake

*Similarity in scaling in larger mammals directly contradicts the basic assumption of the JBP*

Retention time

----- less-than-expected scaling -----

except at low BM

Particle size

----- increase with body mass -----

Digestibility

----- no indication for increase with body mass -----

Methane production

----- linear scaling -----

Are birds different?



# Conclusions

## The “Jarman-Bell-Principle”

In terms of digestive physiology, large body size should not be considered as an advantage in terms of digestive efficiency (from app. 1-10 kg upwards).

For the evolution of large body sizes, a difference between metabolic scaling and intake scaling (which compensates for the lower diet quality) is the better candidate.



# The plan:

- Think
- Extrapolate (using data collections that exist or have to be created/supplemented)
- If possible, link to existing theories



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- Think
- Extrapolate (using data collections that exist or have to be created/supplemented)
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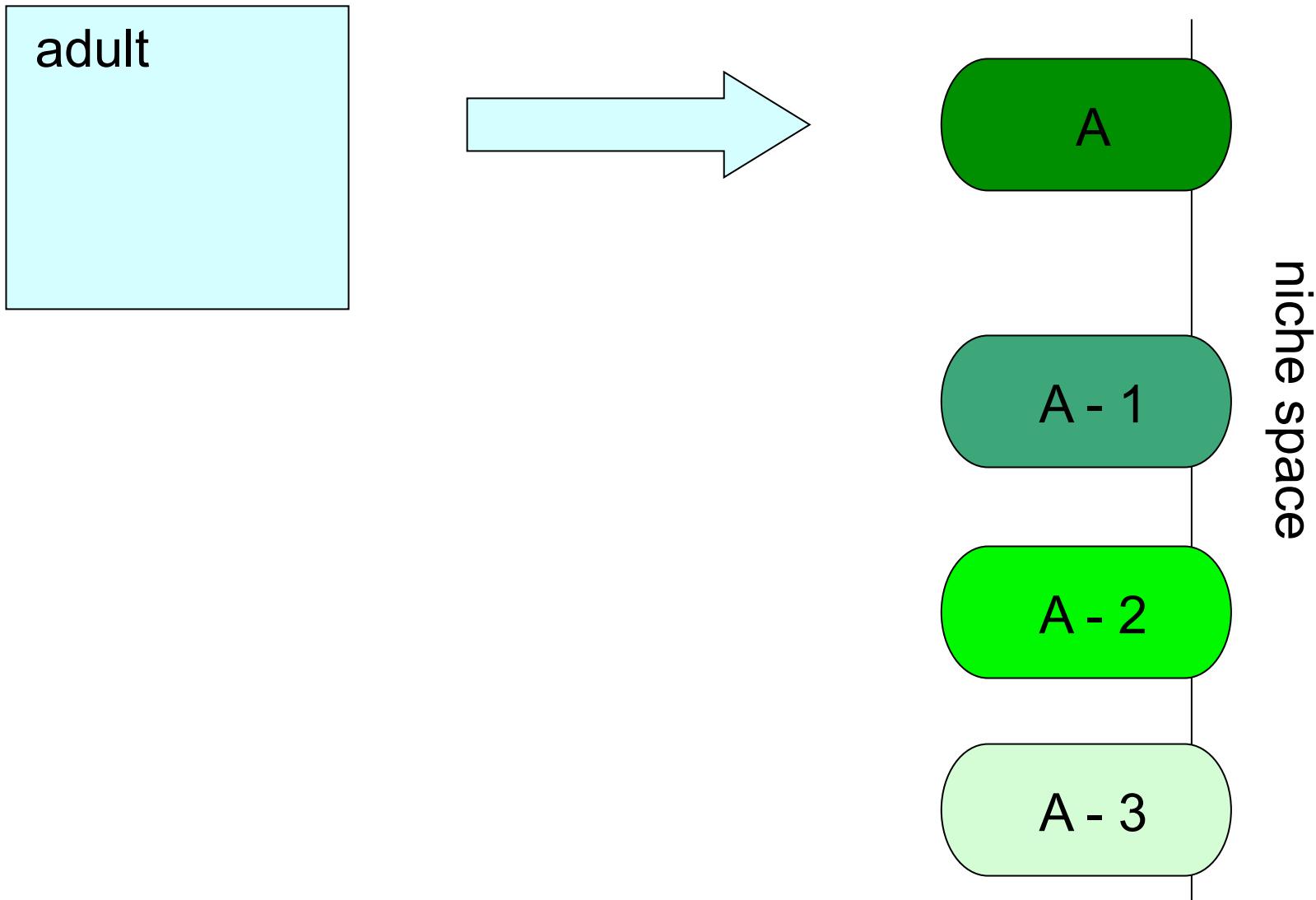


## Assumptions

- Niche stratification according to body size (=body mass)
- Eggs cannot increase endlessly in size because of physical constraints on egg shell thickness (stronger shells needed for larger eggs) and diffusion (thicker shells prevent diffusion of oxygen)
- The K-Pg extinction event affected all animals above a certain body size threshold

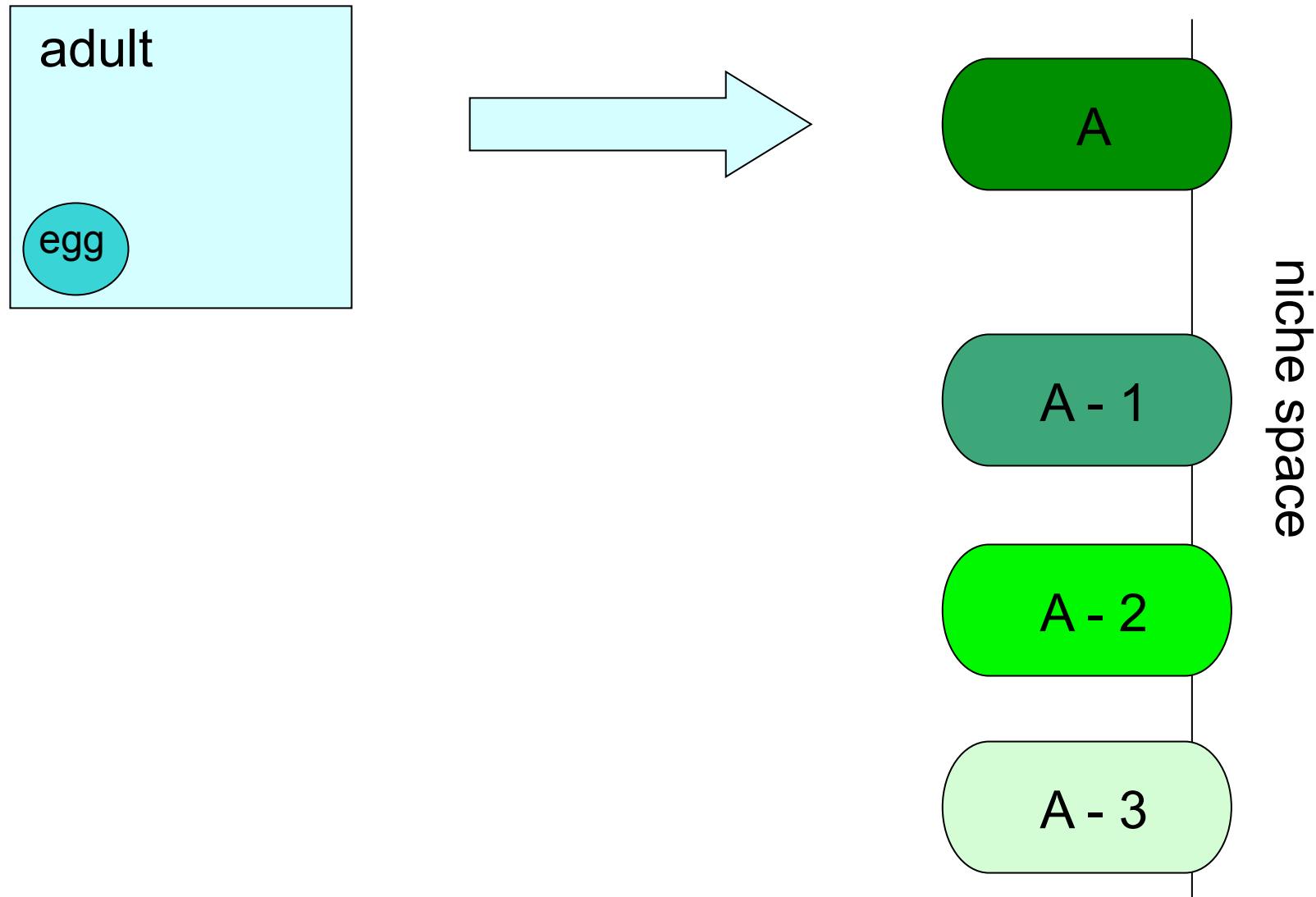


# Niches of parent and offspring



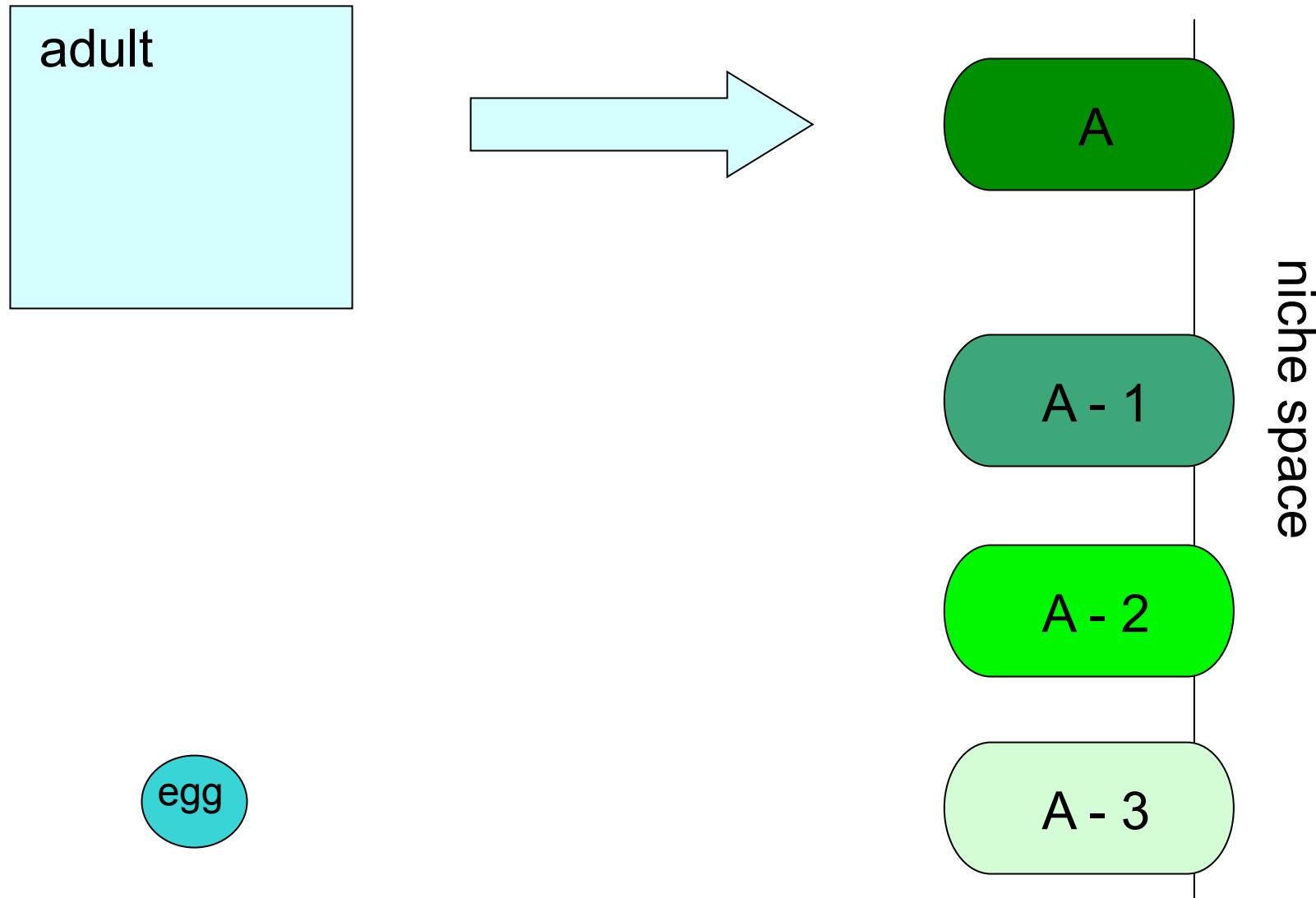


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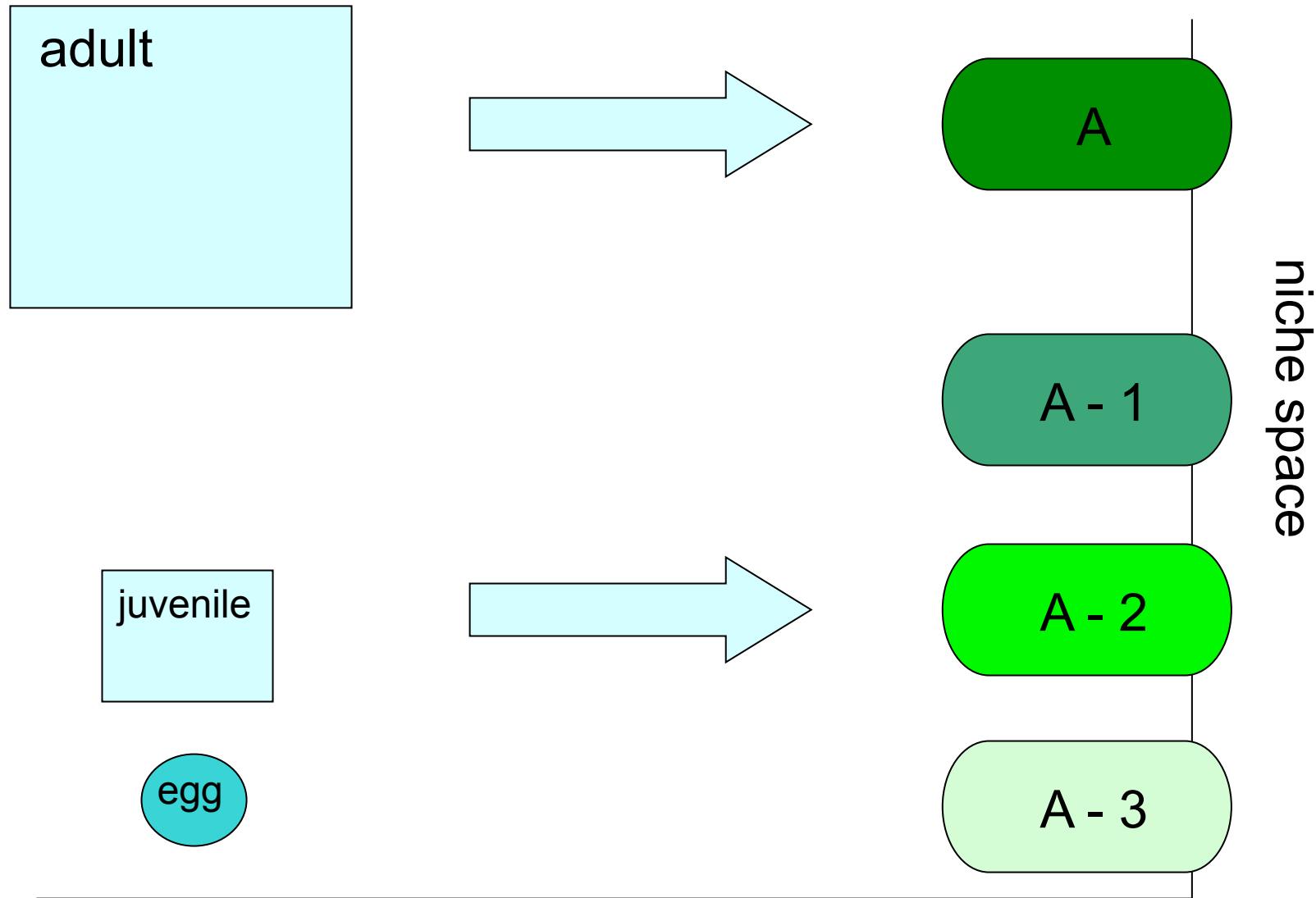


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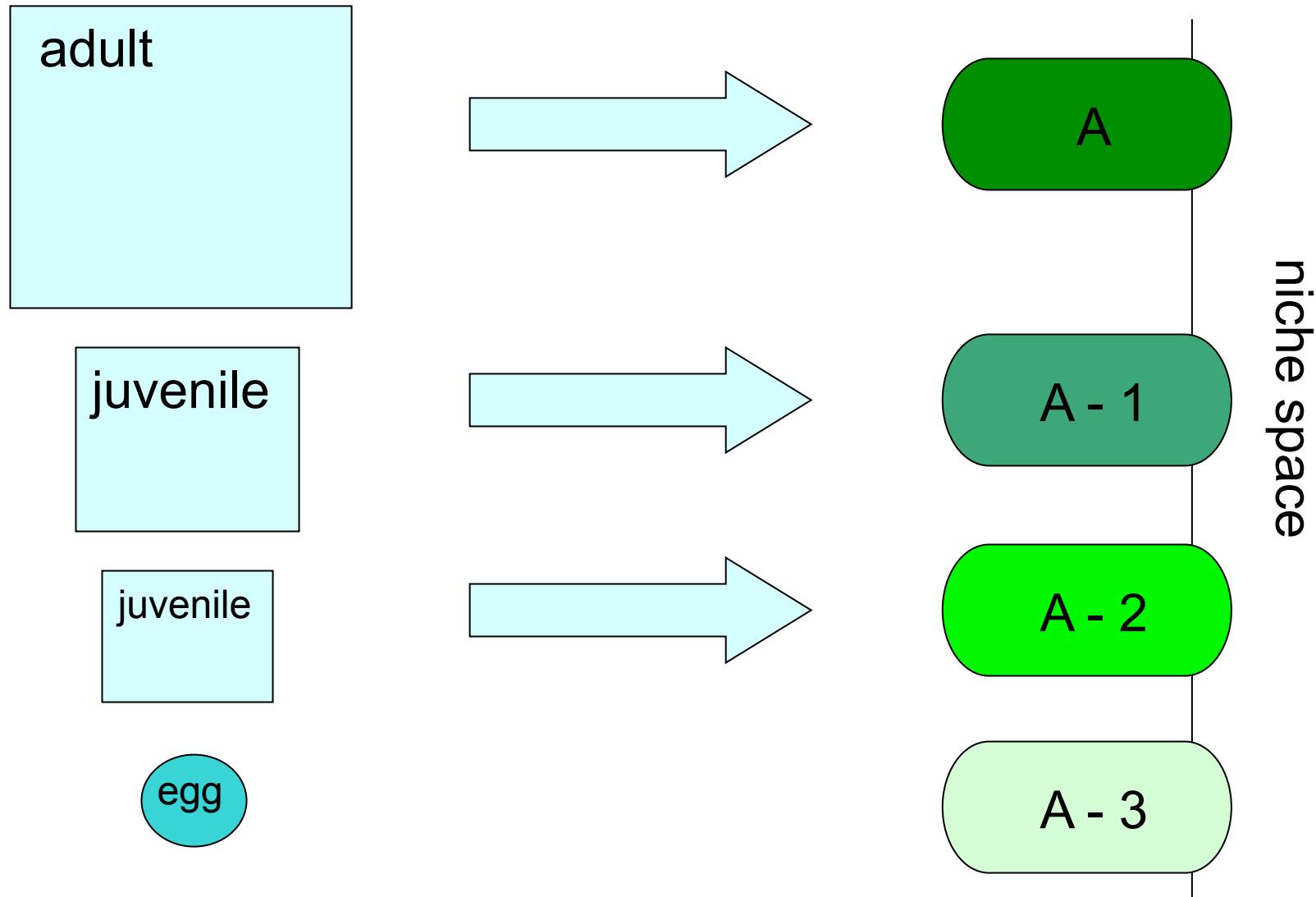


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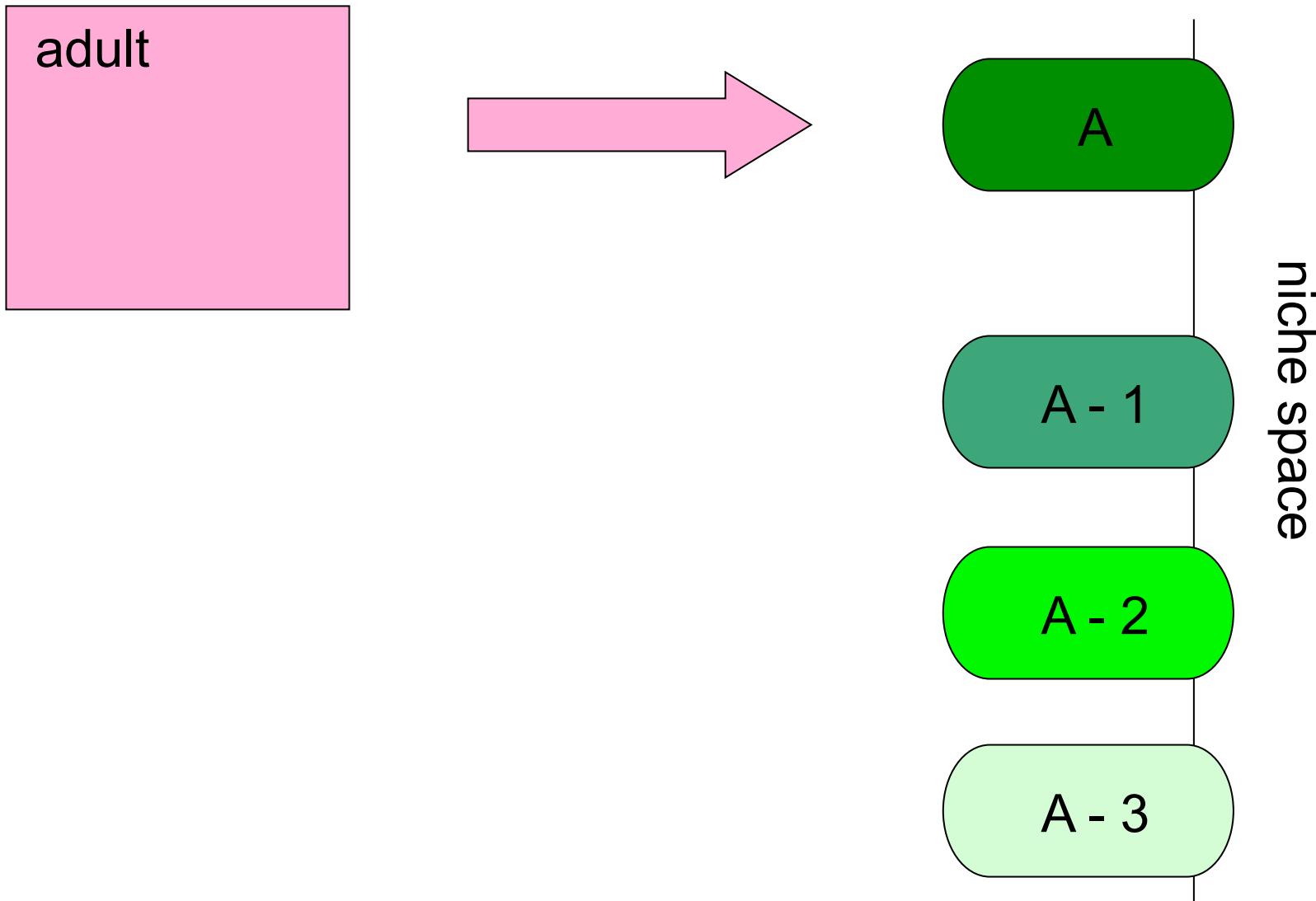


