The art of allometry:

relevance, functional logic and evolutionary history in comparative analyses

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9th International Conference on Behaviour, Physiology and Genetics of Wildlife, Berlin 2013

Research Unit 533
Sauropod Biology
DFG

better late than never

SAUROPOD NUTRITION SQUAD

Overview

Allometry basics

Working with allometries:

- fallacies
- curvature / composite allometries

Case example: allometric (and other) reasoning in large herbivore diversity

Phylogenetic statistics

Allometries as snapshots in evolutionary time – ‘directed evolution’?

Allometry basics

Allometries

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

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

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

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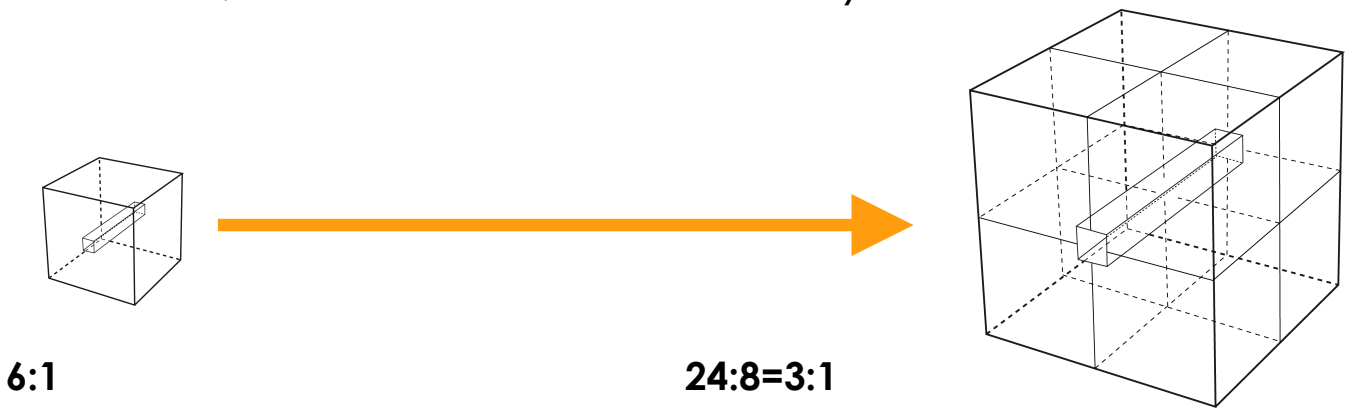
(allometric scaling mostly explained by geometry – e.g. surface-volume shifts, distribution networks etc.)