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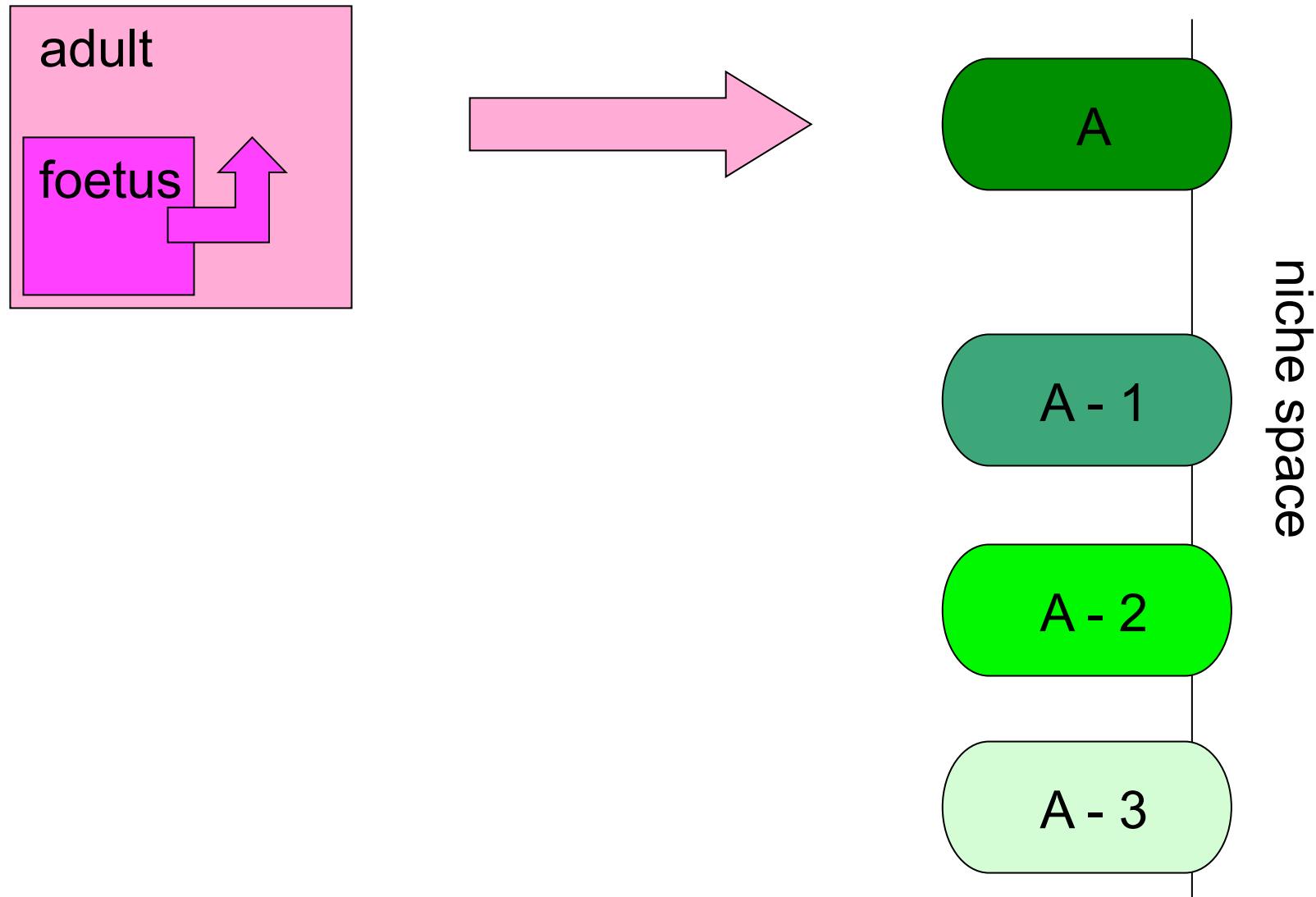


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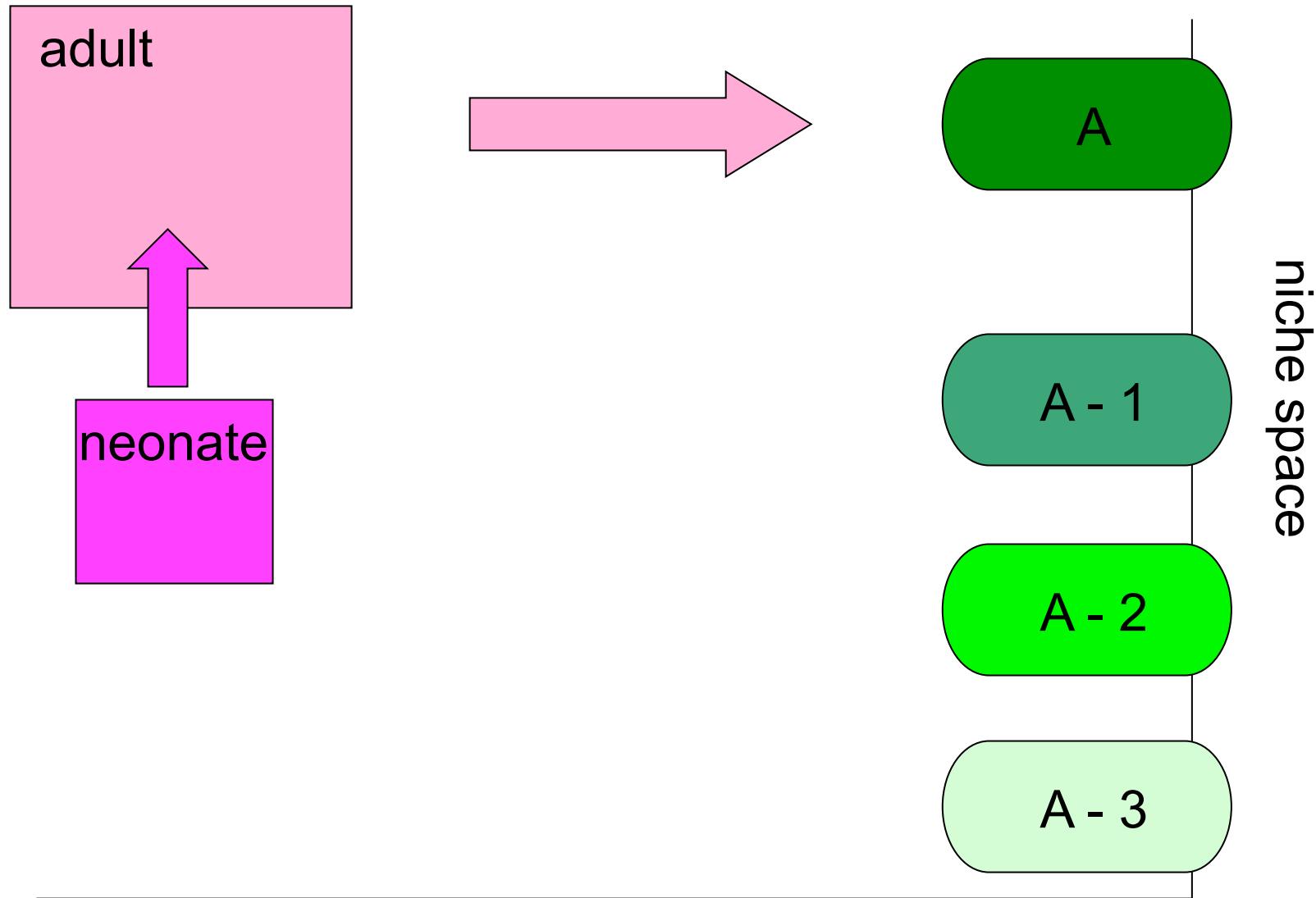


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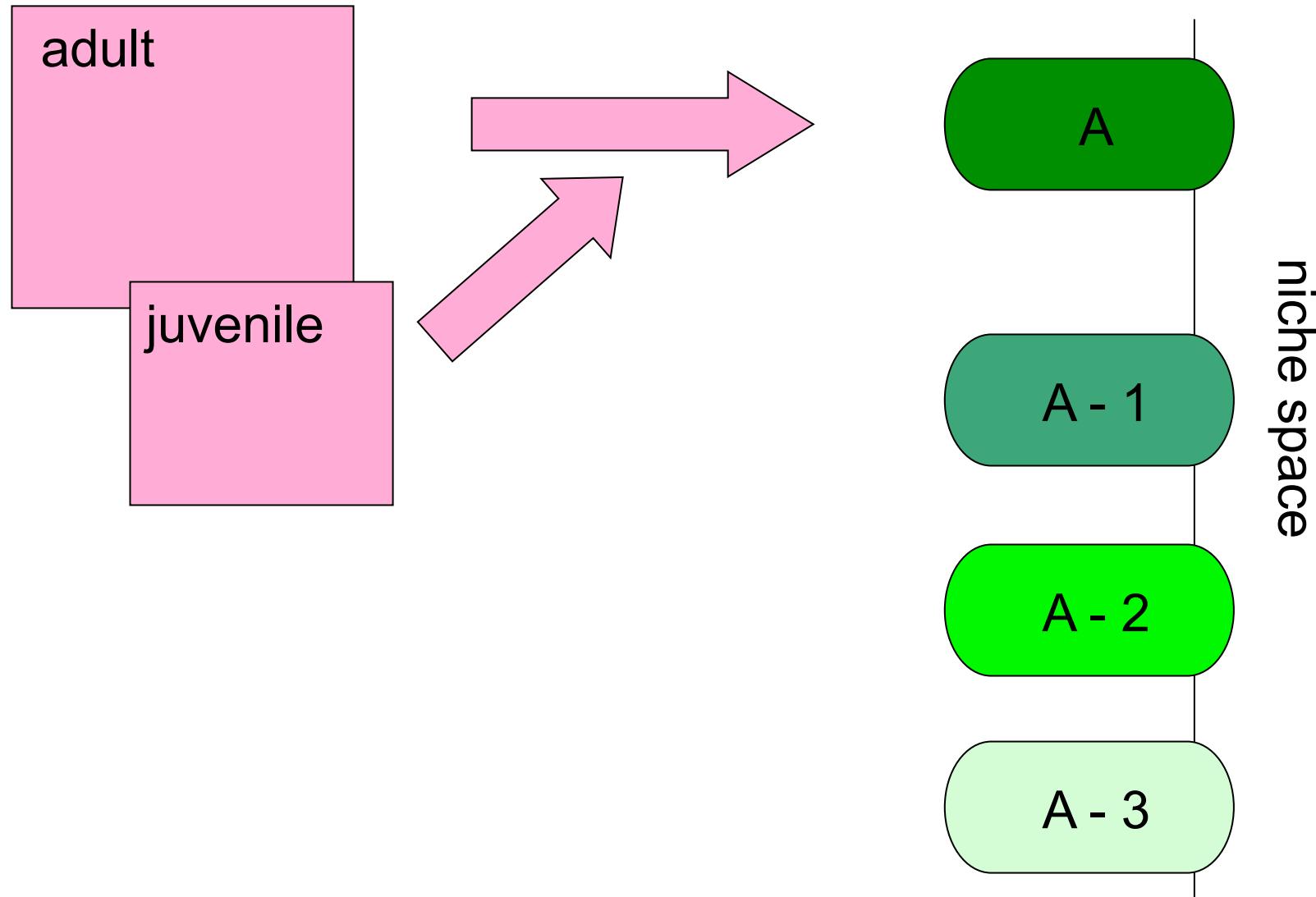


# Niches of parent and offspring





# Niches of parent and offspring





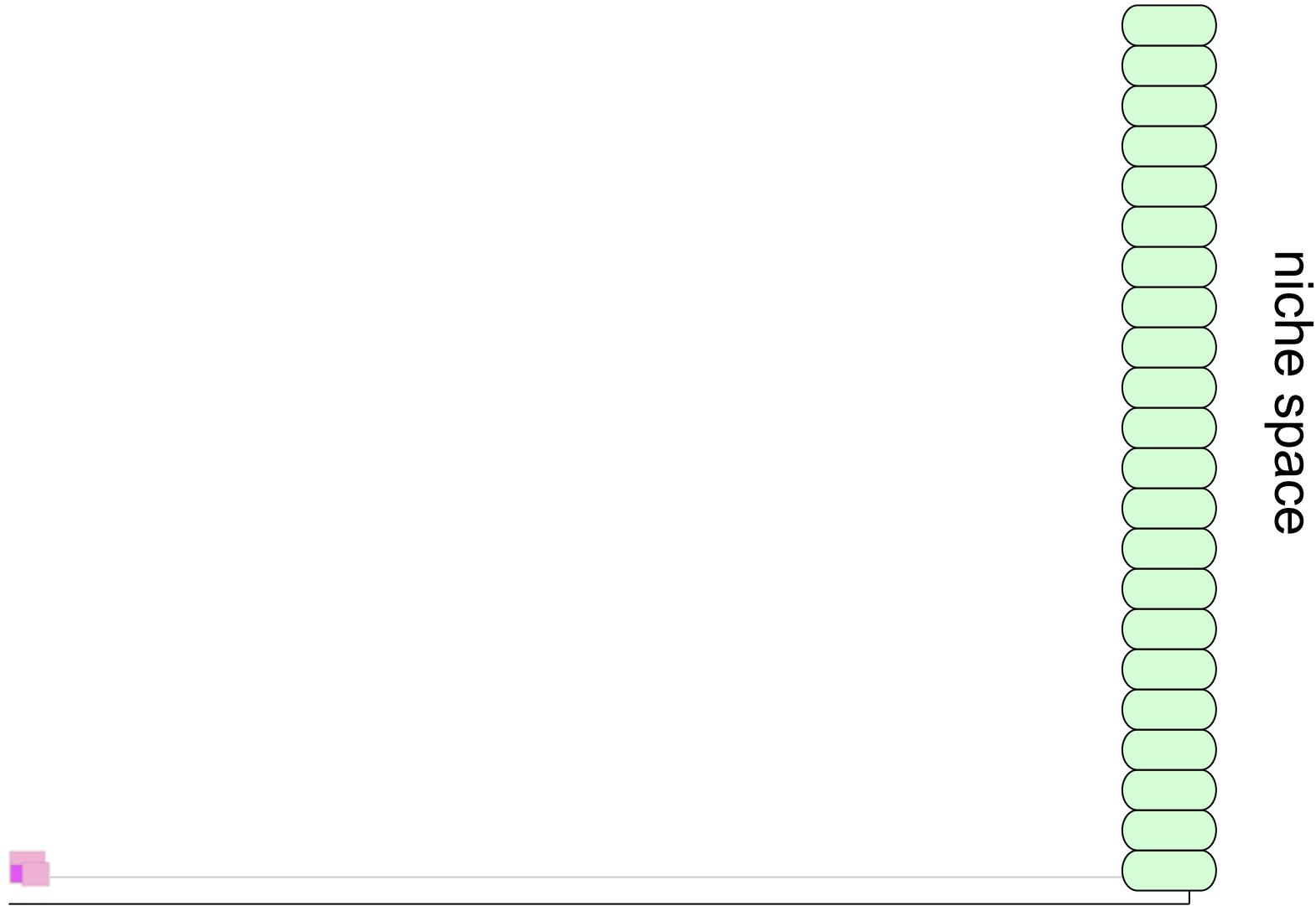
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niche space

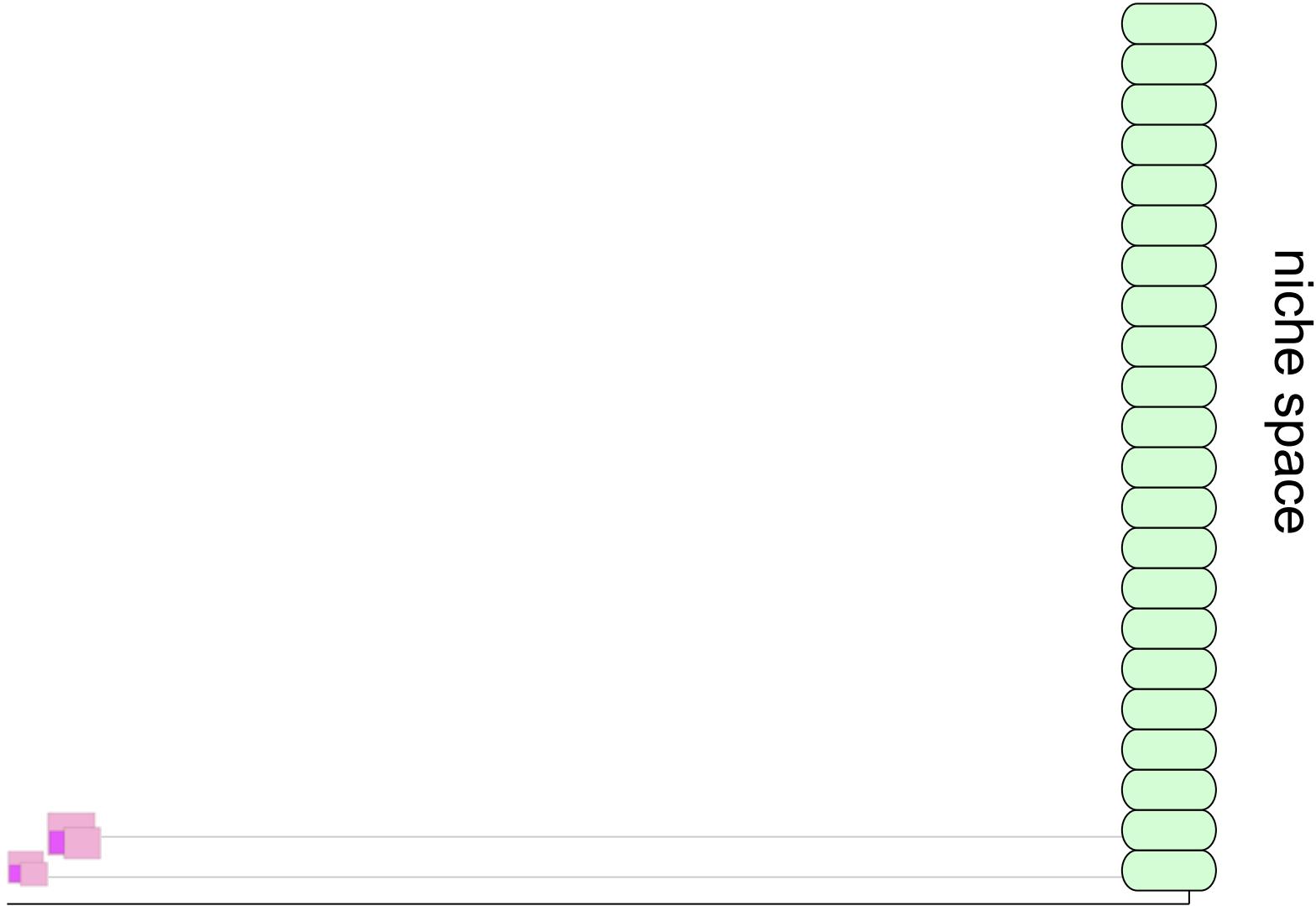


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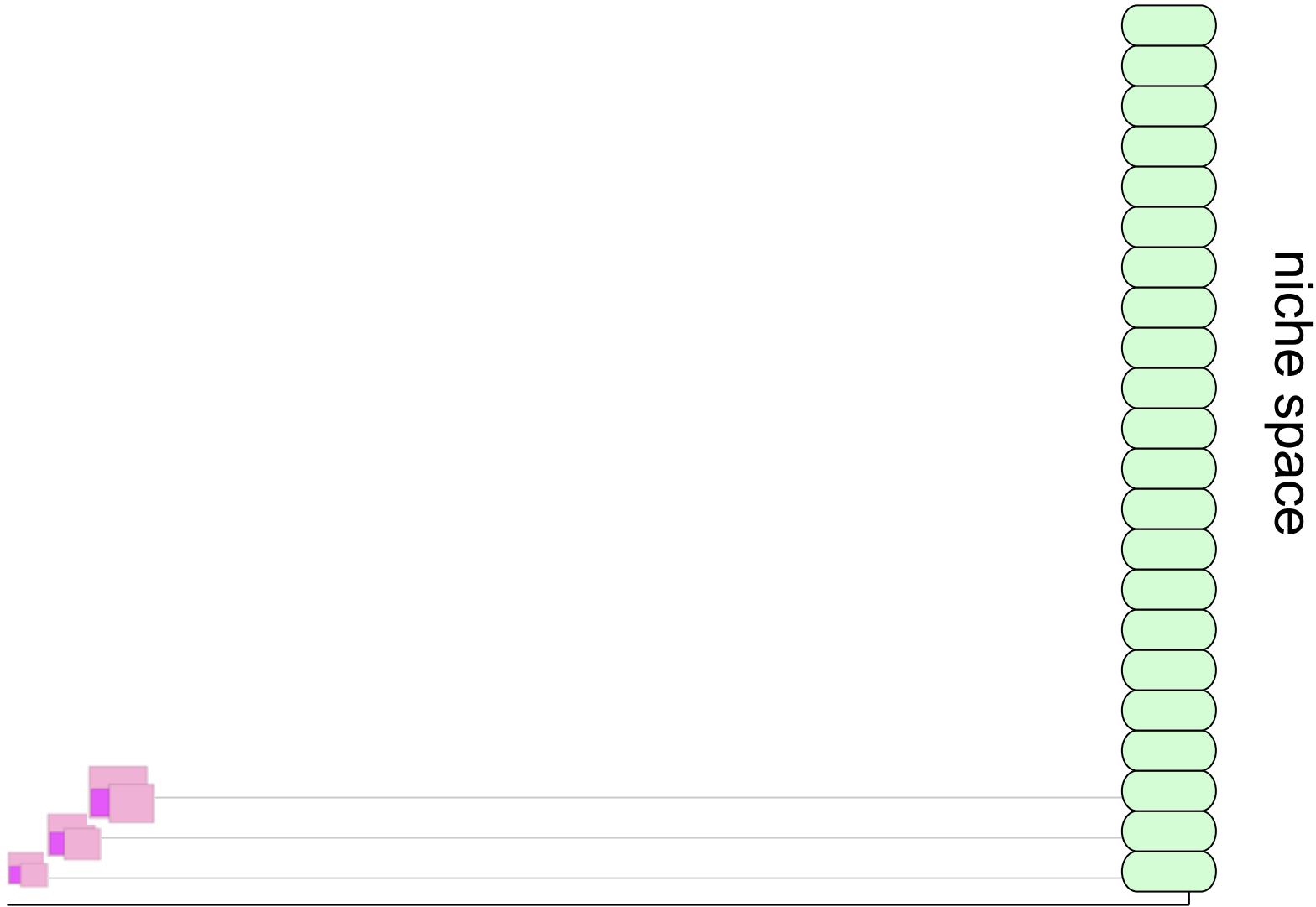


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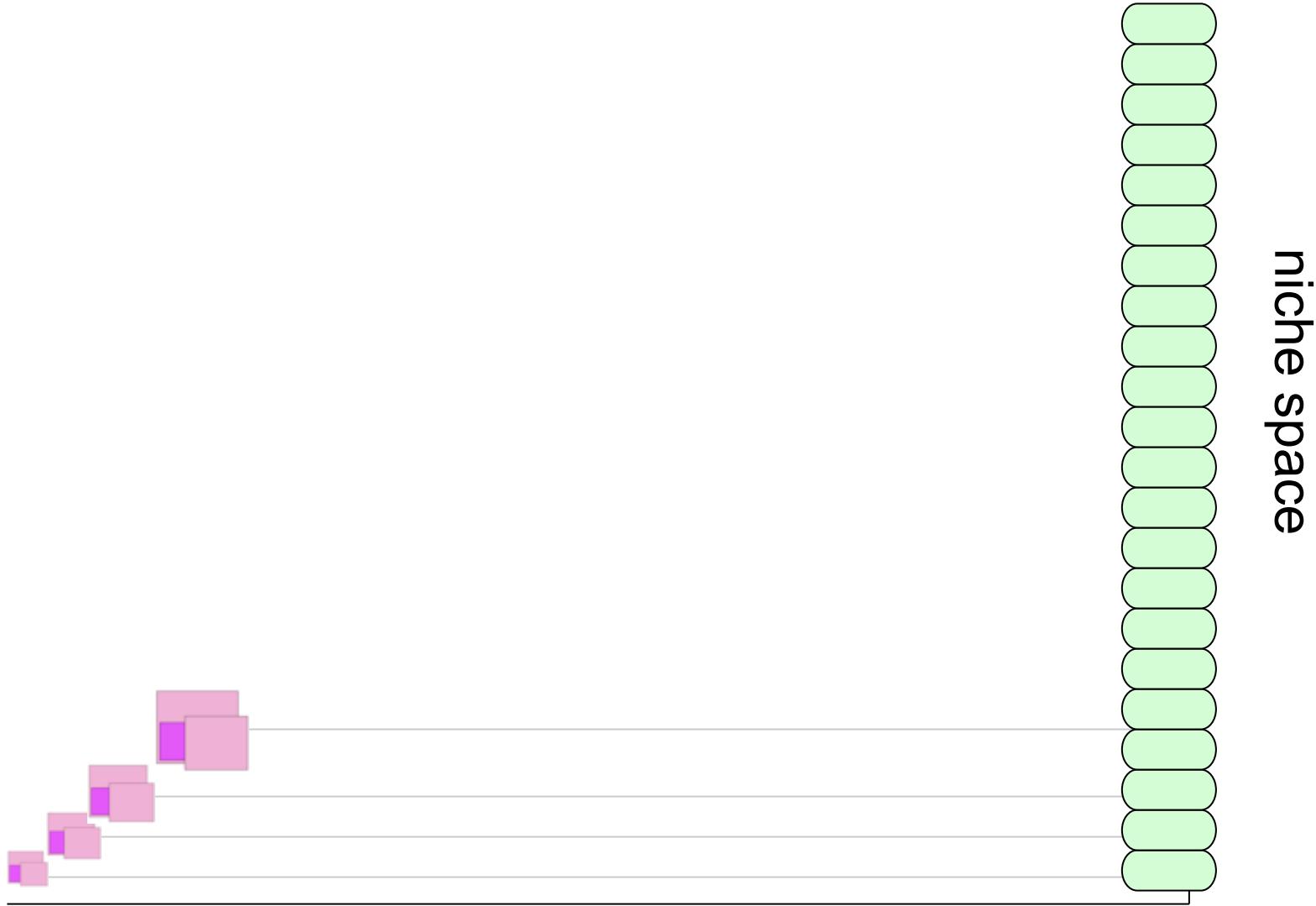


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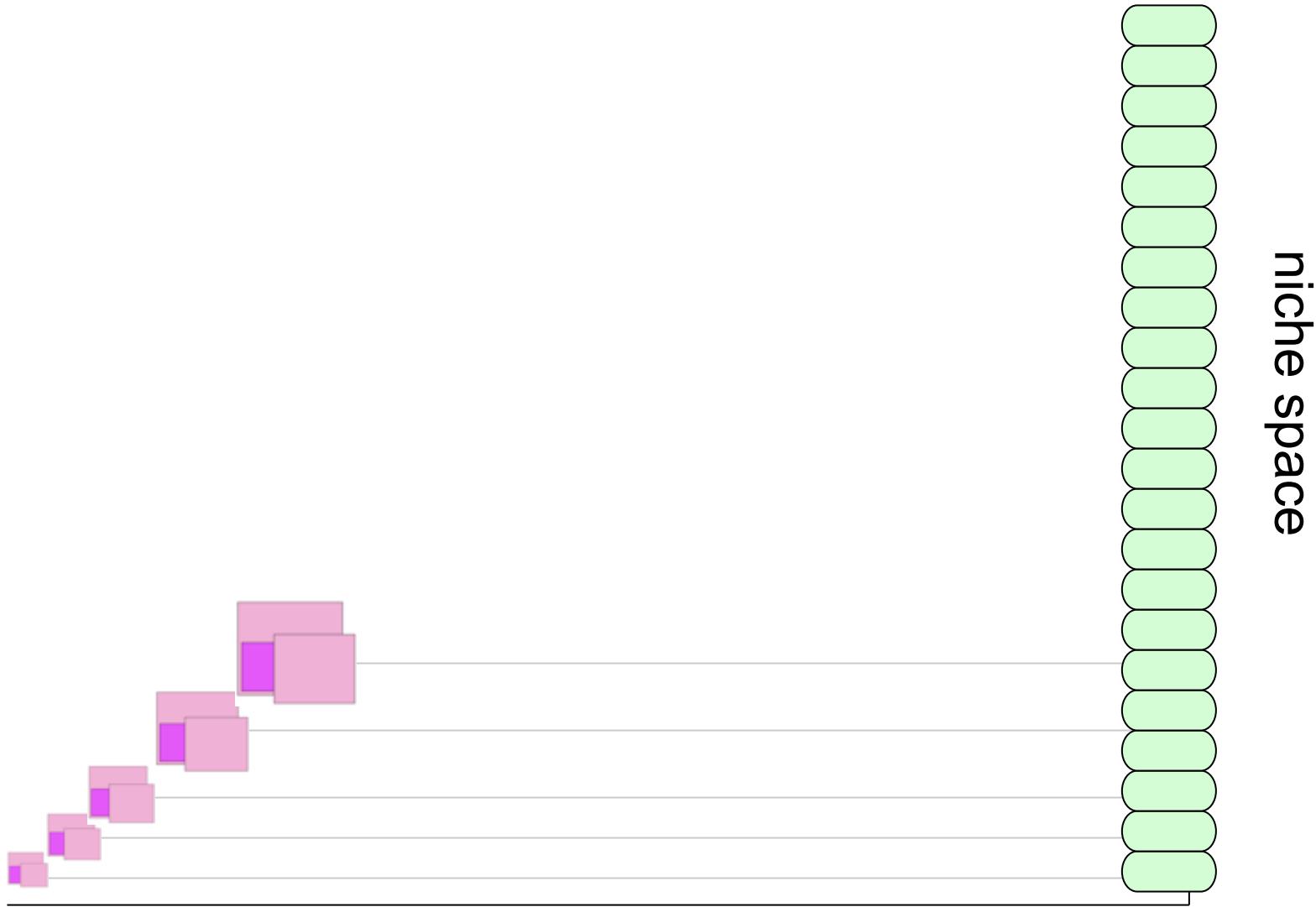


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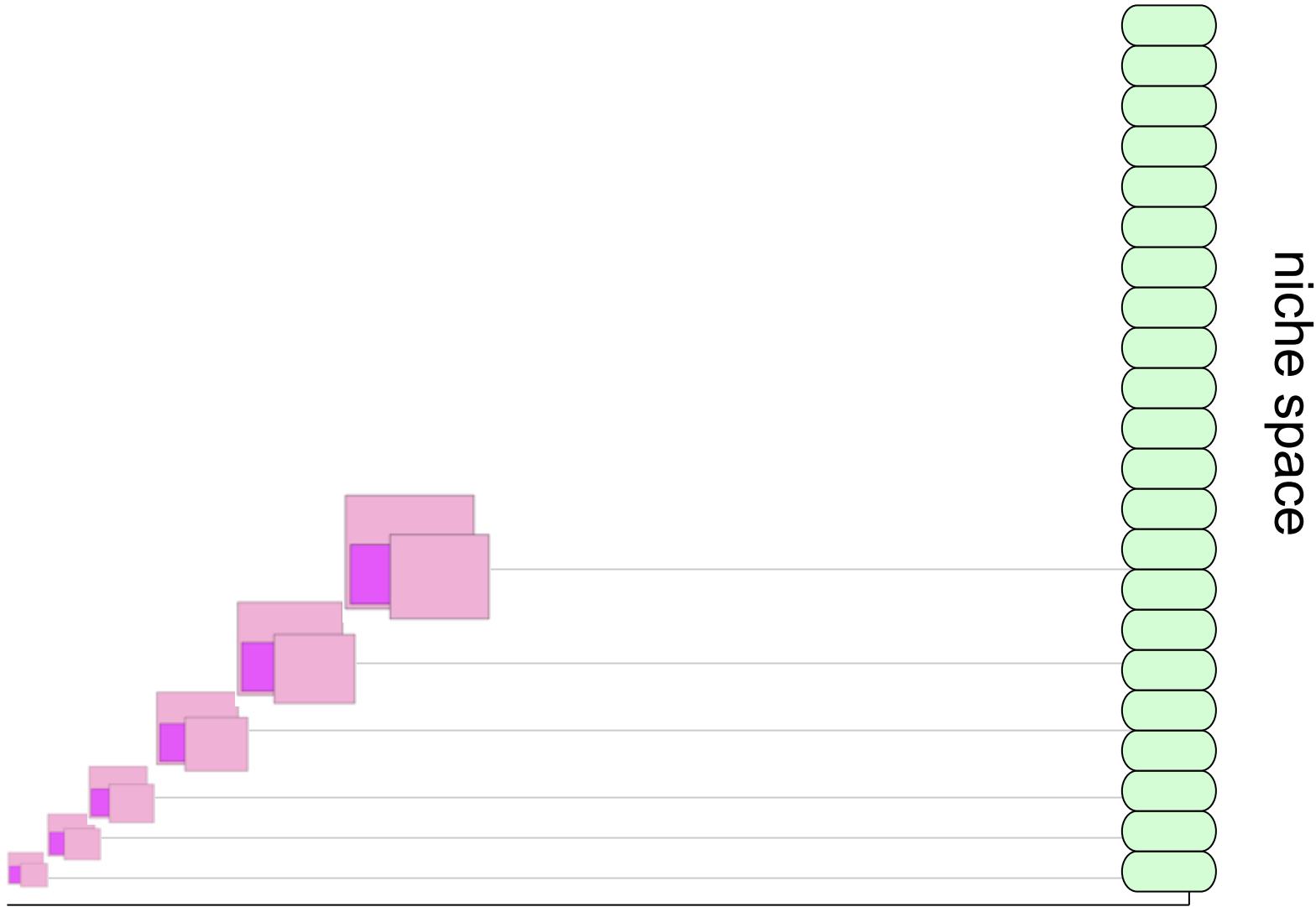


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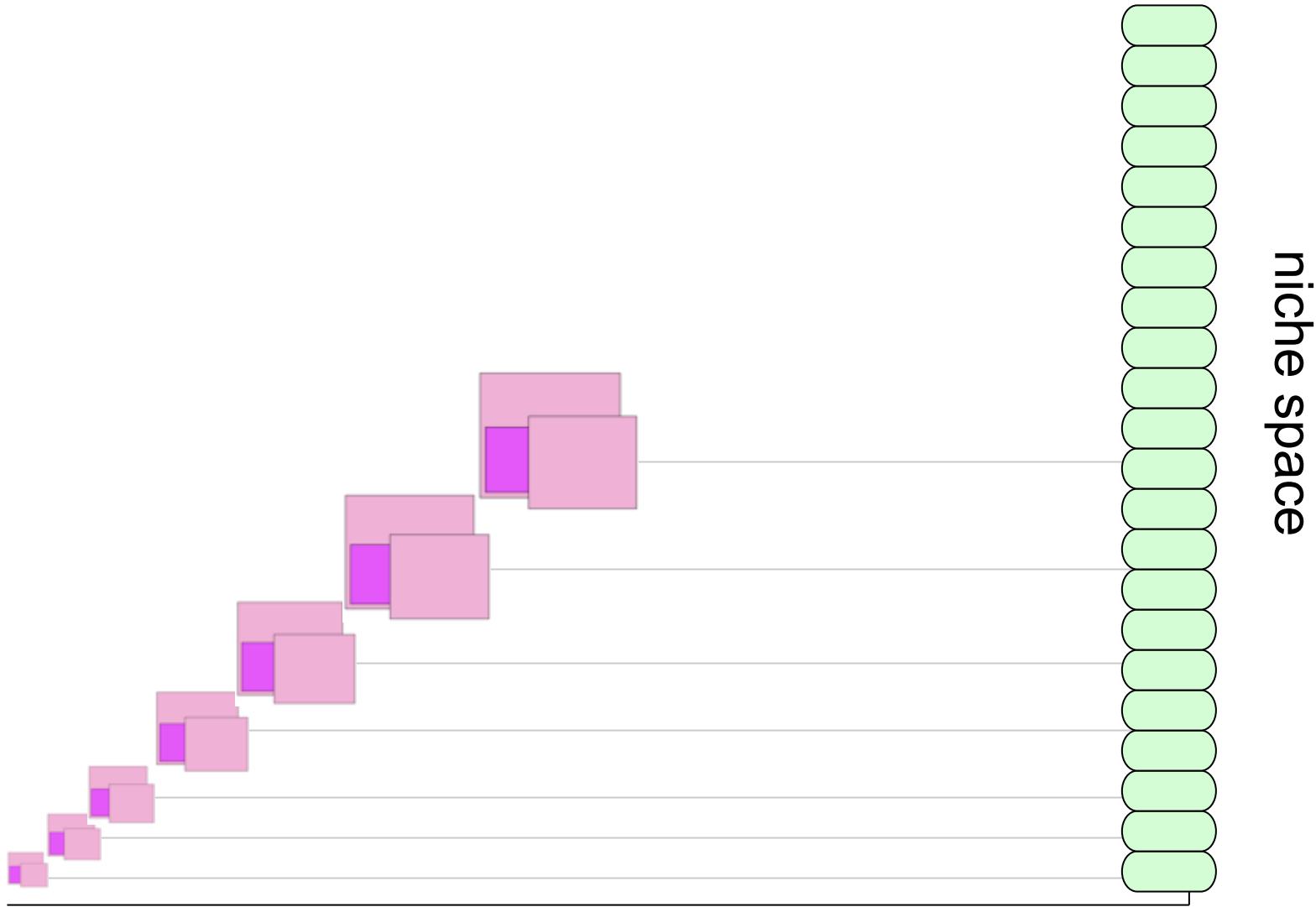


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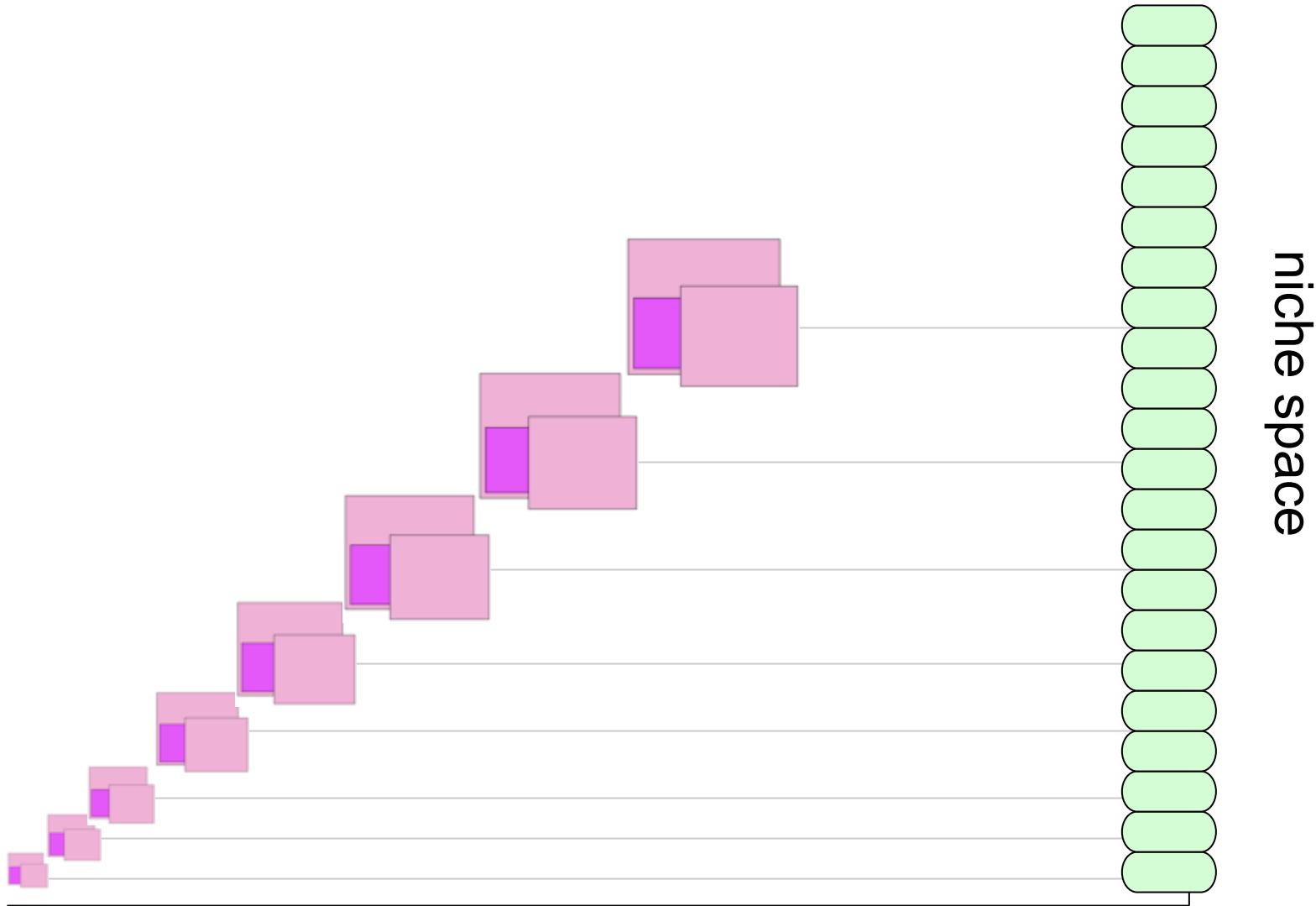