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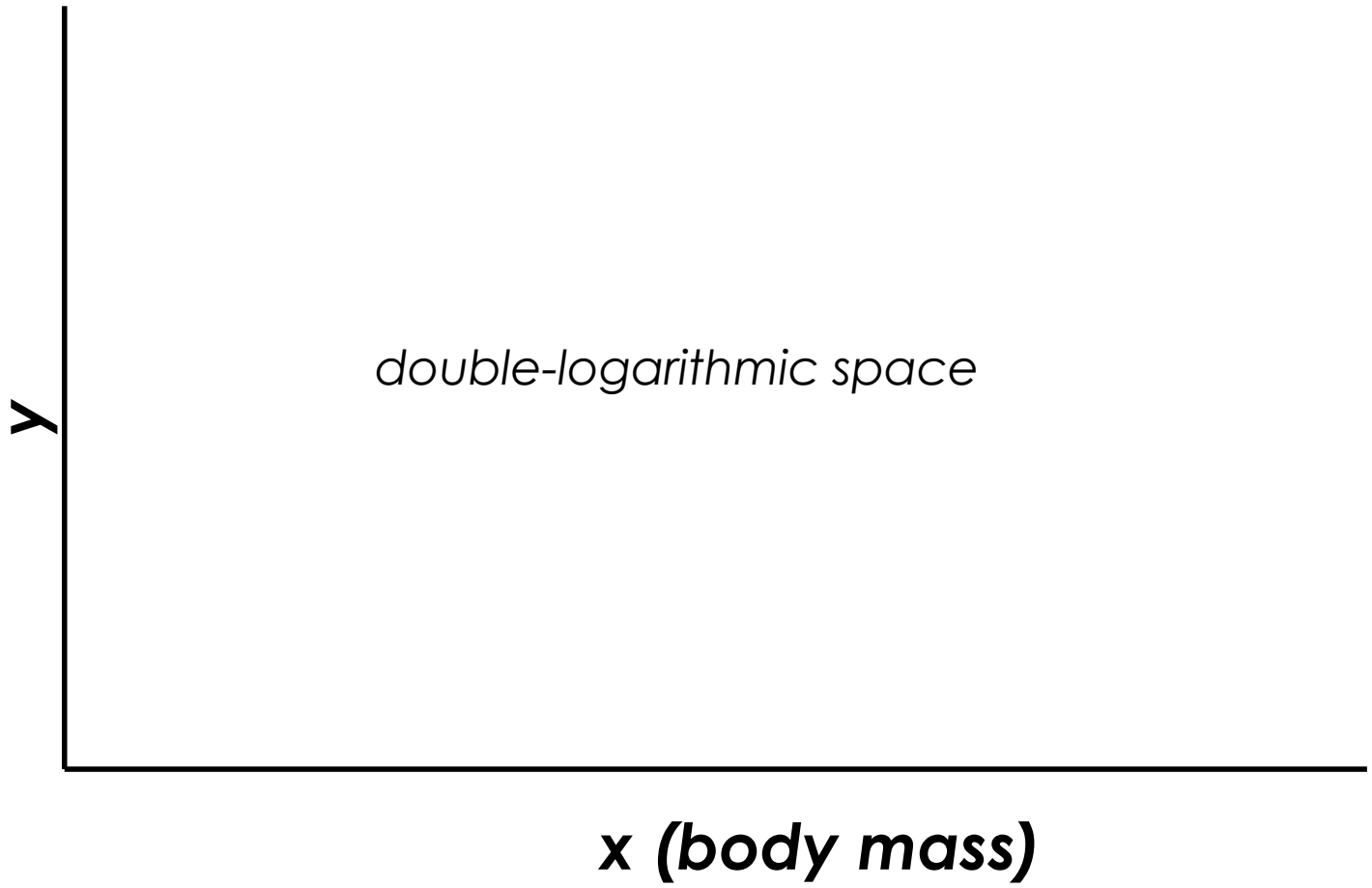