# Niches of parent and offspring



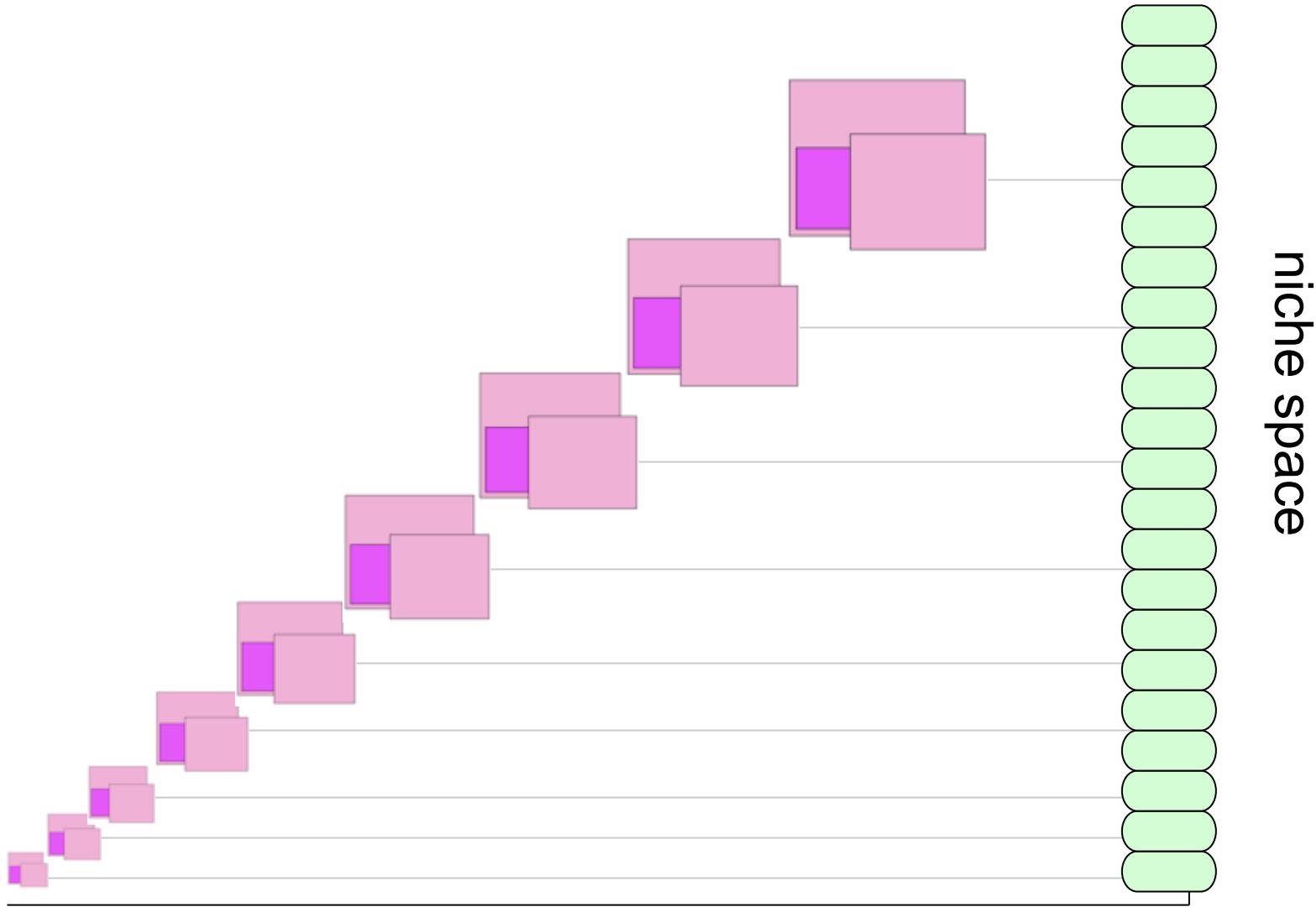


# Niches of parent and offspring



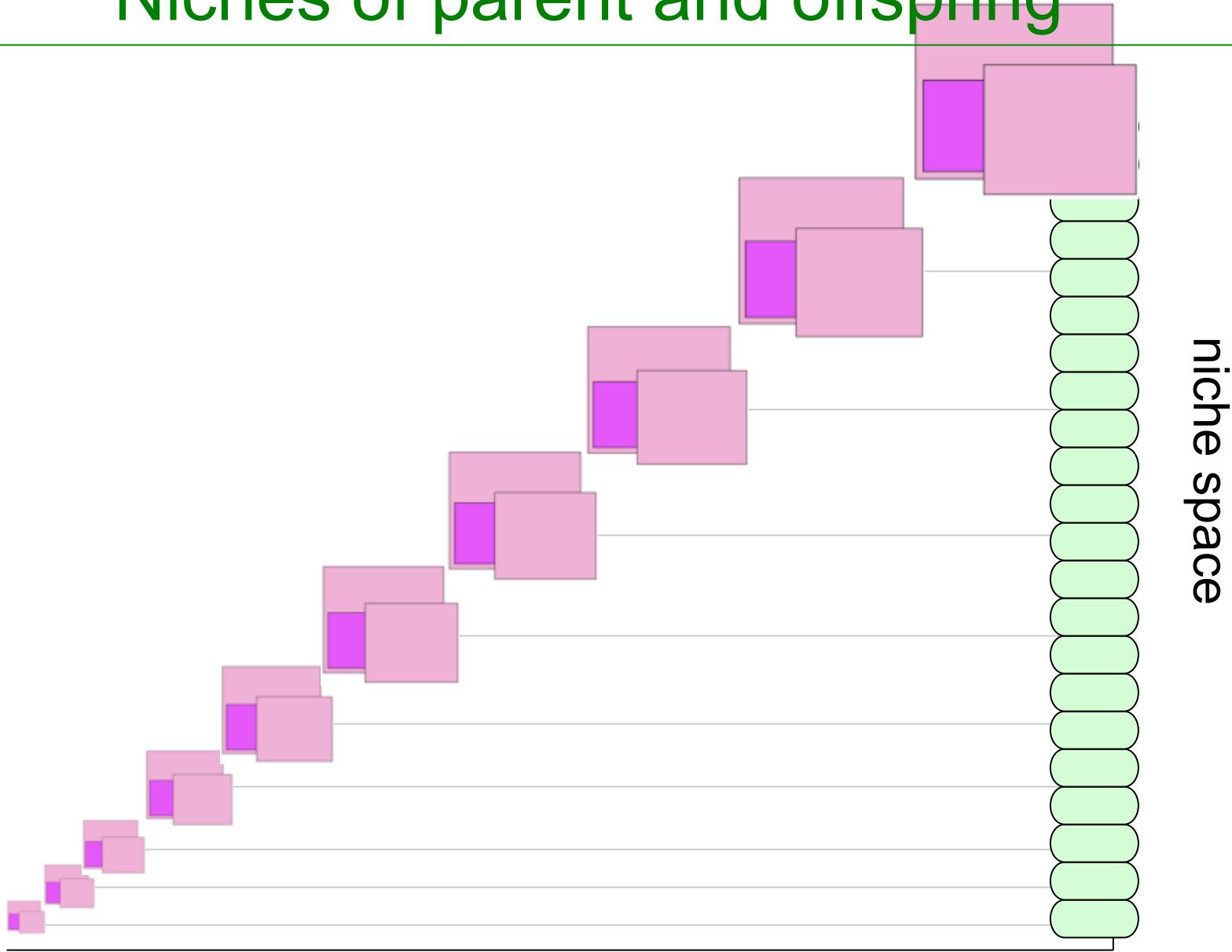


# Niches of parent and offspring





# Niches of parent and offspring



niche space



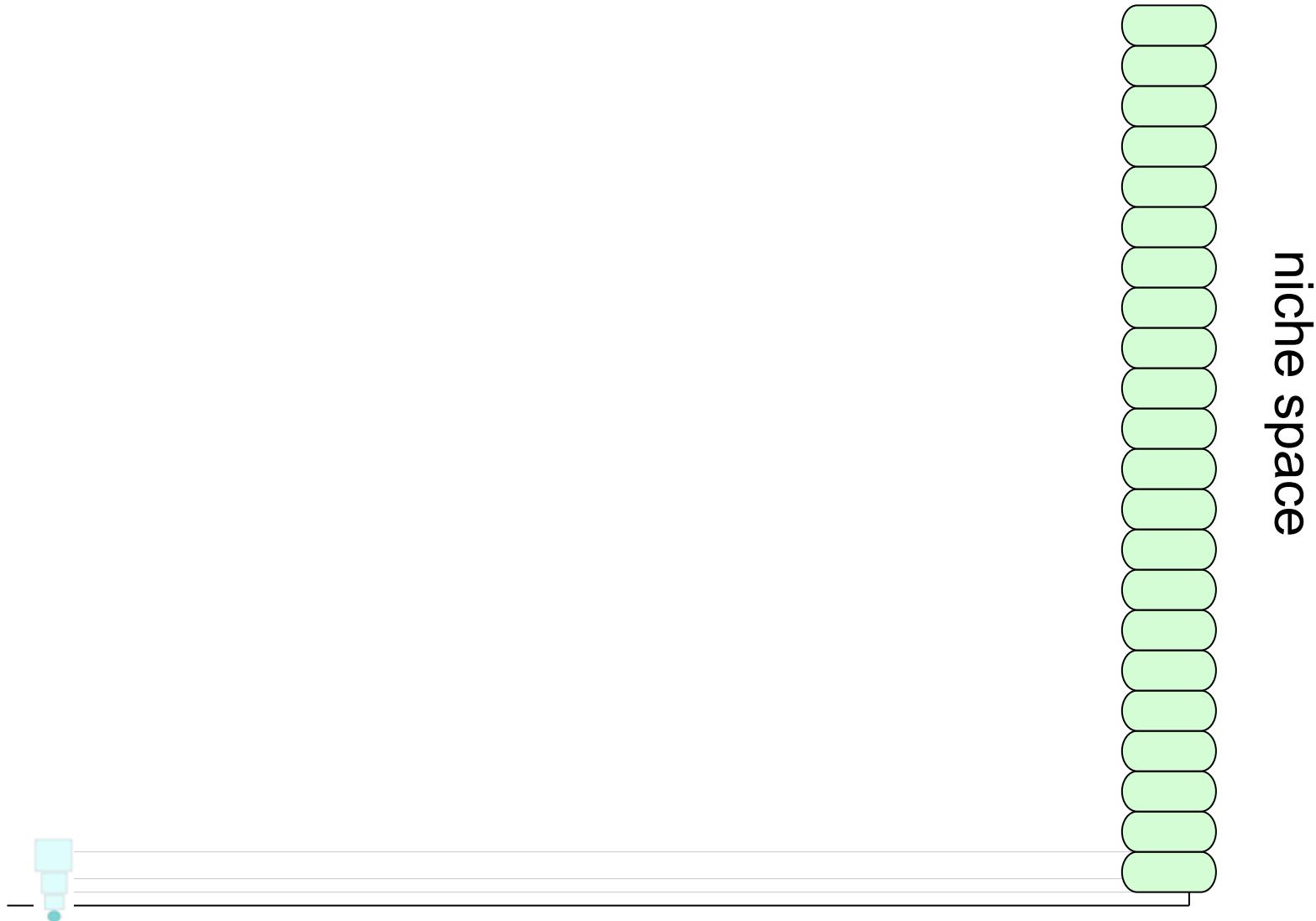
# Niches of parent and offspring



niche space



# Niches of parent and offspring





# Niches of parent and offspring





# Niches of parent and offspring



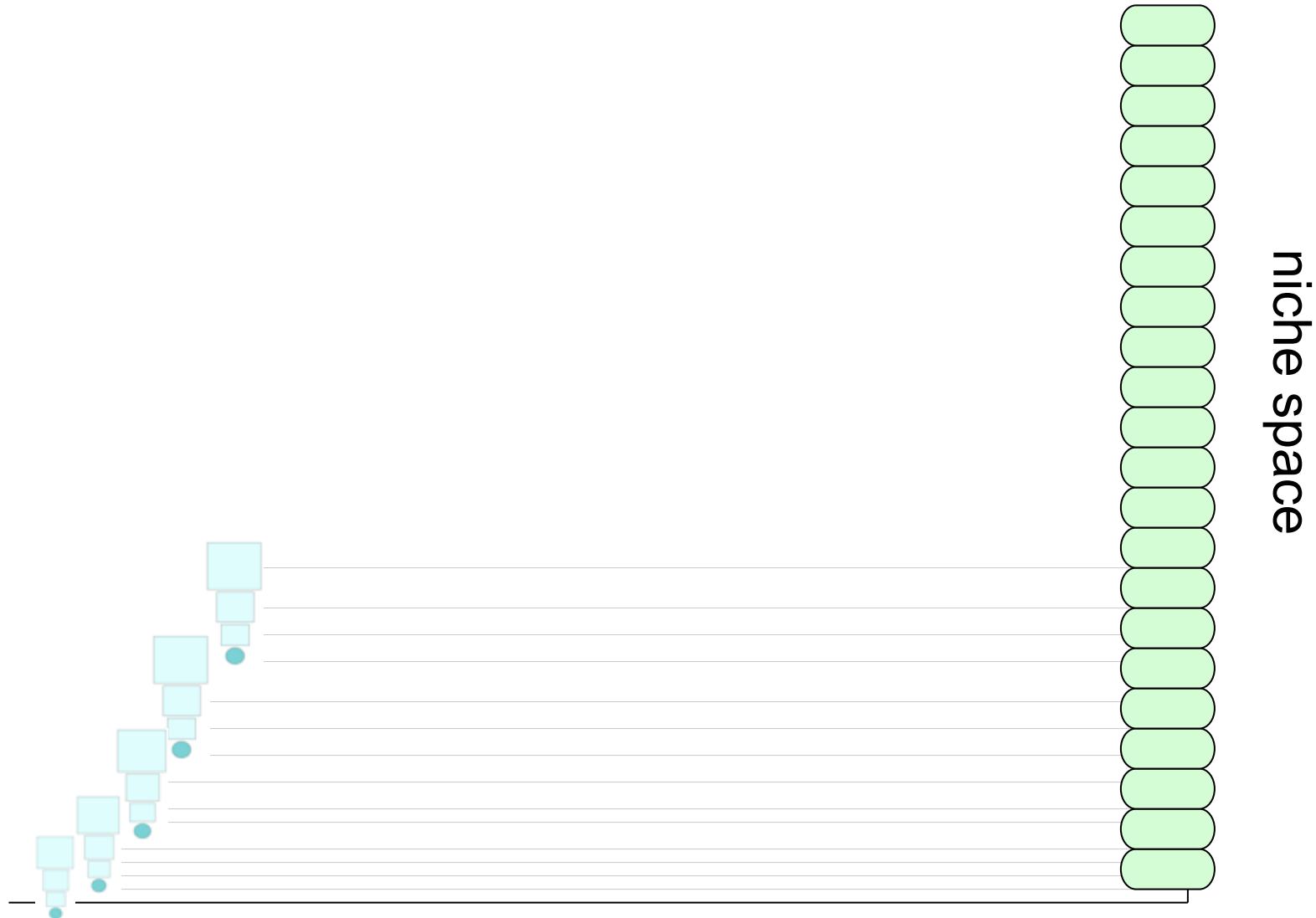


# Niches of parent and offspring



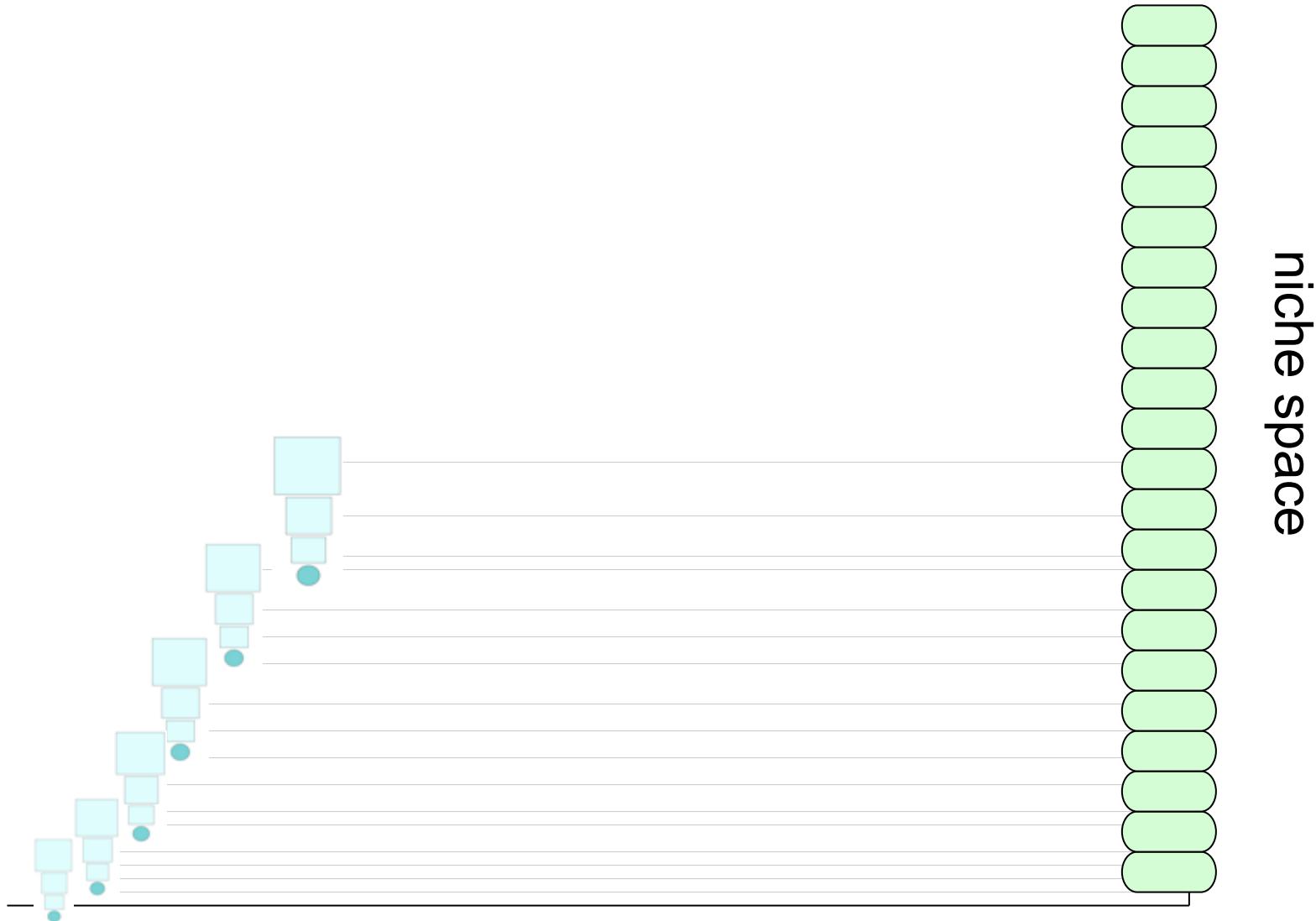


# Niches of parent and offspring



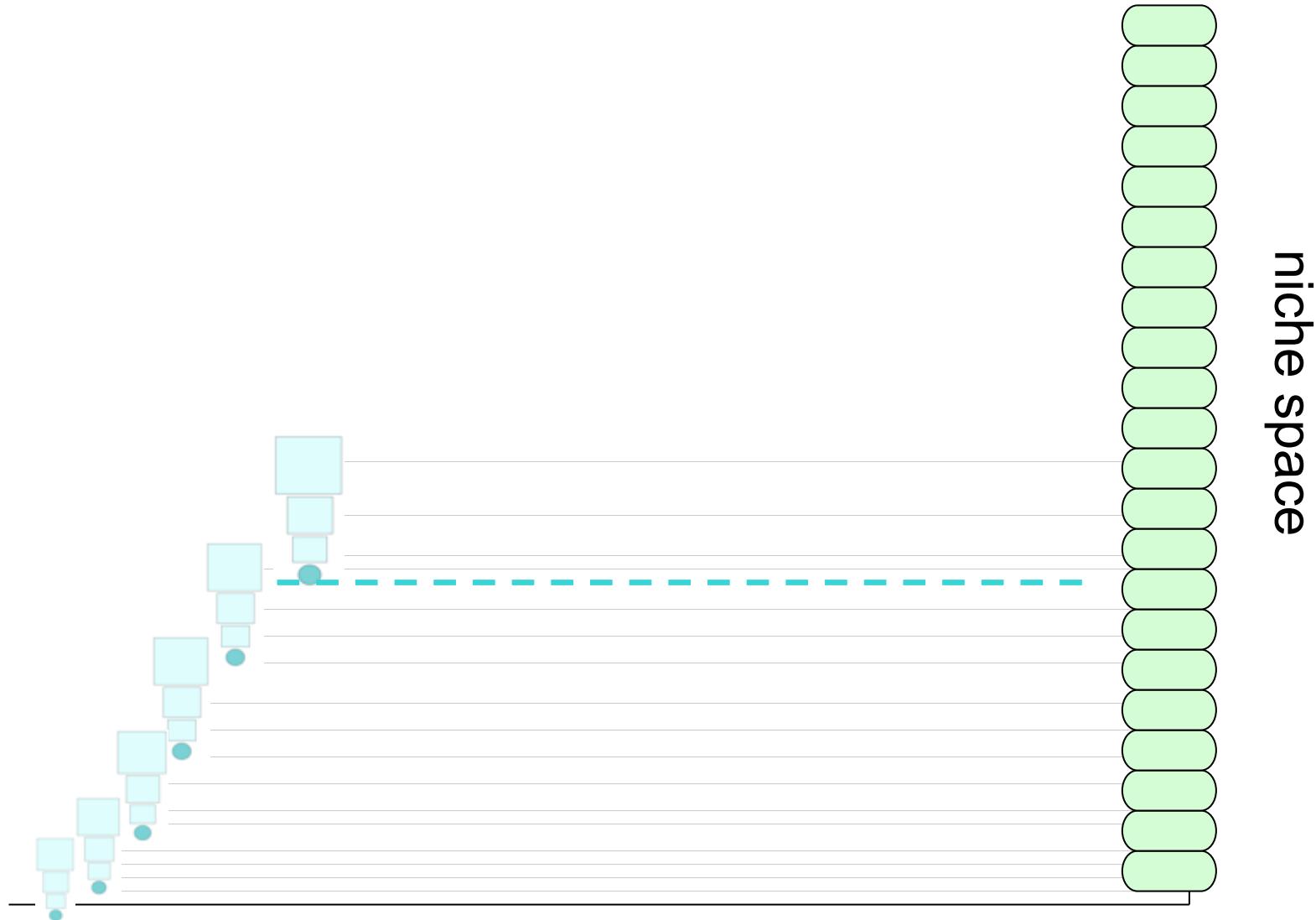


# Niches of parent and offspring



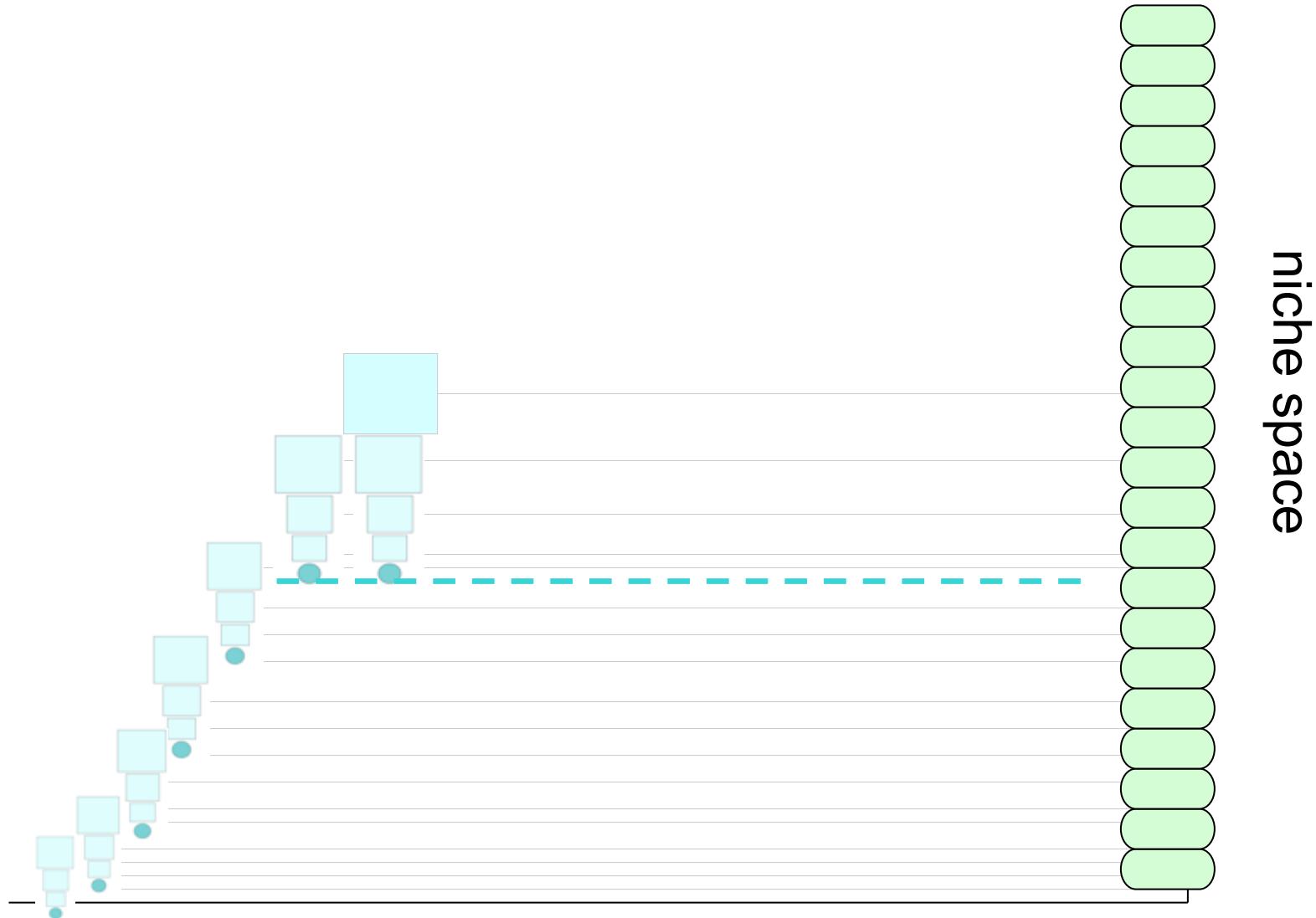


# Niches of parent and offspring



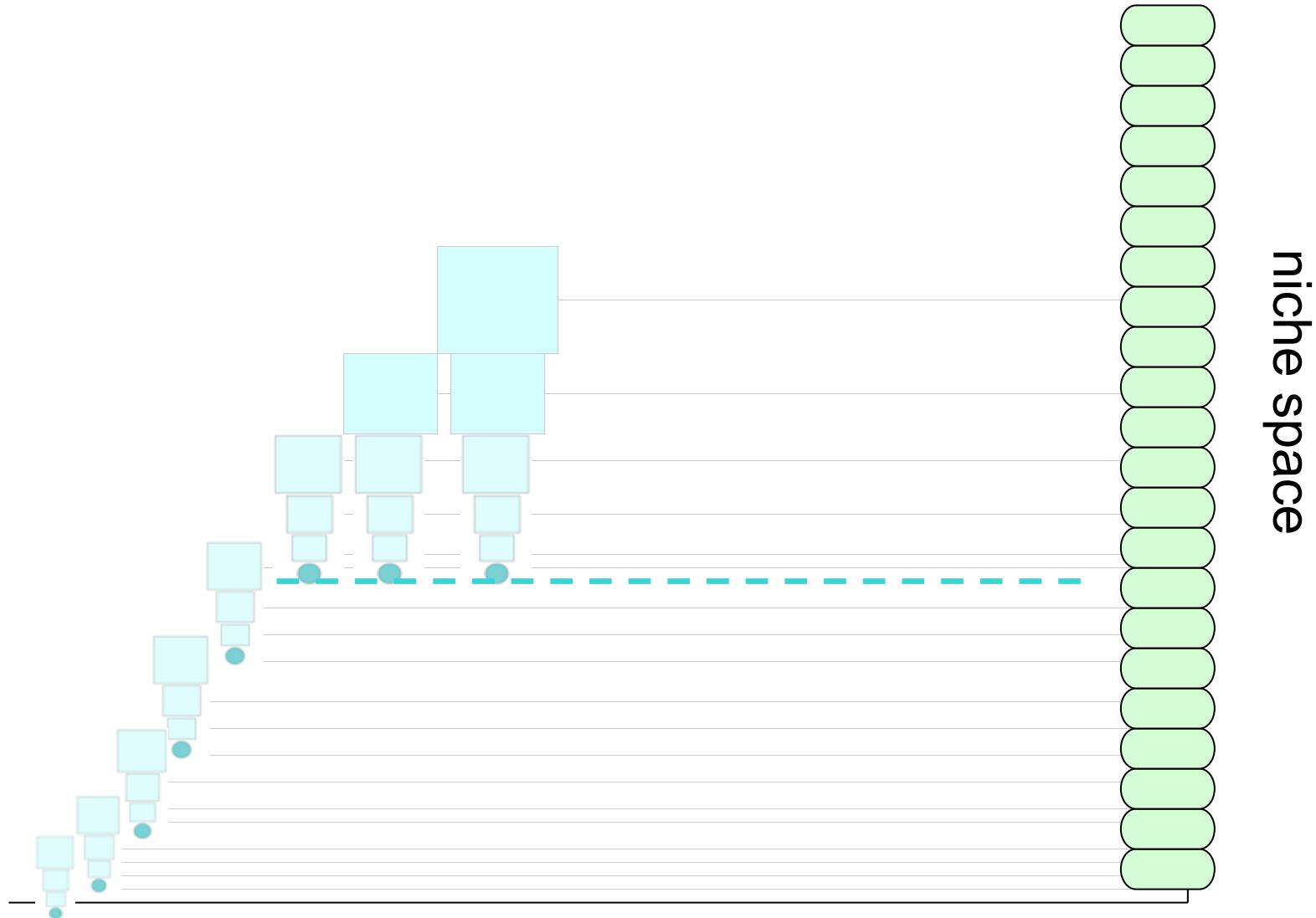


# Niches of parent and offspring



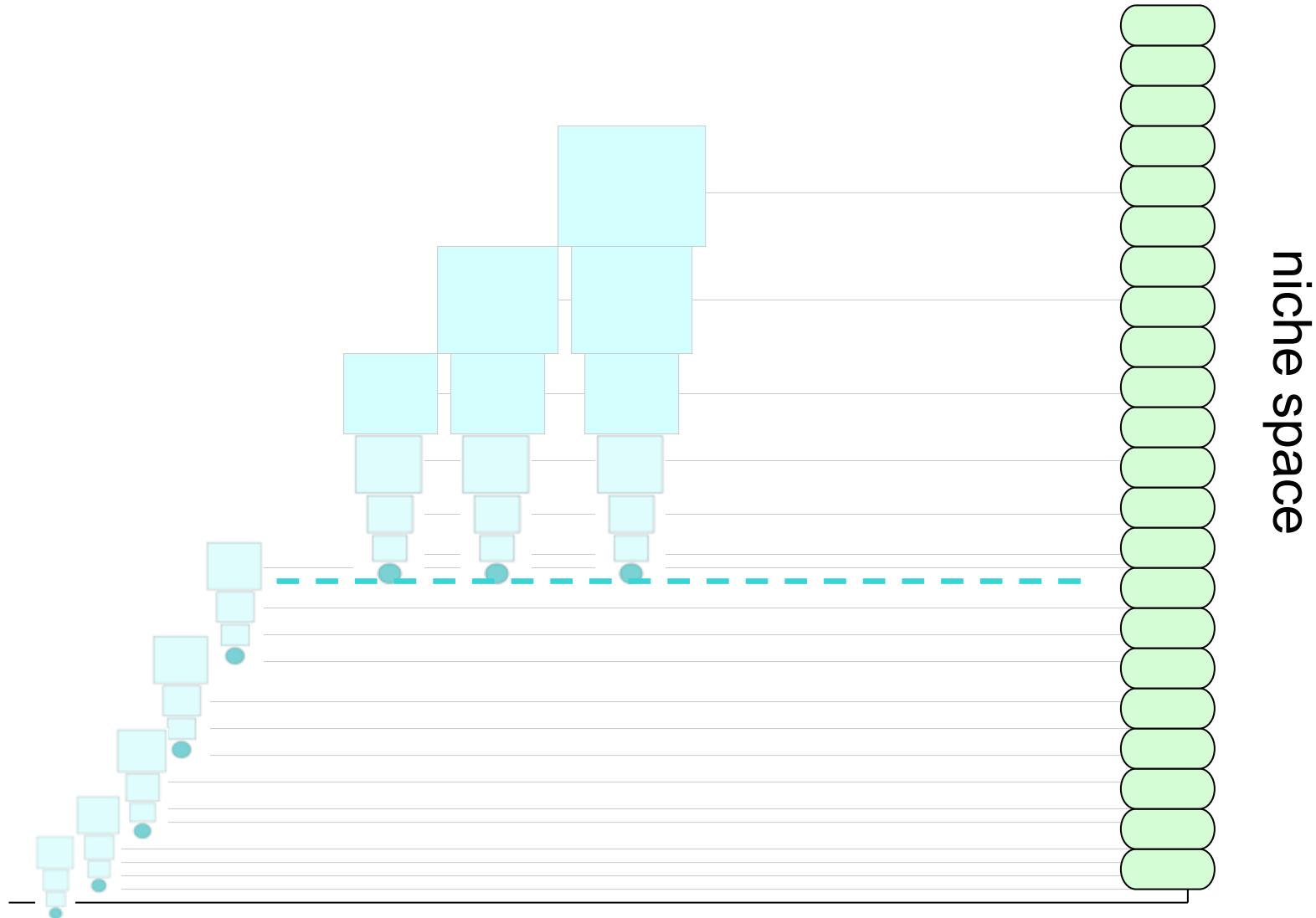


# Niches of parent and offspring



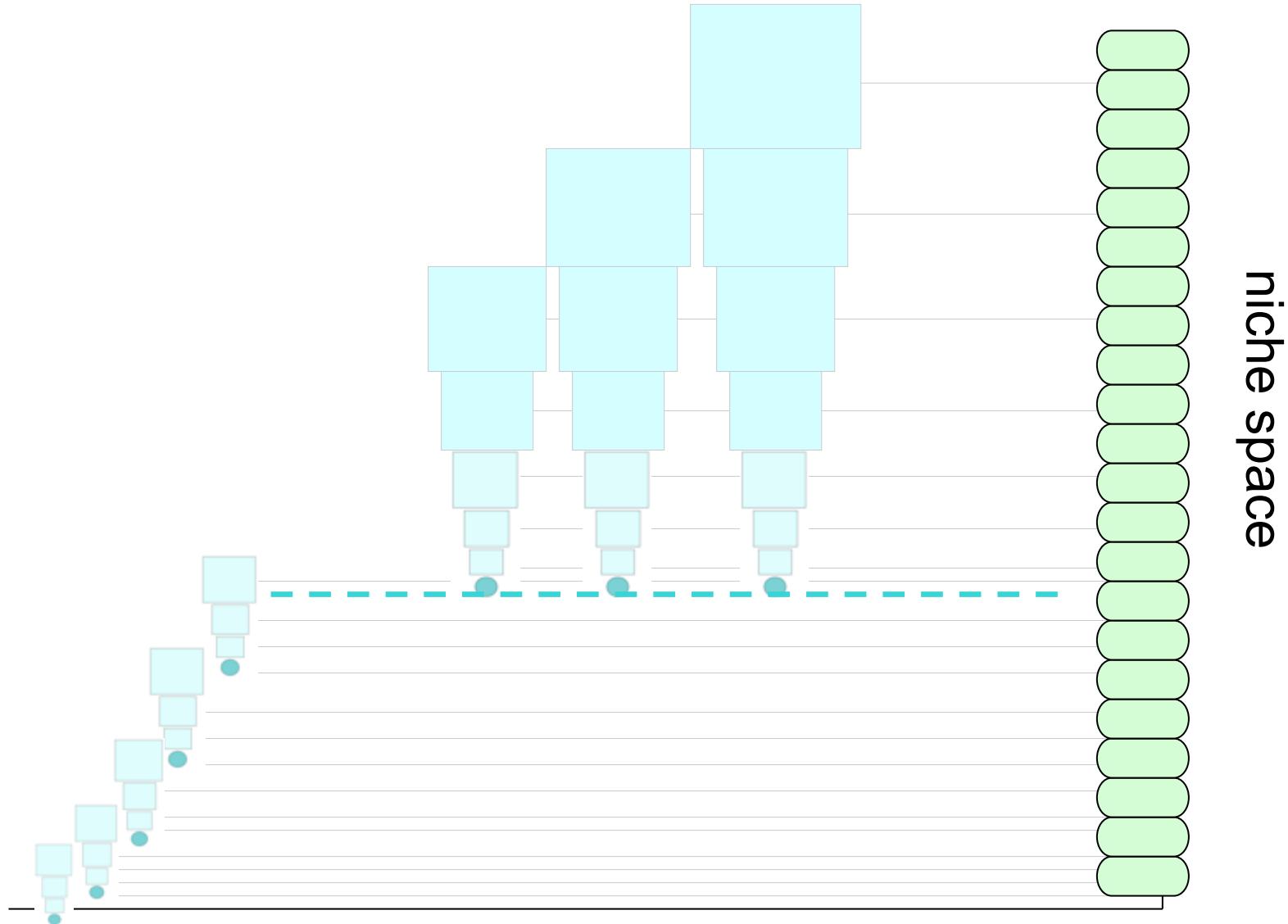


# Niches of parent and offspring



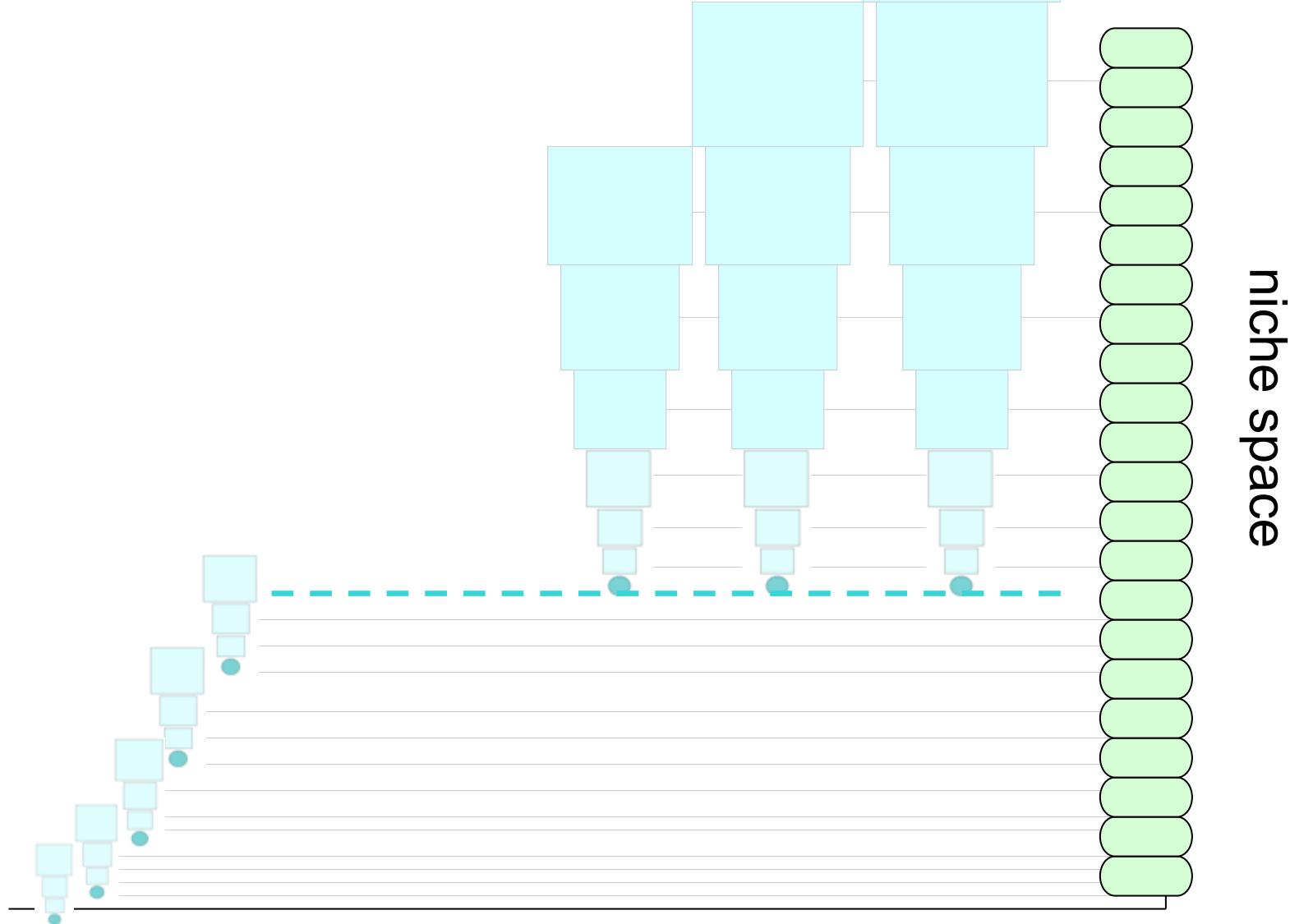


# Niches of parent and offspring



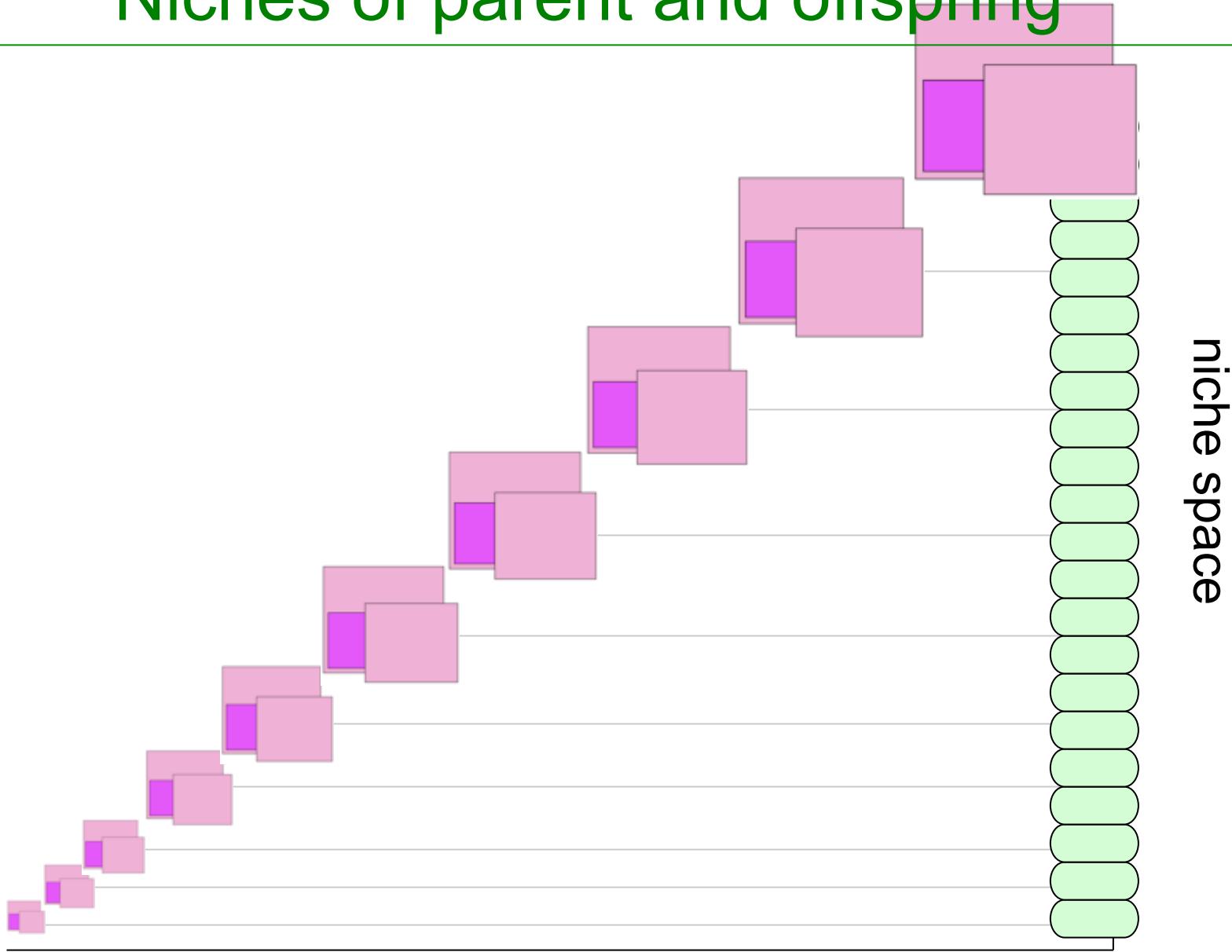


# Niches of parent and offspring





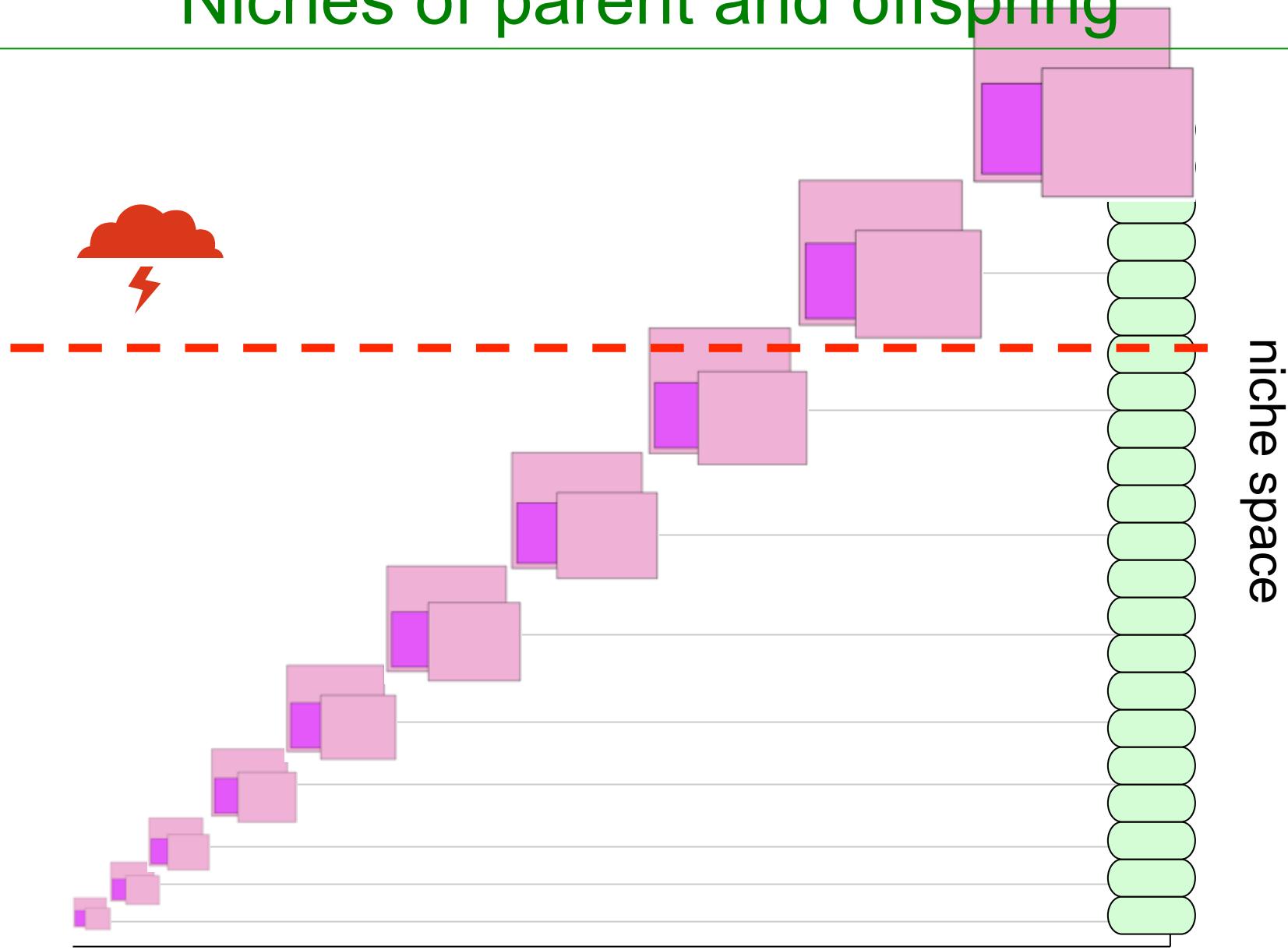
# Niches of parent and offspring



niche space

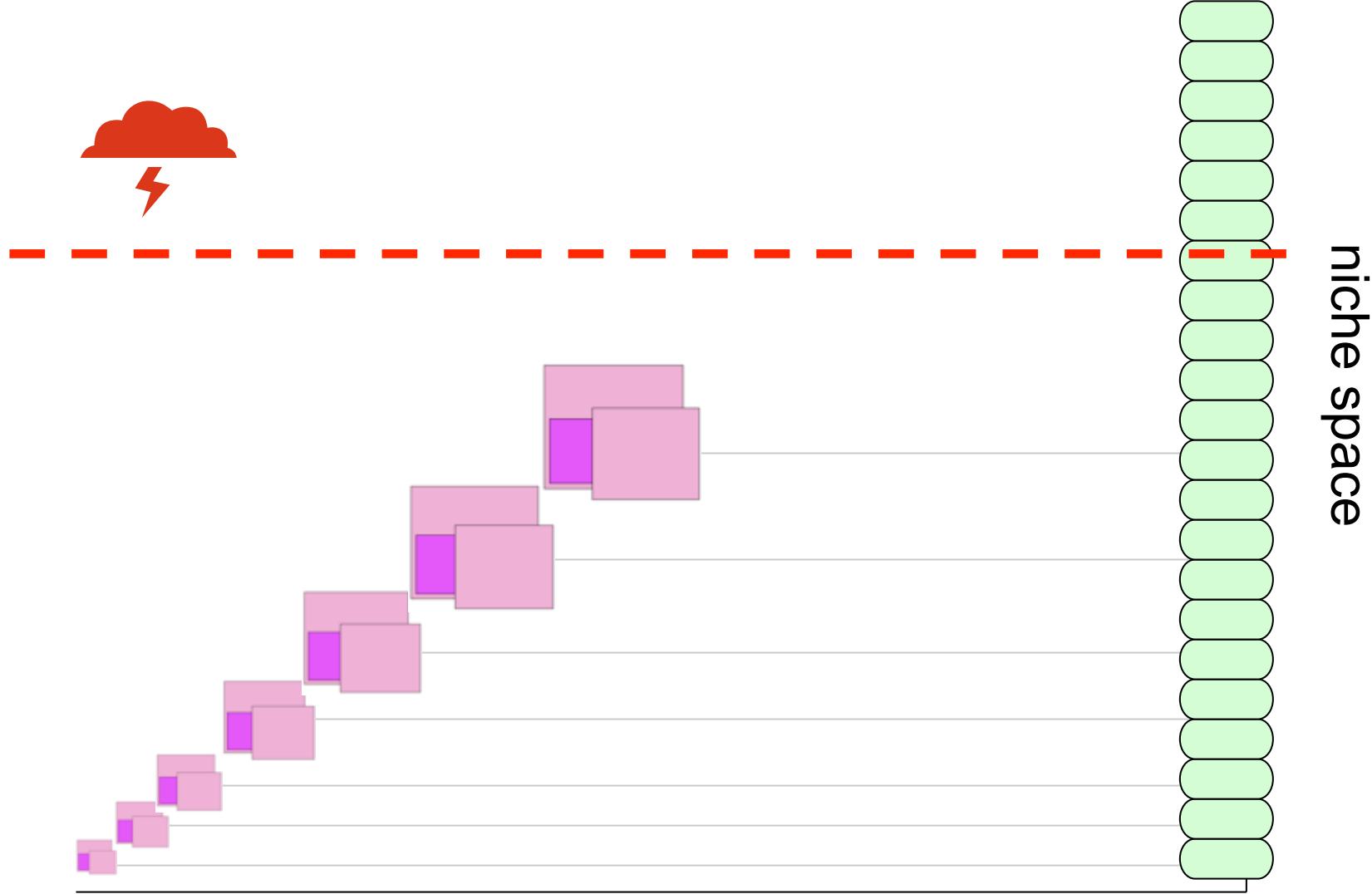


# Niches of parent and offspring



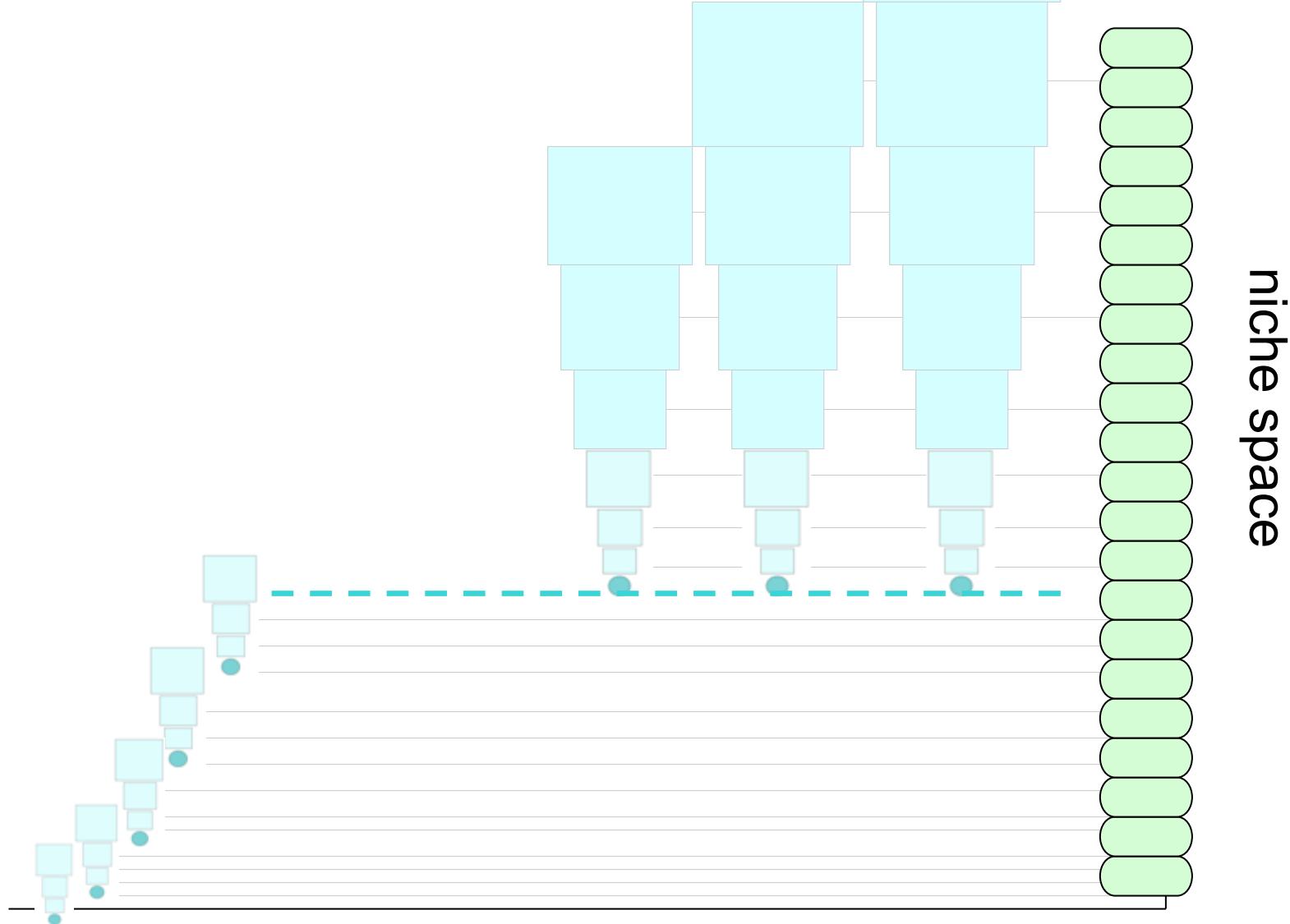


# Niches of parent and offspring



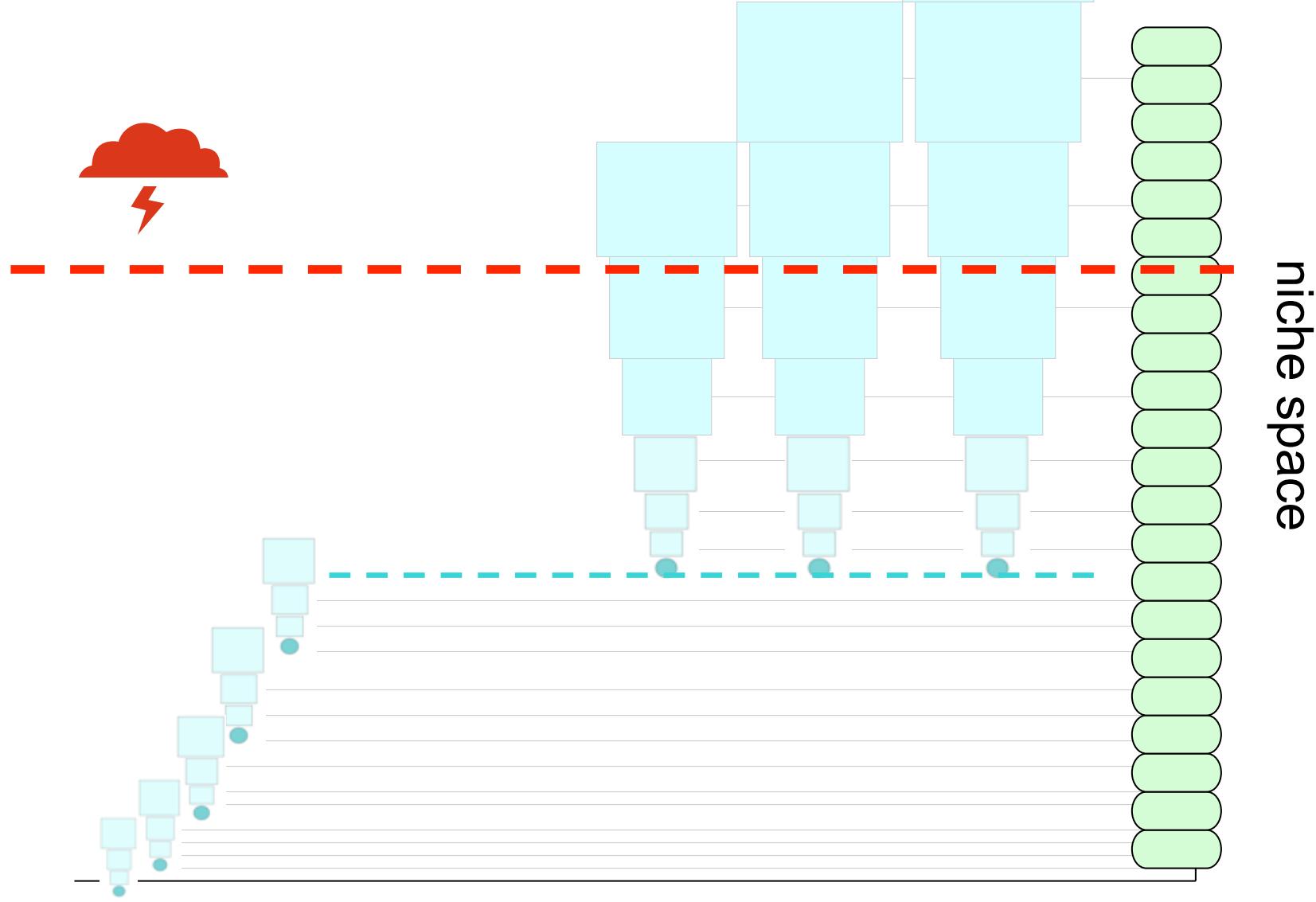


# Niches of parent and offspring



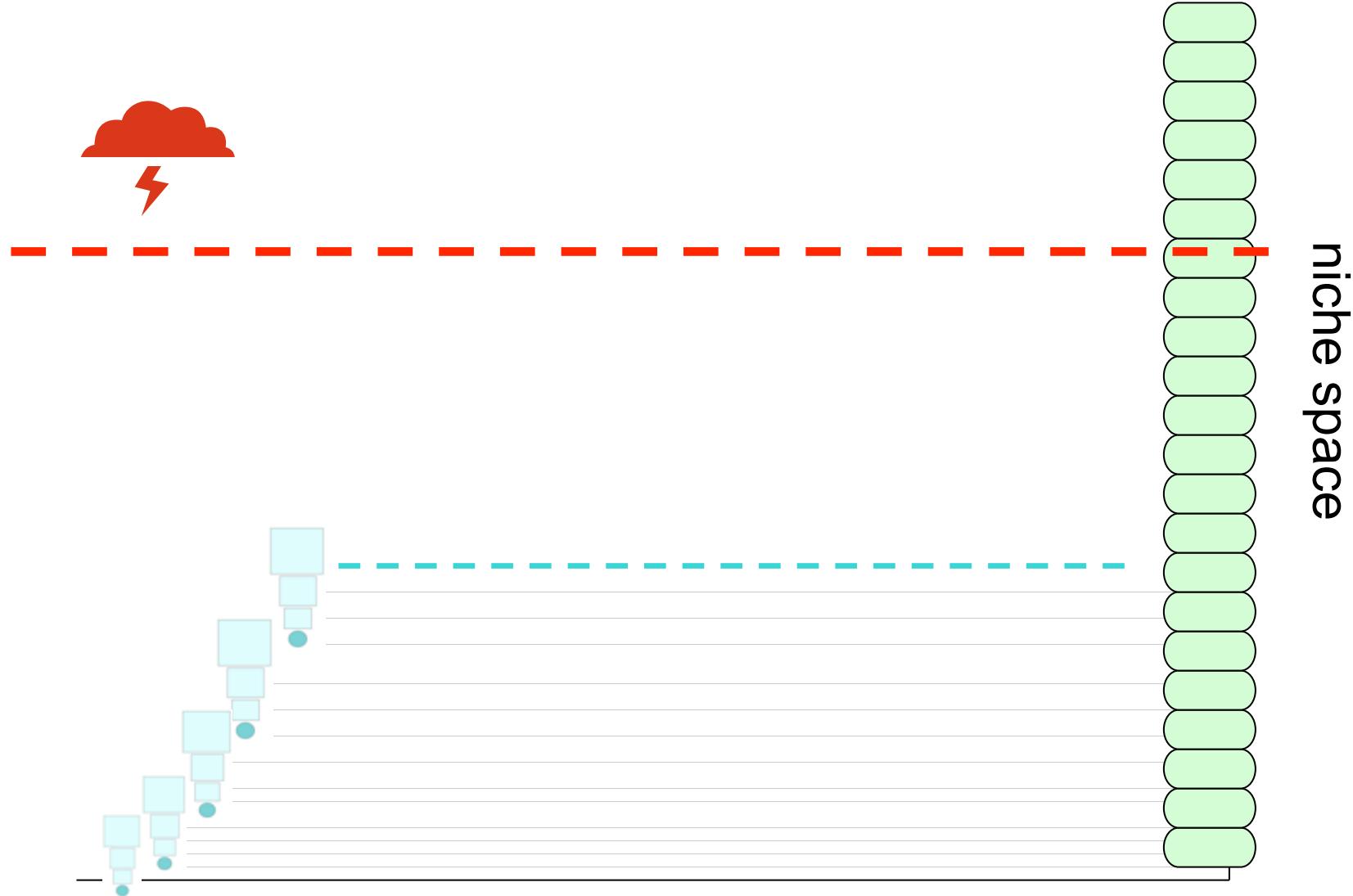


# Niches of parent and offspring





# Niches of parent and offspring





## Resulting hypothesis I

The reproductive mode of dinosaurs (oviparity), with its intrinsic limited juvenile start size linked to ontogenetic niche stratification, may have led to a parallel decrease of small dinosaur species with the increase of larger species, because offspring of large species fill the niche space of the smaller species.

A catastrophic event, truncating adult body size, could therefore, in theory, wipe out the whole reproductive dinosaur population.



## Resulting hypothesis II

In contrast, the reproductive mode of mammals (and also that of many birds due to parental care) does not lead to an ontogenetic niche stratification, but offspring use the parents' niche.

Thus, with increasing body mass of larger species, niches of smaller species are not usurped by the larger species' offspring to the same extent.

Die-offs of larger species would not leave niches of smaller life forms empty.



## Work plan

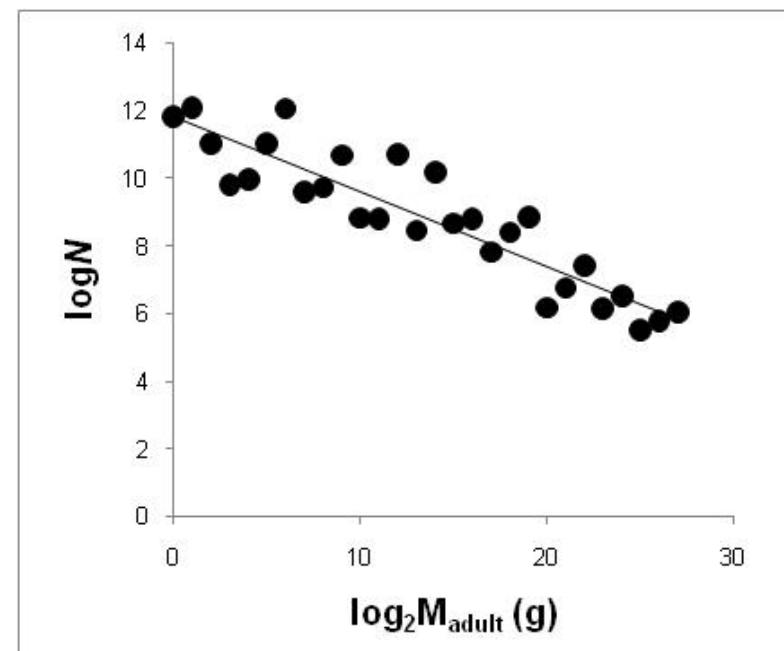
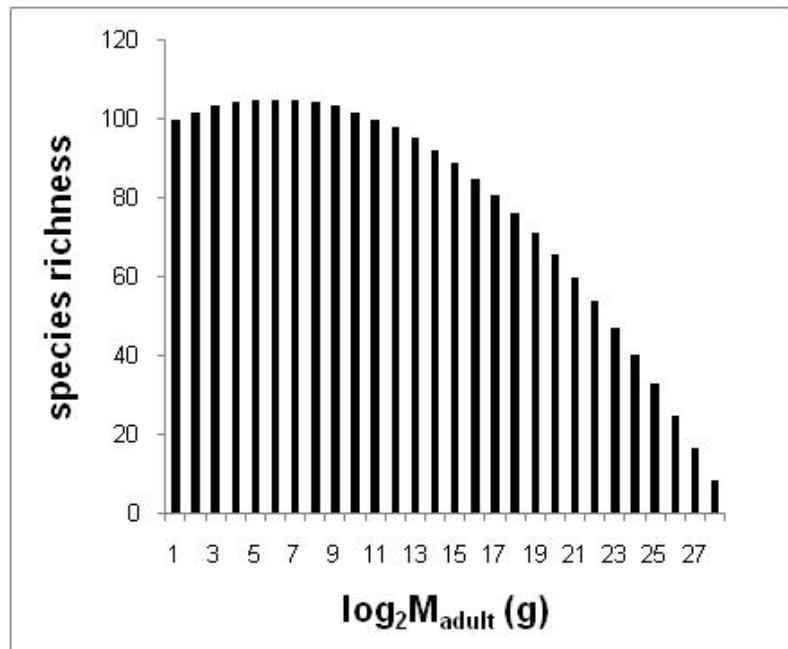
Check species assemblages for distribution patterns (is there a ‘gap’)?