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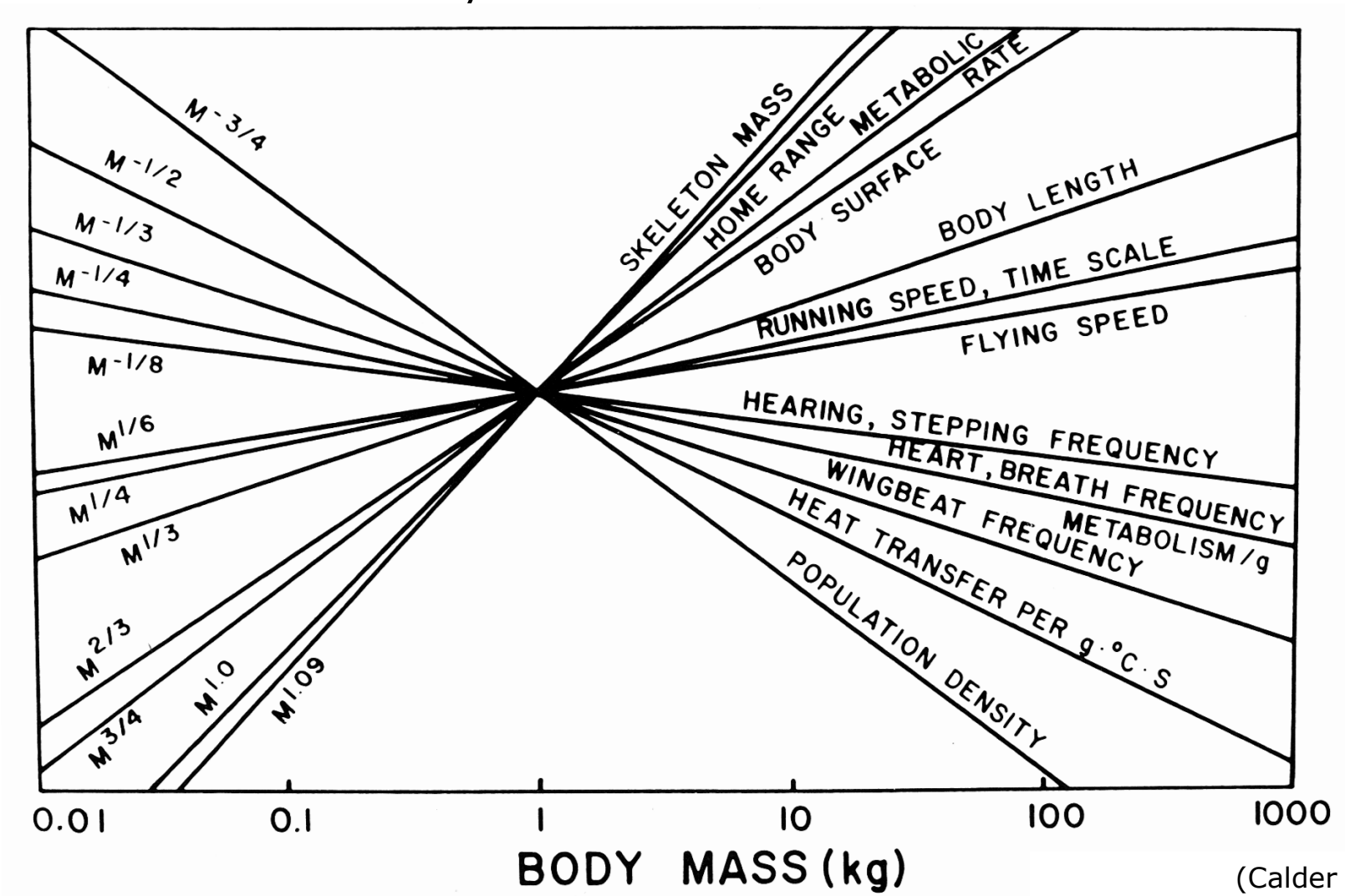

(Calder 1983)

Interpreting allometries

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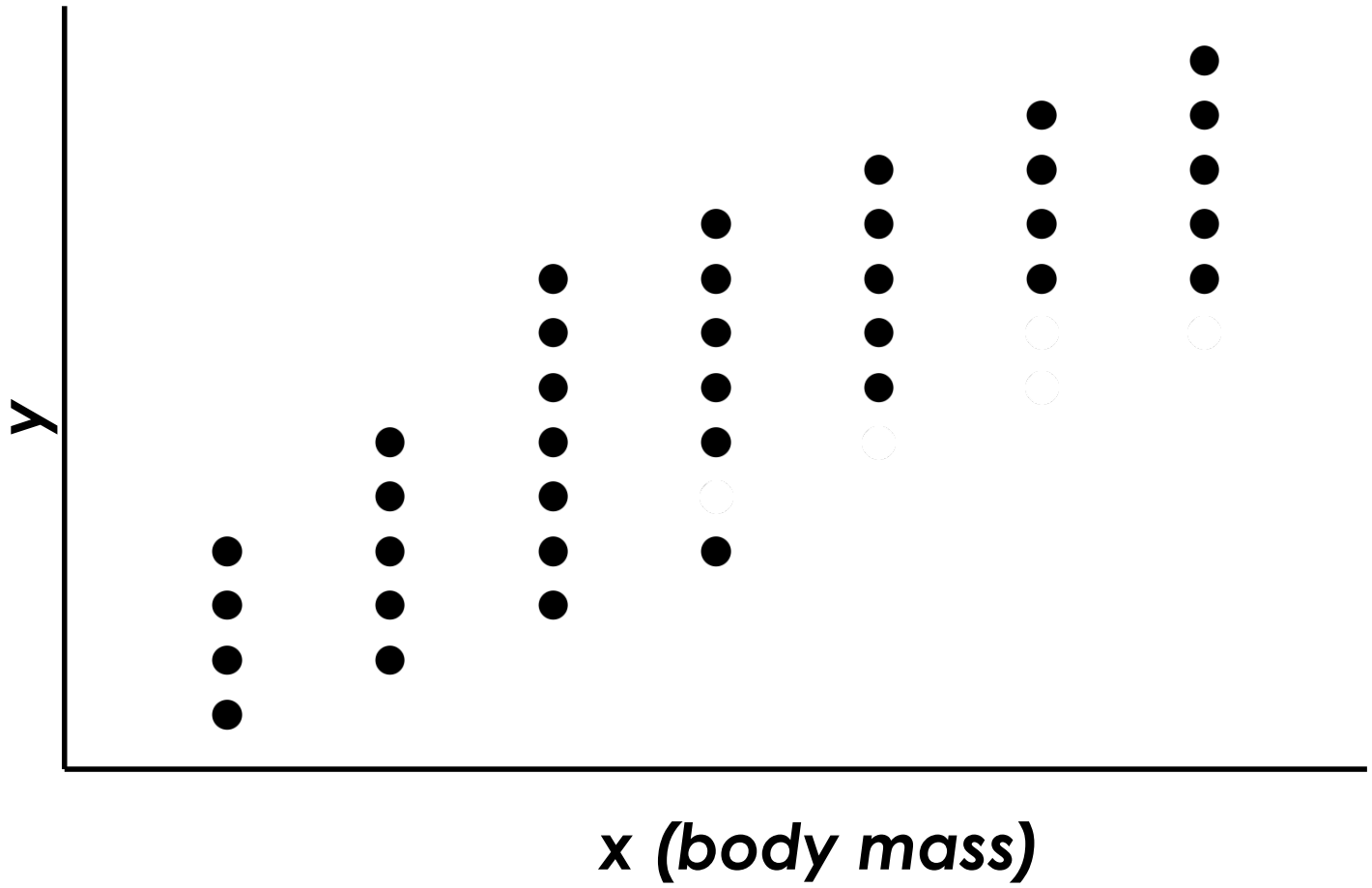