Design deterministic model to test effect of interspecific competition on body mass distribution of mammals and dinosaurs before and after a simulated K-Pg-event





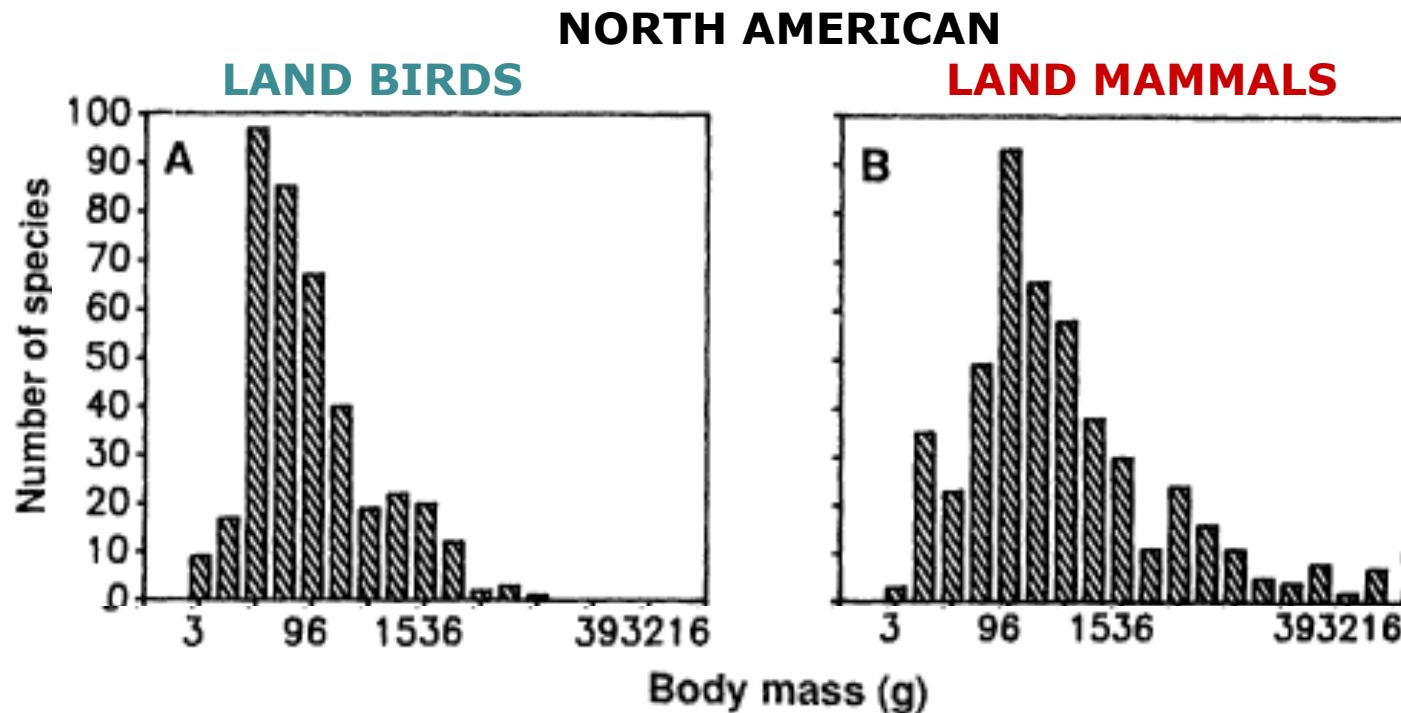
## Species/abundance distributions - mammals



Hutchinson & MacArthur (1958): intuitive, quantitative model of more niche space at lower  $M$



## Species distributions - mammals/birds

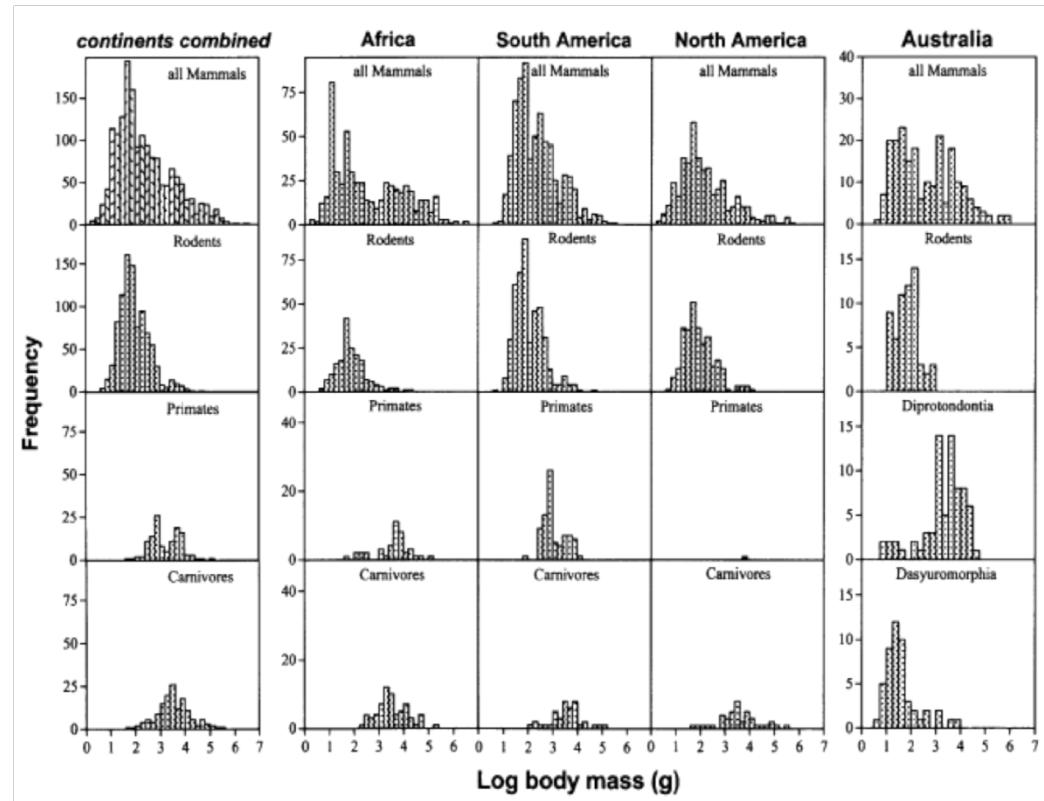


Brown & Maurer (1989) *Science* 243:1145-1150



# Species distributions - mammals

## MAMMALS: PERSISTENT OVER MULTIPLE SCALES



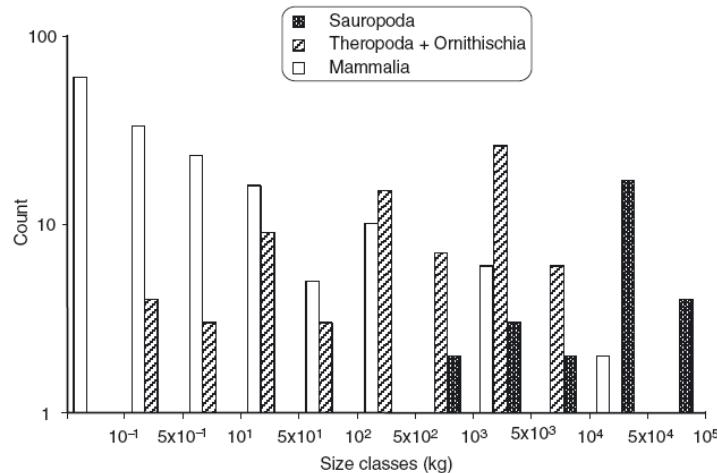
Smith et al. (2004) *Am Nat* 163:672-691





# Species distributions - dinosaurs

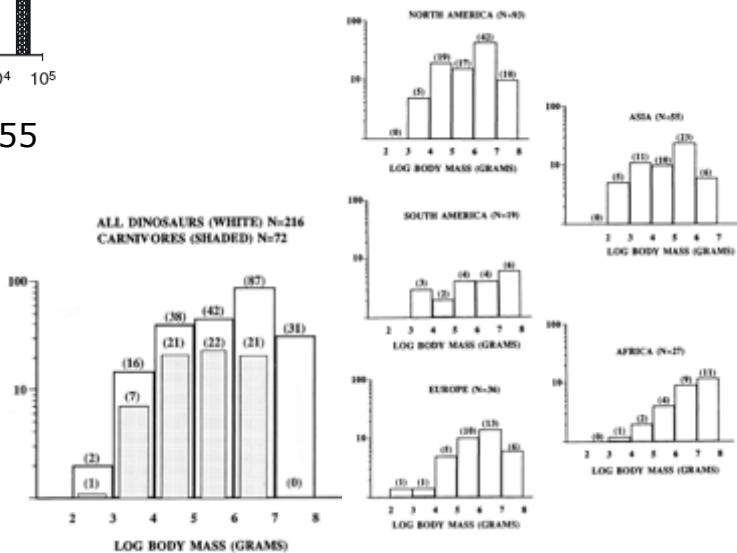
## DINOSAURS: FEW SMALL TAXA



Sander et al. (2011) *Biol Rev* 86:117-155



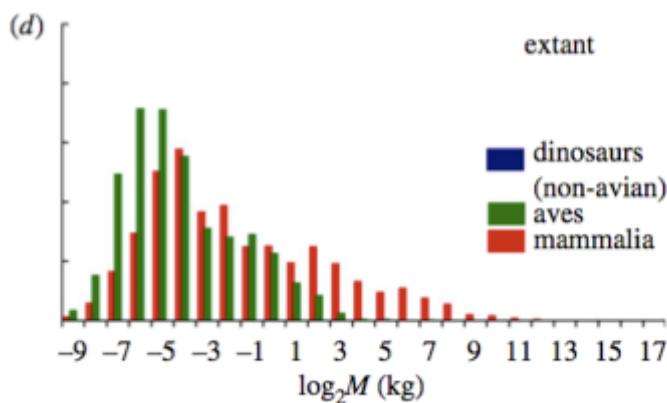
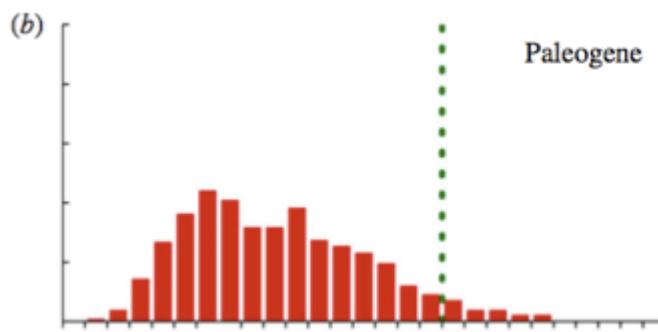
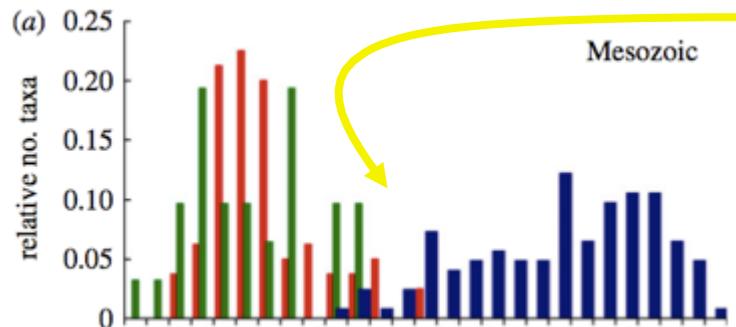
## MULTIPLE SCALES



Peczkis (1995) *J Vert Paleontol* 14:520-533



# Species distributions





## Deterministic model

- Populations of different sized species of:

Dinosaurs:  $i_1, i_2 \dots i_k = \{2 \text{ g to } \sim 131 \text{ tons}\}$

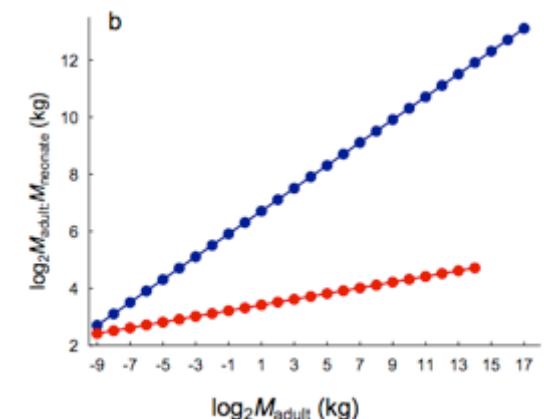
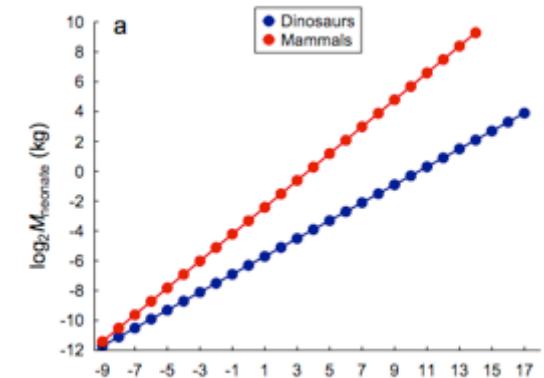
Mammals:  $i_1, i_2 \dots i_k = \{2 \text{ g to } \sim 16 \text{ tons}\}$

- Each structured by size ( $\log_2 M$  increments,  $j$ ) from neonate-adult

$$M_{\text{neonate}} = a M_{\text{adult}}^b$$

$$b_{\text{dinosaurs}} \sim 0.6$$

$$b_{\text{mammals}} \sim 0.9$$





## Deterministic model

- Populations of different sized species of:

Dinosaurs:  $i_1, i_2 \dots i_k = \{2 \text{ g to } \sim 131 \text{ tons}\}$

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- Each structured by size ( $\log_2 M$  increments,  $j$ ) from neonate-adult

$$M_{\text{neonate}} = a M_{\text{adult}}^b$$

$$b_{\text{dinosaurs}} \sim 0.6$$

$$b_{\text{mammals}} \sim 0.9$$

- For each  $M_{i,j}$ , estimate:
  1. initial abundance  $n$  (allometry)
  2. survivorship  $p$  ( $r$ -selecting or  $K$ -selecting)
  3. fecundity  $f$  (allometry; add  $f_i n_{i,k}$  to  $n_{i,1}$ )

- Assume: each  $\log_2 M$  step = ontogenetic niche shift



# Deterministic model



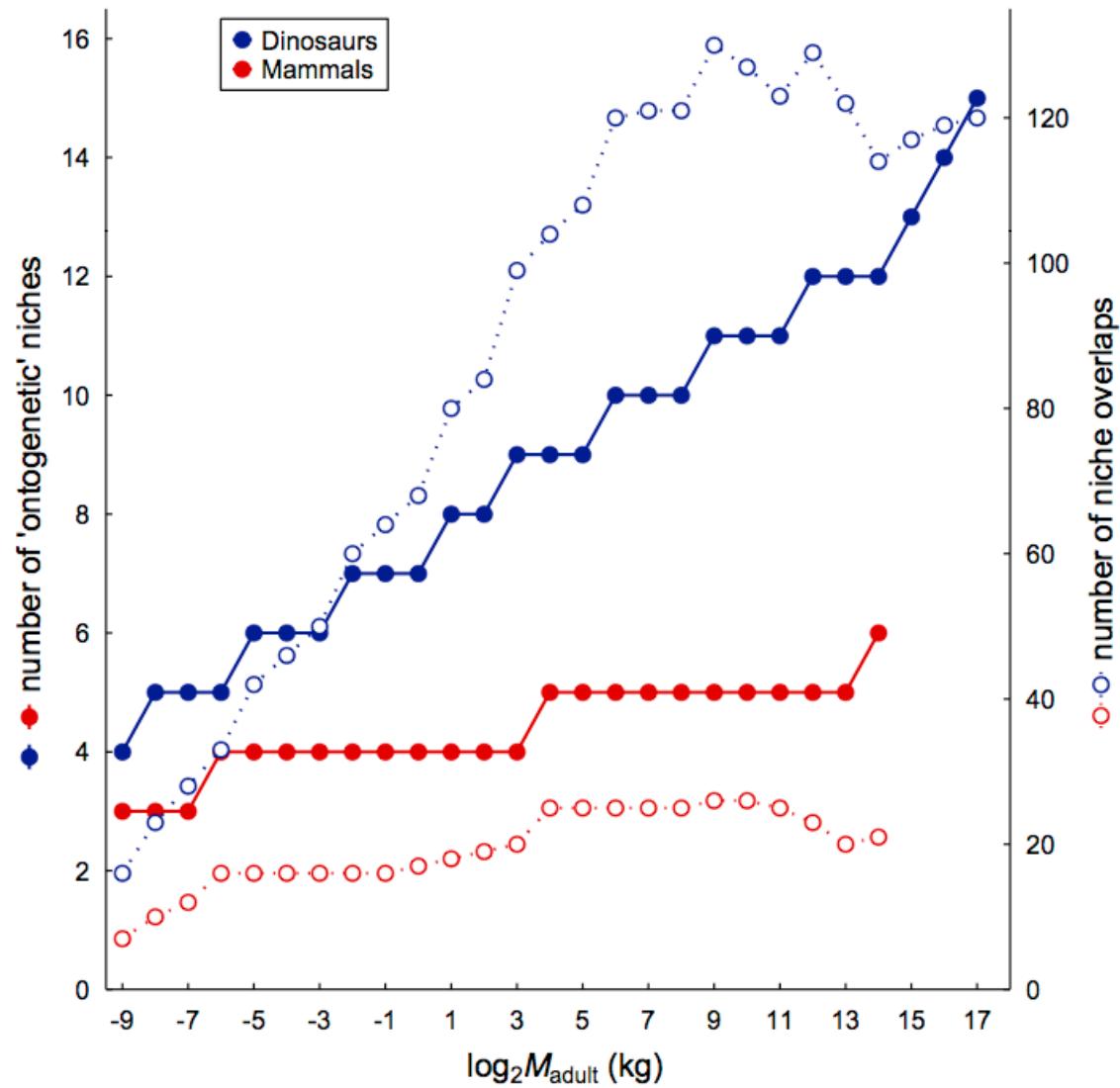
$\log_2 M_{\text{adult}} (\text{kg})$	log <sub>2</sub> $M$ classes represented in $M$ category (ontogenetic 'niches')															# of $M$ niches									
	-11	-10	-9	-8	-7	-6	-5	-4	-3	-2	-1	0	1	2	3	4	5	6	7	8	9	10	11	12	13
-9	x	x	x																						3
-8		x	x	x																					3
-7		x	x	x																					3
-6			x	x	x																				3
-5			x	x	x																				3
-4			x	x	x																				3
-3			x	x	x	x																			4
-2			x	x	x	x																			4
-1			x	x	x	x																			4
0			x	x	x	x	x																		4
1			x	x	x	x	x																		4
2			x	x	x	x	x																		4
3			x	x	x	x	x																		4
4			x	x	x	x	x																		4
5			x	x	x	x	x																		4
6			x	x	x	x	x																		4
7			x	x	x	x	x																		5
8			x	x	x	x	x																		5
9			x	x	x	x	x																		5
10			x	x	x	x	x																		5
11			x	x	x	x	x																		5
12			x	x	x	x	x																		5
13			x	x	x	x	x														x	x	x	x	5
14			x	x	x	x	x														x	x	x	x	5
# of interactions	1	2	3	3	3	4	4	4	4	4	4	4	4	4	4	4	5	5	5	5	5	4	3	2	1



$\log_2 M_{adult}$ (kg)	log <sub>2</sub> $M$ classes represented in $M$ category (ontogenetic 'niches')																		# of $M$ niches										
	-11	-10	-9	-8	-7	-6	-5	-4	-3	-2	-1	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
-9	x	x	x																									3	
-8	x	x	x	x																								4	
-7	x	x	x	x																								4	
-6	x	x	x	x	x																							4	
-5	x	x	x	x	x																							5	
-4	x	x	x	x	x	x																						5	
-3	x	x	x	x	x	x	x																				6		
-2	x	x	x	x	x	x	x	x																			6		
-1	x	x	x	x	x	x	x	x	x																		6		
0	x	x	x	x	x	x	x	x	x	x																	7		
1	x	x	x	x	x	x	x	x	x	x	x																7		
2	x	x	x	x	x	x	x	x	x	x	x	x															8		
3	x	x	x	x	x	x	x	x	x	x	x	x	x														8		
4	x	x	x	x	x	x	x	x	x	x	x	x	x	x													8		
5	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x											9			
6	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x										9			
7	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x									10			
8	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x								10			
9	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x							10			
10	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x							11		
11	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x						11		
12	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x				12			
13	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x			12			
14	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x			12			
15	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		13			
16	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		13			
17	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	14			
# of interactions	2	3	5	6	6	7	8	8	9	10	10	11	12	12	13	14	13	12	11	10	9	8	7	6	5	4	3	2	1



## Deterministic model





## Deterministic model

Competition-induced mortality ( $\alpha$ ) occurs amongst all similarly-sized individuals (symmetric)

- Density of each  $i$  after competition:

$$N_i = p_{i,j} n_{i,j} - \alpha(\Sigma[p_{i,j} n_j] - p_{i,j} n_{i,j})$$

- Independent  $\alpha$  for **D** on **M** and **M** on **D**:

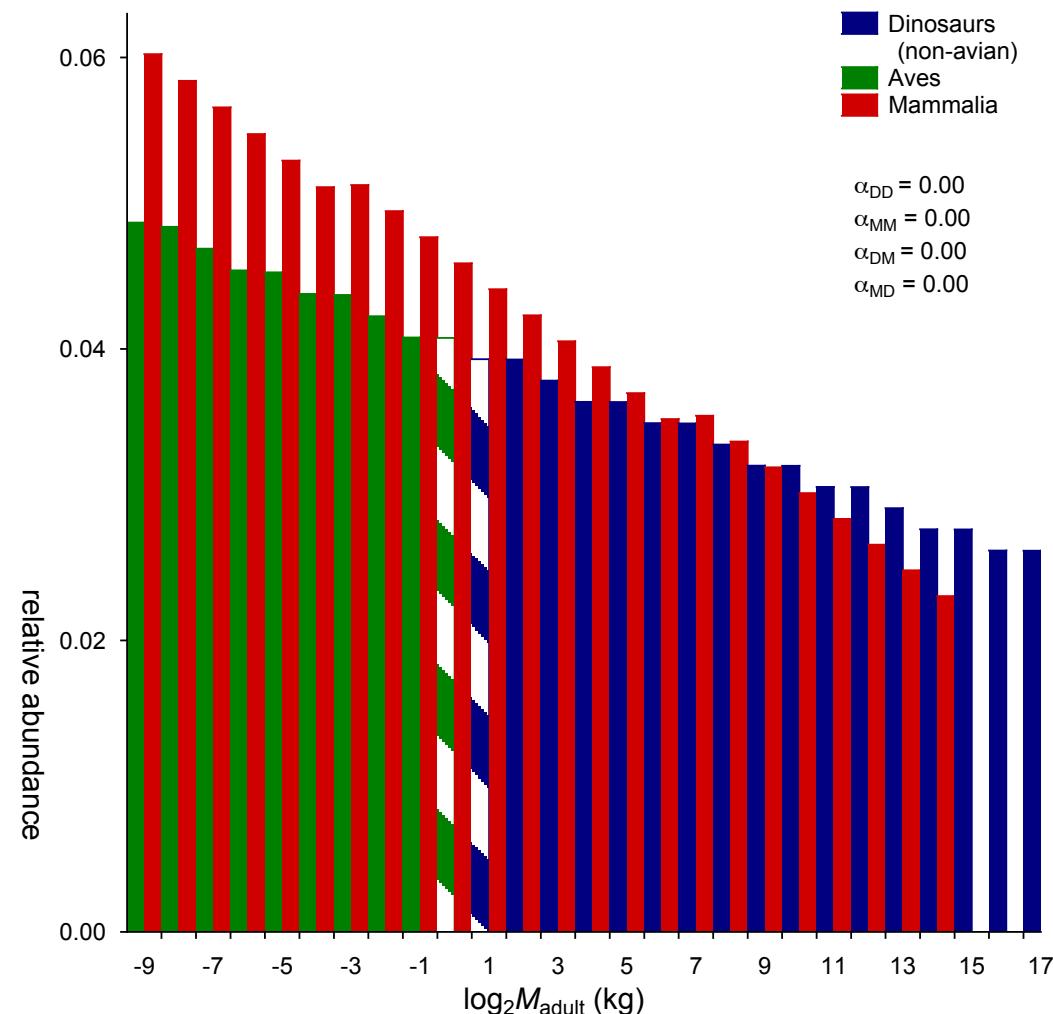
Dinosaurs:  $N_{Di} = \Sigma[n_{Di,j} - \alpha_{DD}(\Sigma n_{Dj} - n_{Di,j}) - \alpha_{MD}(\Sigma n_{Mj})]$

Mammals:  $N_{Mi} = \Sigma[n_{Mi,j} - \alpha_{MM}(\Sigma n_{Mj} - n_{Mi,j}) - \alpha_{DM}(\Sigma n_{Dj})]$