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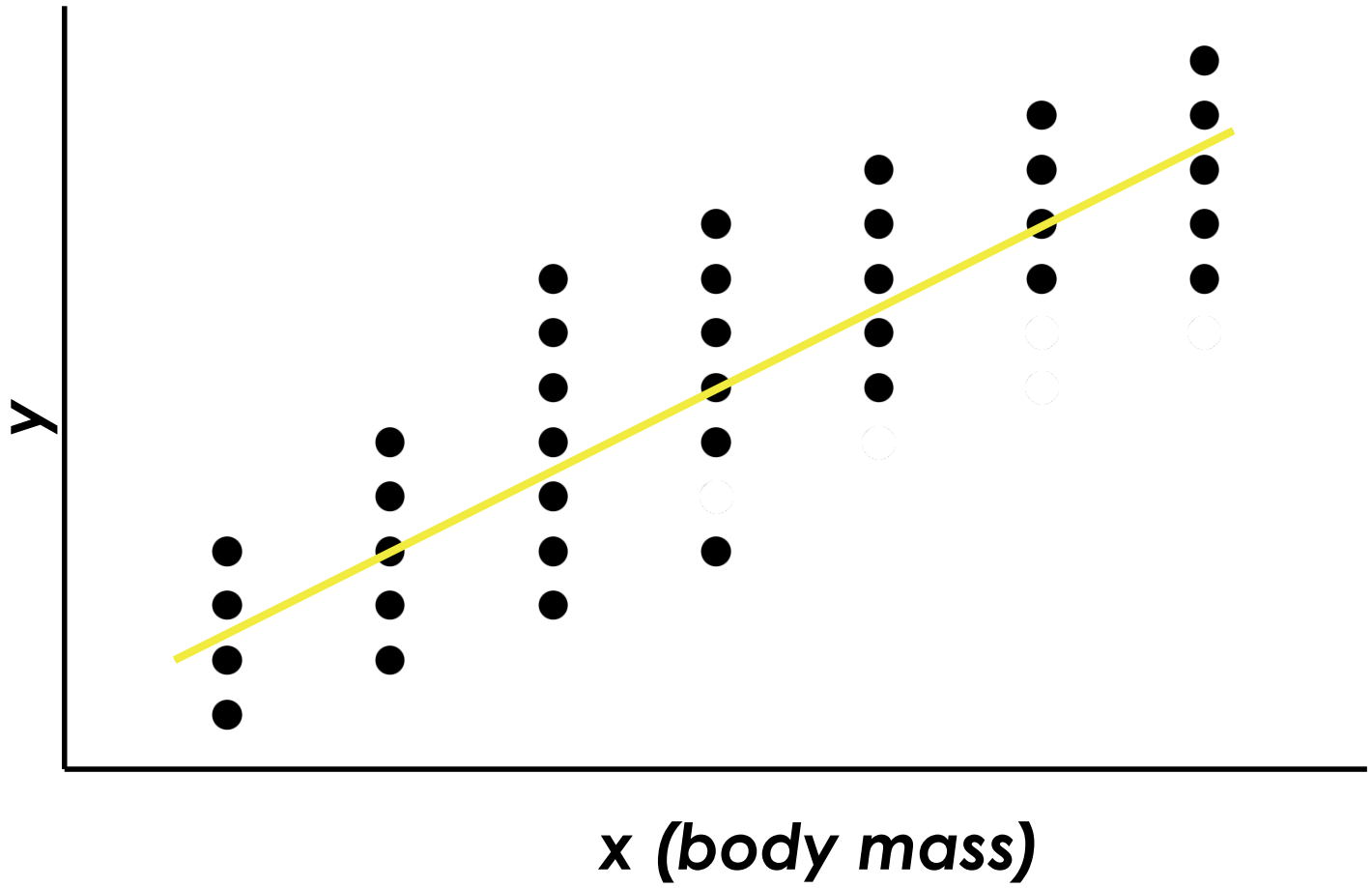

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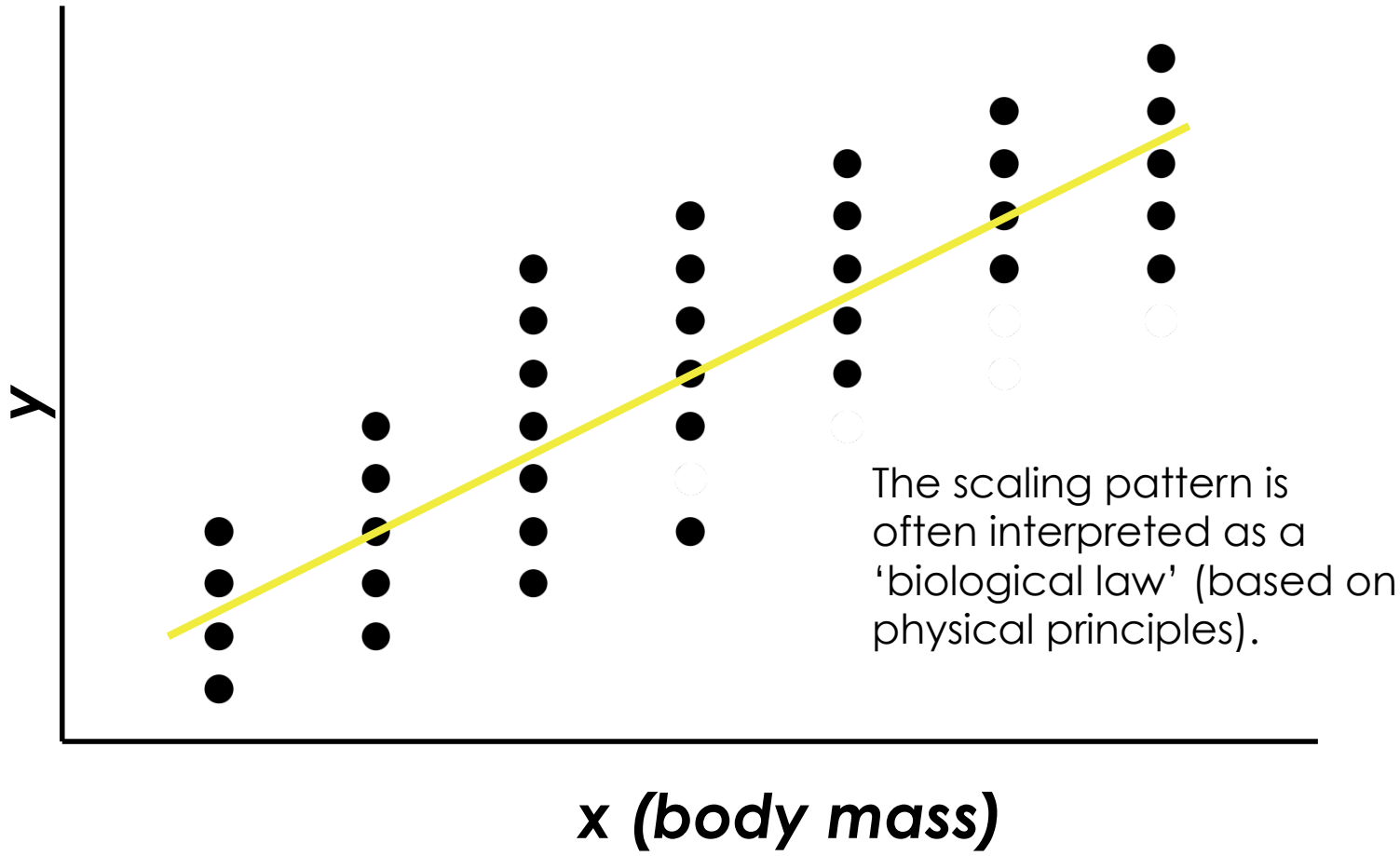