- Simulate  $K-T$ : kill all individuals  $> 25$  kg

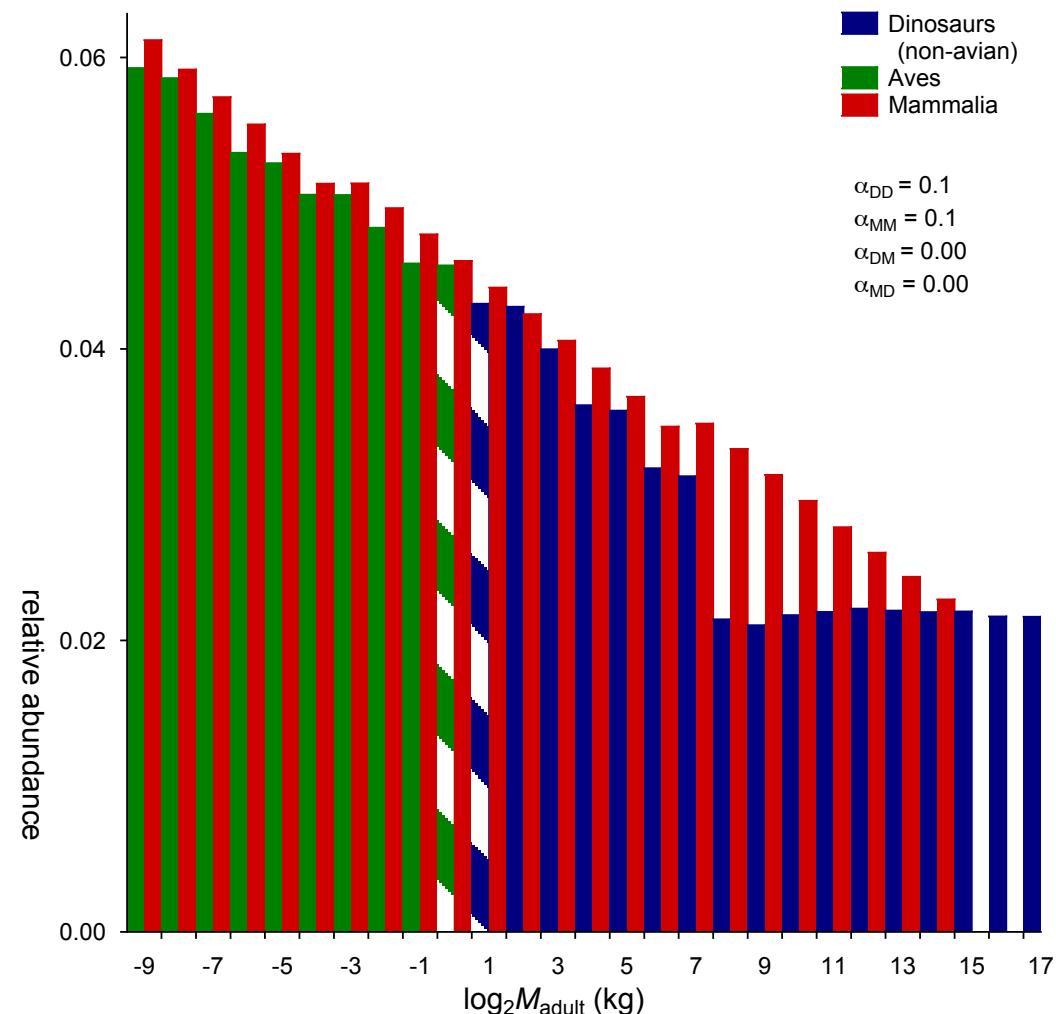


## Model results - no competition



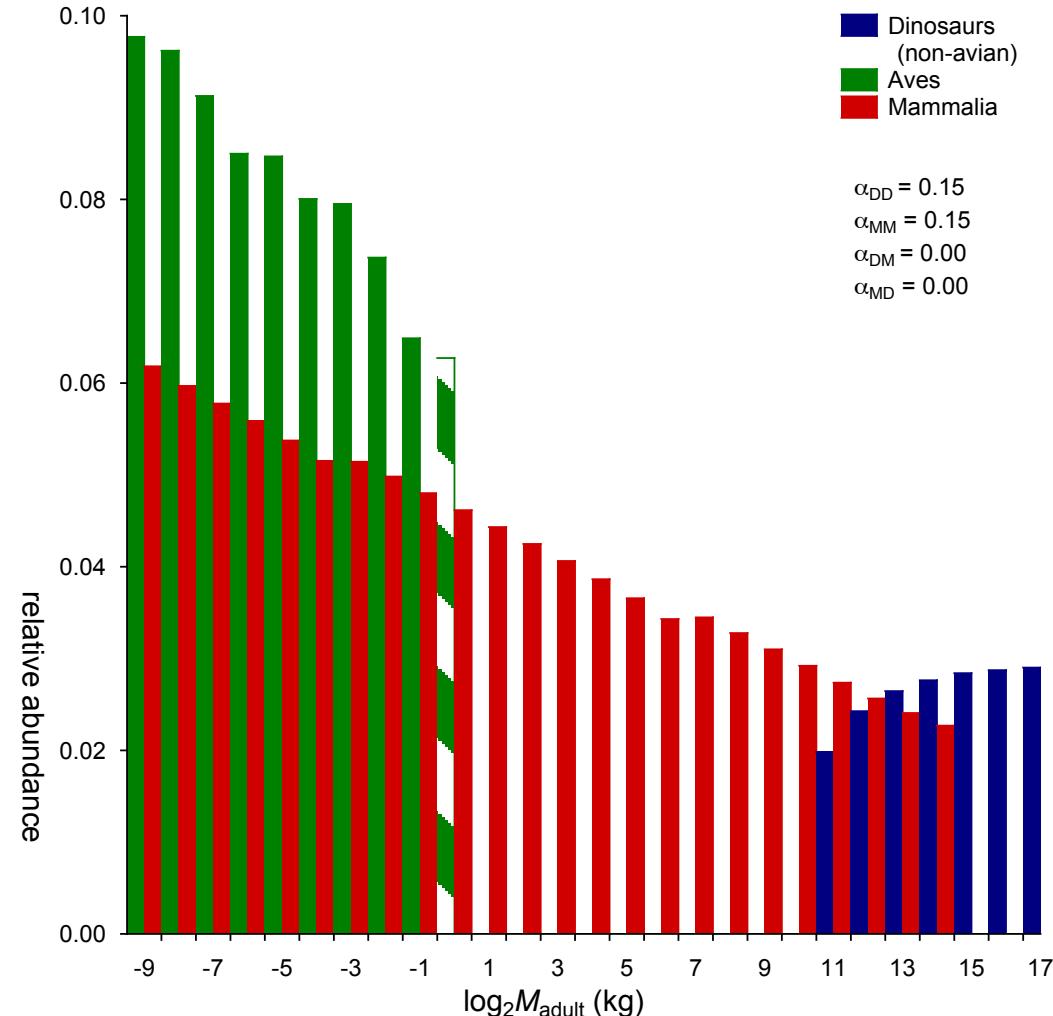


## Model results - mild competition-induced mortality



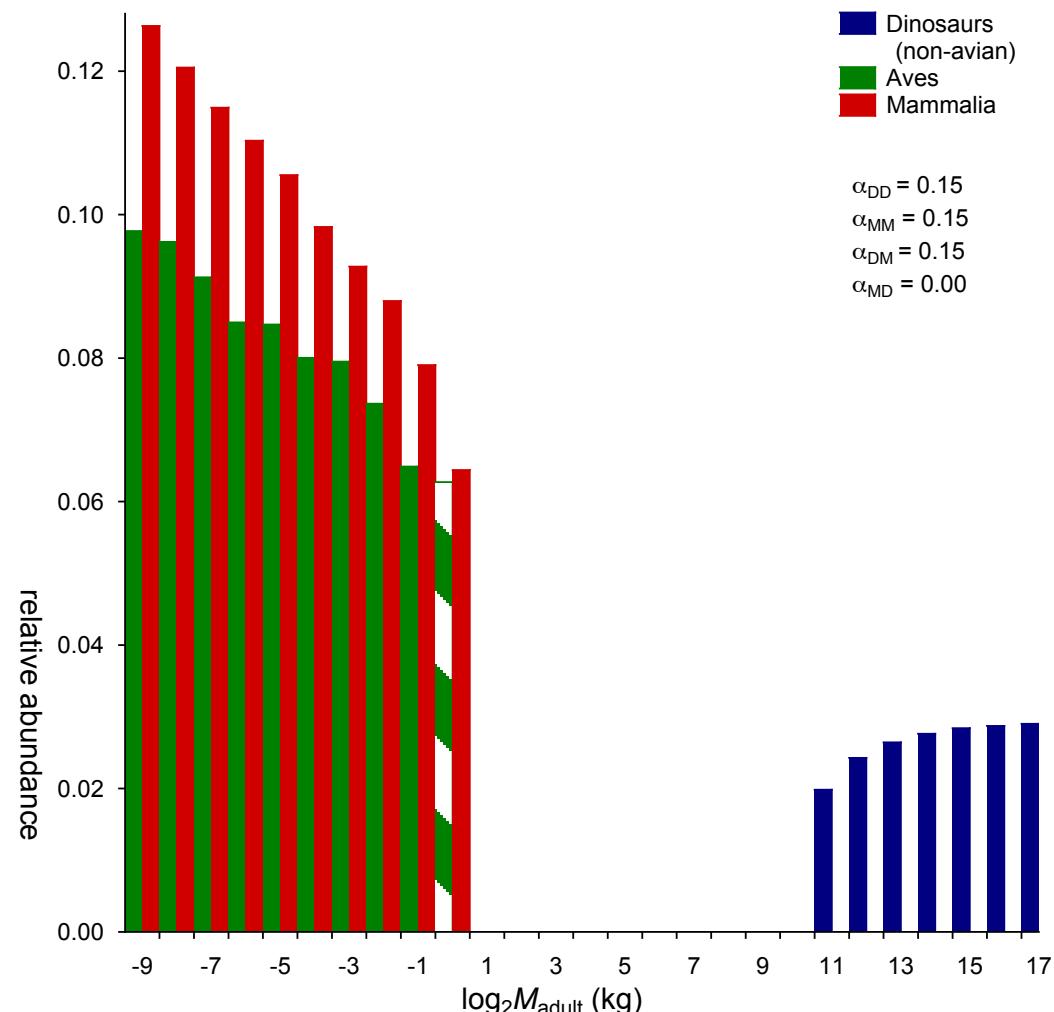


## Model results - stronger competition



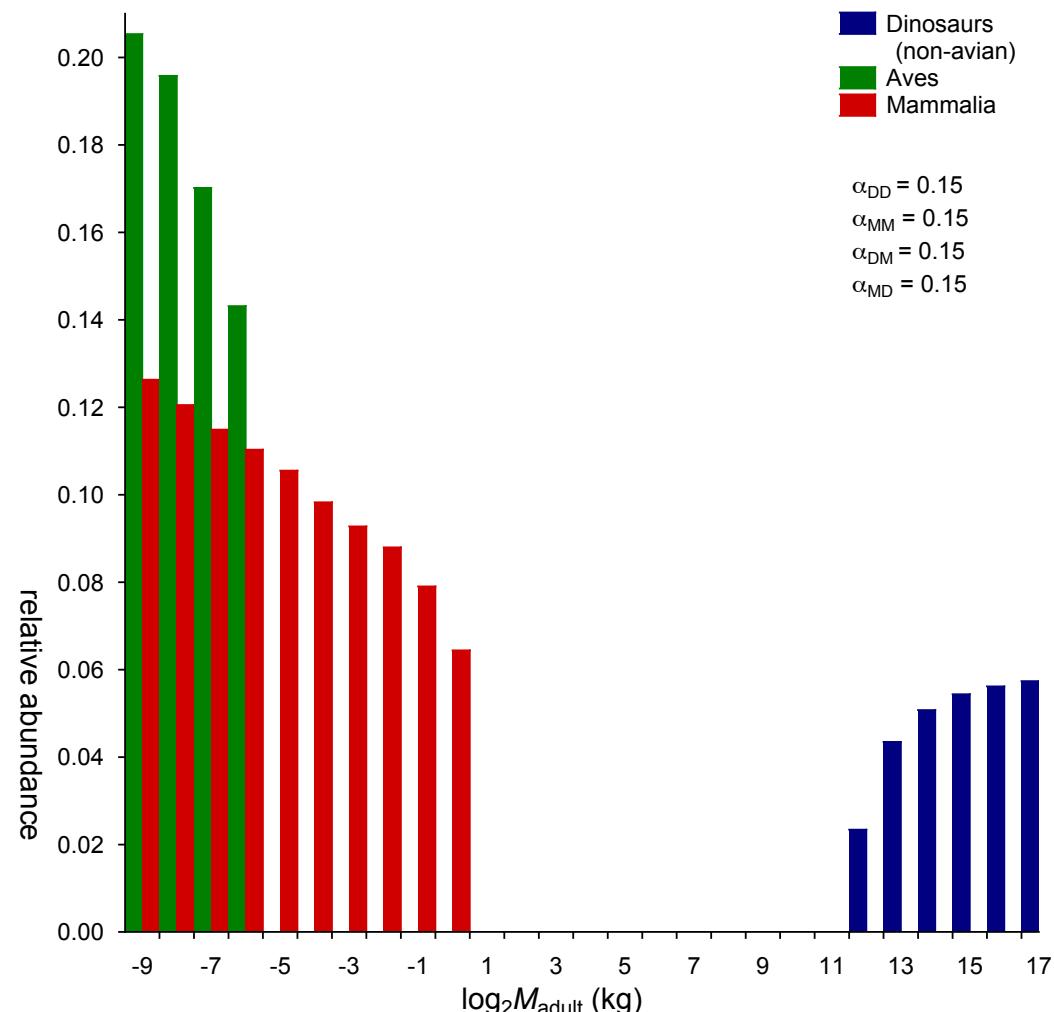


## Model results - including competition from [dinosaurs](#) on [mammals](#)



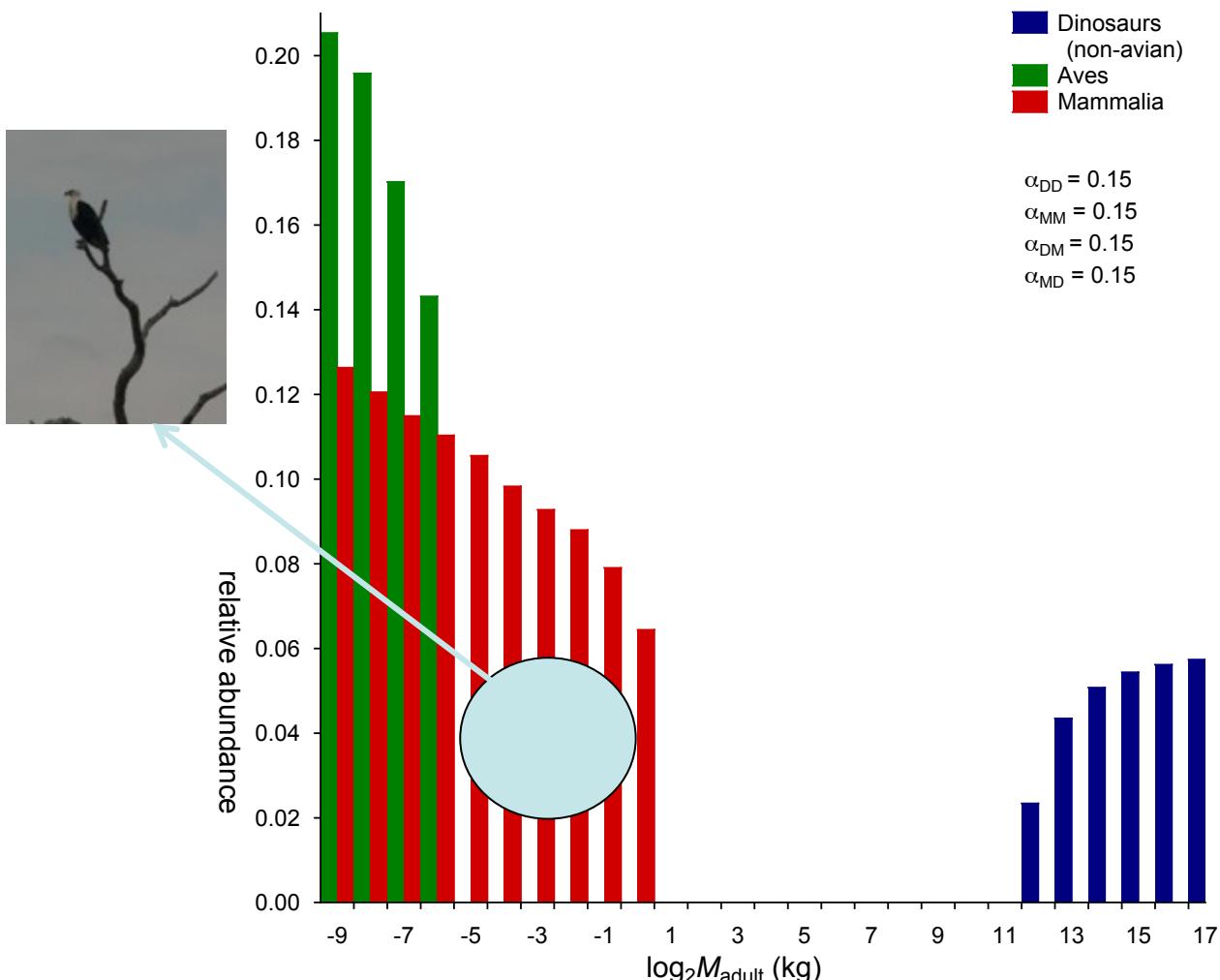


## Model results - ... and from mammals on dinosaurs



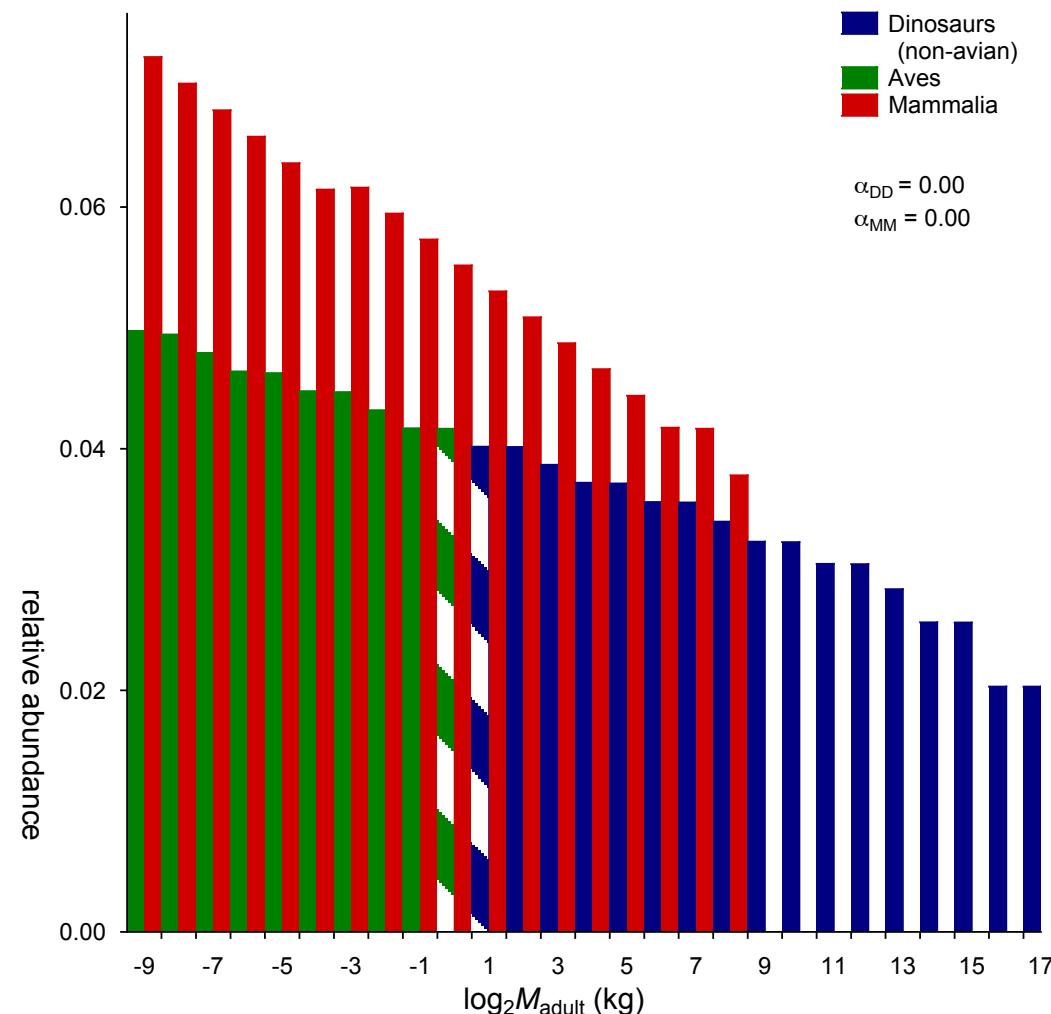


## Model results - ... and from mammals on dinosaurs



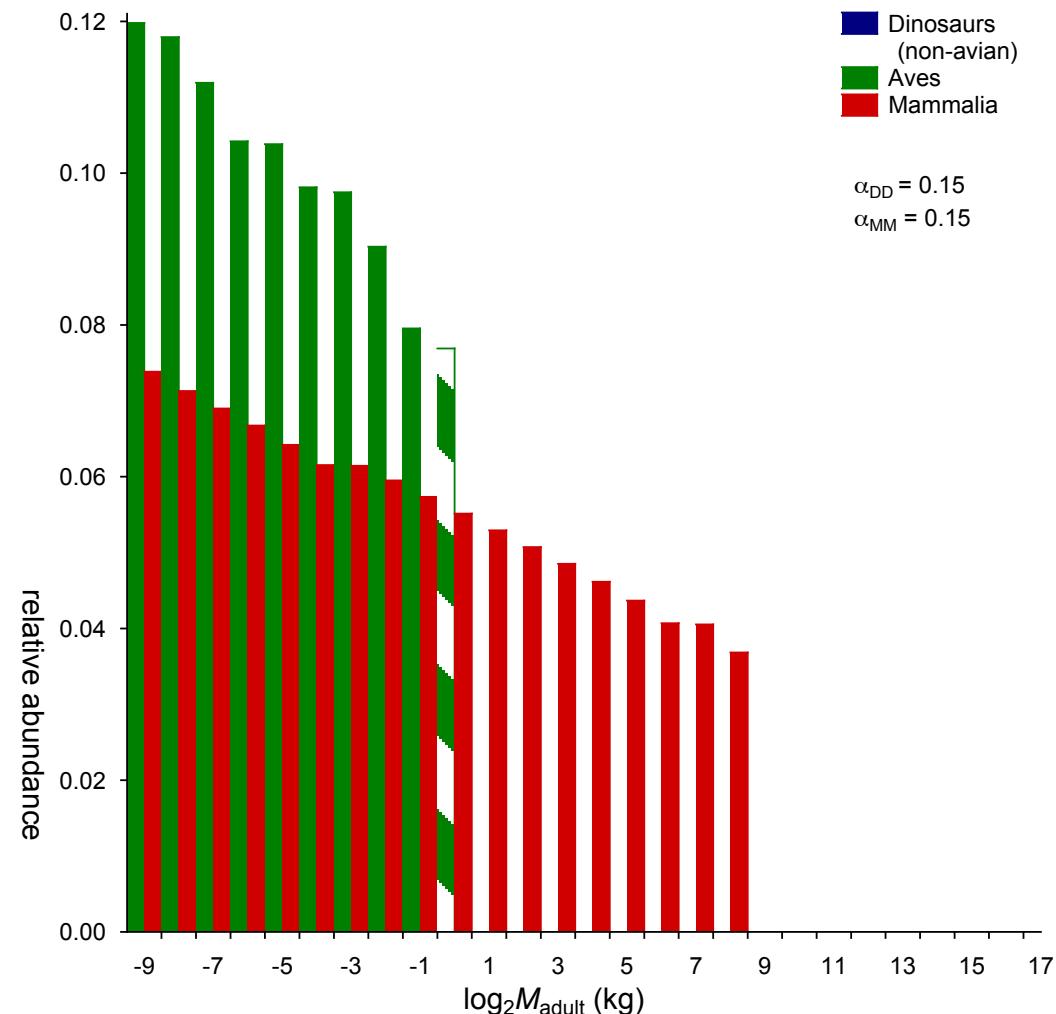


## Model results - after K/Pg, no competition



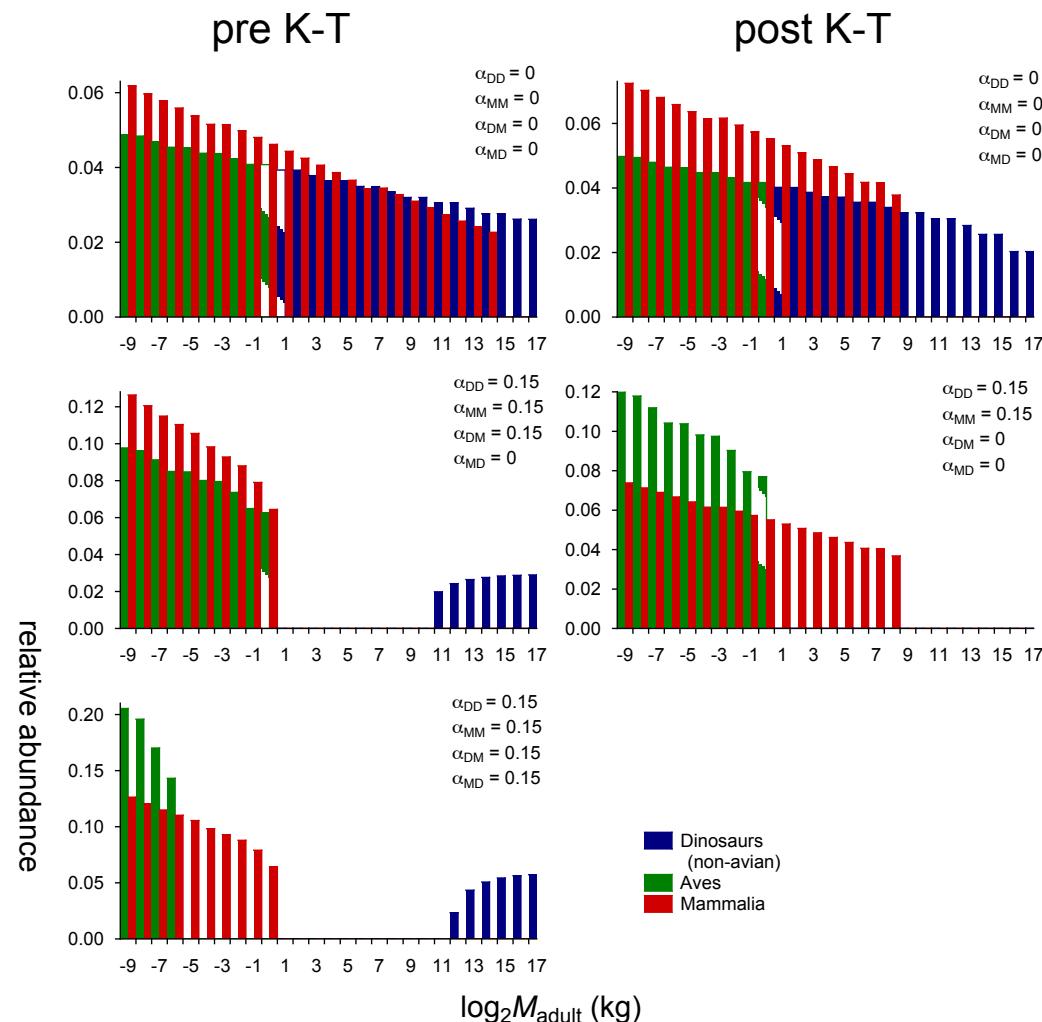


## Model results - after K/Pg, with competition





## Model results - summary



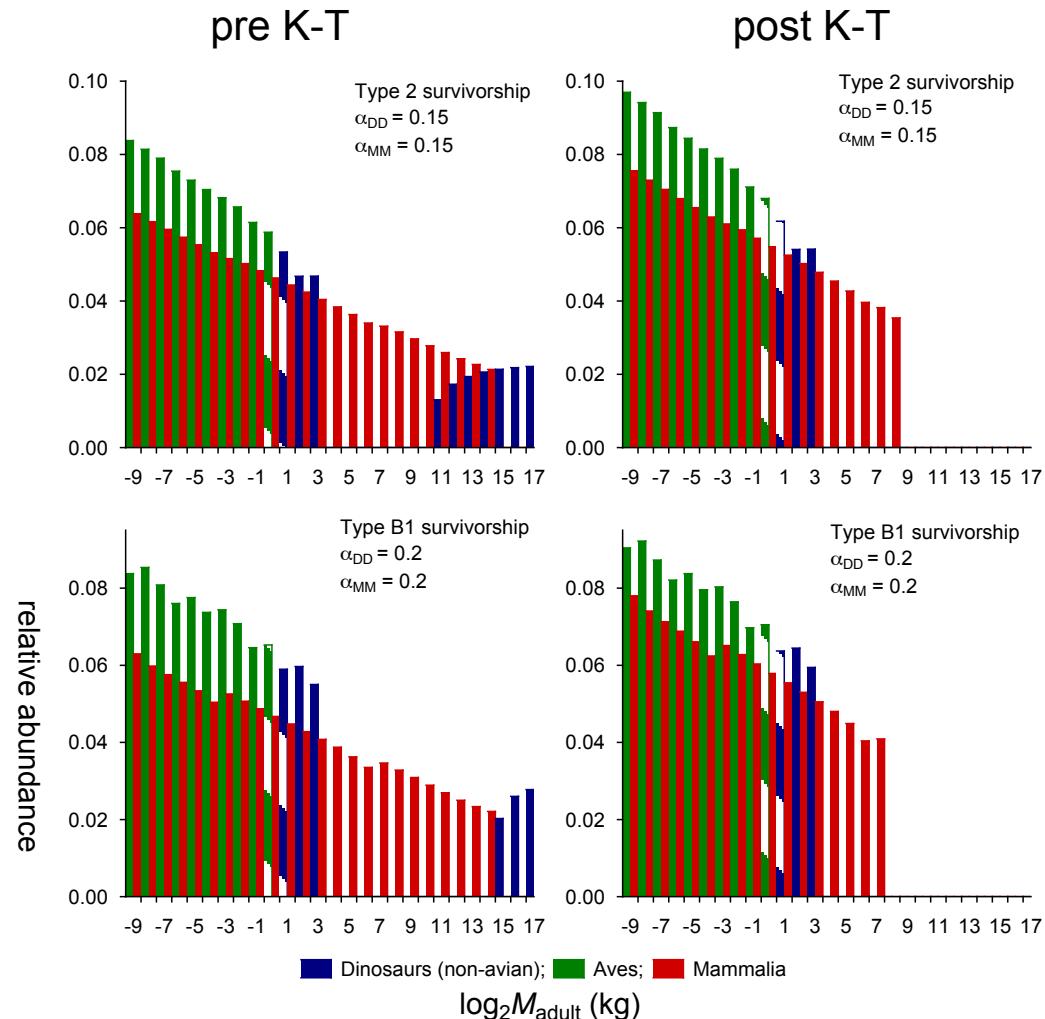


## Deterministic model

- Robustness and sensitivity
  - Changes and variability in  $M$  effects on:
    1. life history strategy
    2. reproductive output
    3.  $M_{adult} : M_{neonate}$  ratio
    4. competition co-efficient ( $\alpha$ )
    5. symmetry of  $\alpha$
    6. abundance
  - Stochastic parameter estimates (bounded within empirical limits for birds/herpetiles or mammals),  $10^3$  iterations

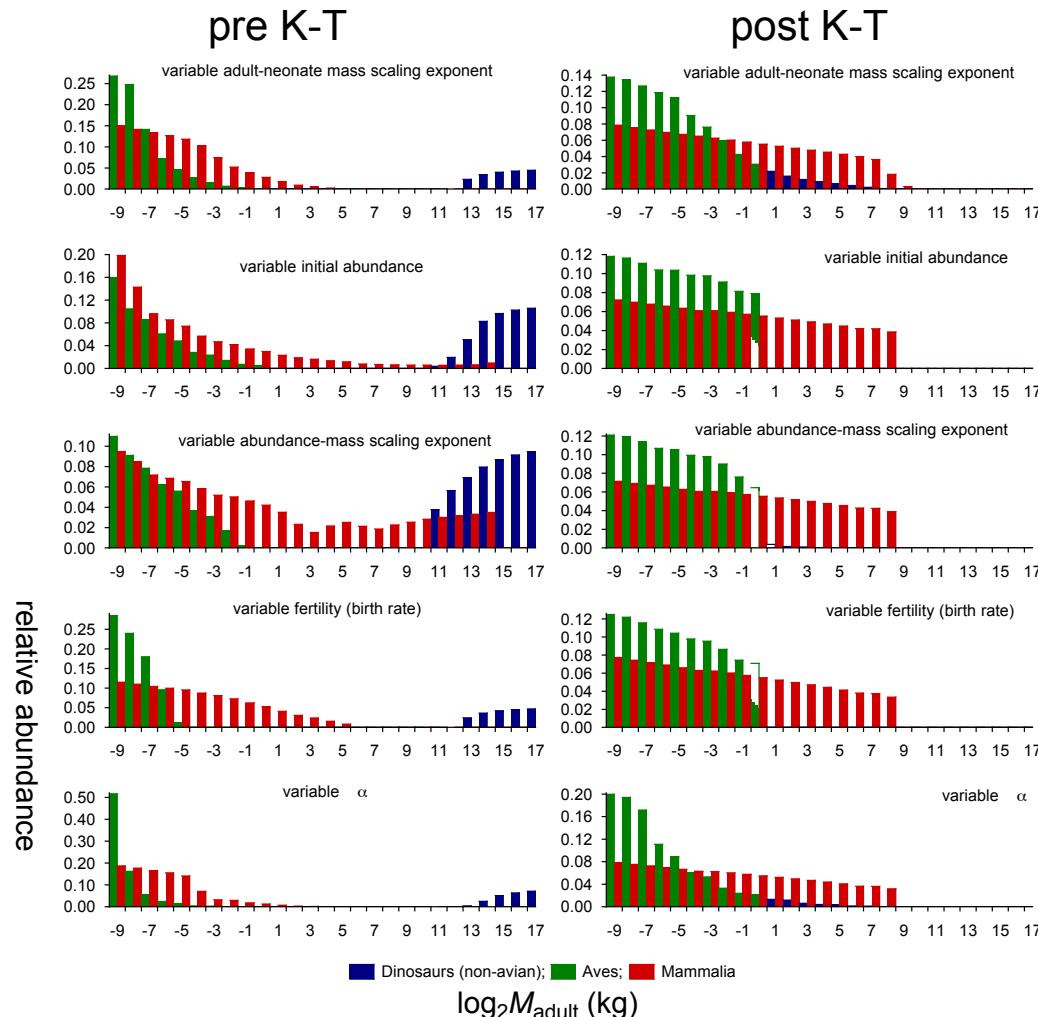


# Model results - variation in life history





## Model results - variation in neonate scaling, demography, and ecology





# Conclusions

## **Size-specific competition influences S**

- Effects largest amongst species with high intraspecific niche breadth (e.g. large, oviparous)...
- ... favouring large-bodied taxa

## **Explains paucity of small-bodied dinosaurs**

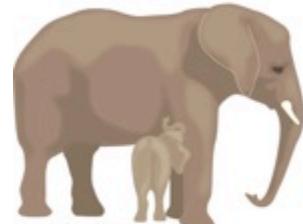
- Dominance of large dinosaurs then limited max BM of other vertebrate groups in Mesozoic...
- ... resultant dominance of small taxa amongst mammals further limited small dinosaurs (=aerial niche?)

## **Extinction event above BM threshold = remaining S too low for recovery (even with high f)**



# Ontogenetic niche shifts in dinosaurs influenced size, diversity and extinction in terrestrial vertebrates

Daryl Codron<sup>1–4,\*</sup>, Chris Carbone<sup>5</sup>,  
Dennis W. H. Müller<sup>1</sup> and Marcus Clauss<sup>1</sup>



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