Using allometries

Using allometric relationships to extrapolate data for other species.

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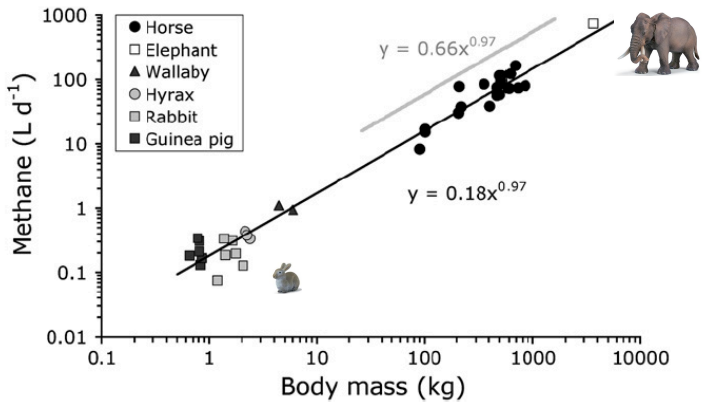
Methane output of rabbits (*Oryctolagus cuniculus*) and guinea pigs (*Cavia porcellus*) fed a hay-only diet: Implications for the scaling of methane production with body mass in non-ruminant mammalian herbivores

Ragna Franz [a], Carla R. Soliva [b], Michael Kreuzer [b], Jürgen Hummel [c], Marcus Clauss [a,*]

Comparative Biochemistry and Physiology, Part A 158 (2011) 177–181



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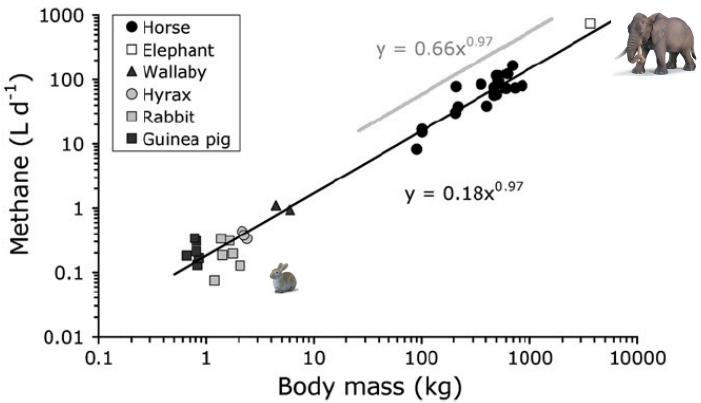

Could methane produced by sauropod dinosaurs have helped drive Mesozoic climate warmth?

David M. Wilkinson[1,*],
Euan G. Nisbet[2],
and Graeme D. Ruxton[3]

Current Biology Vol 22 No 9
R292

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Using allometric relationships to compare different animal groups.

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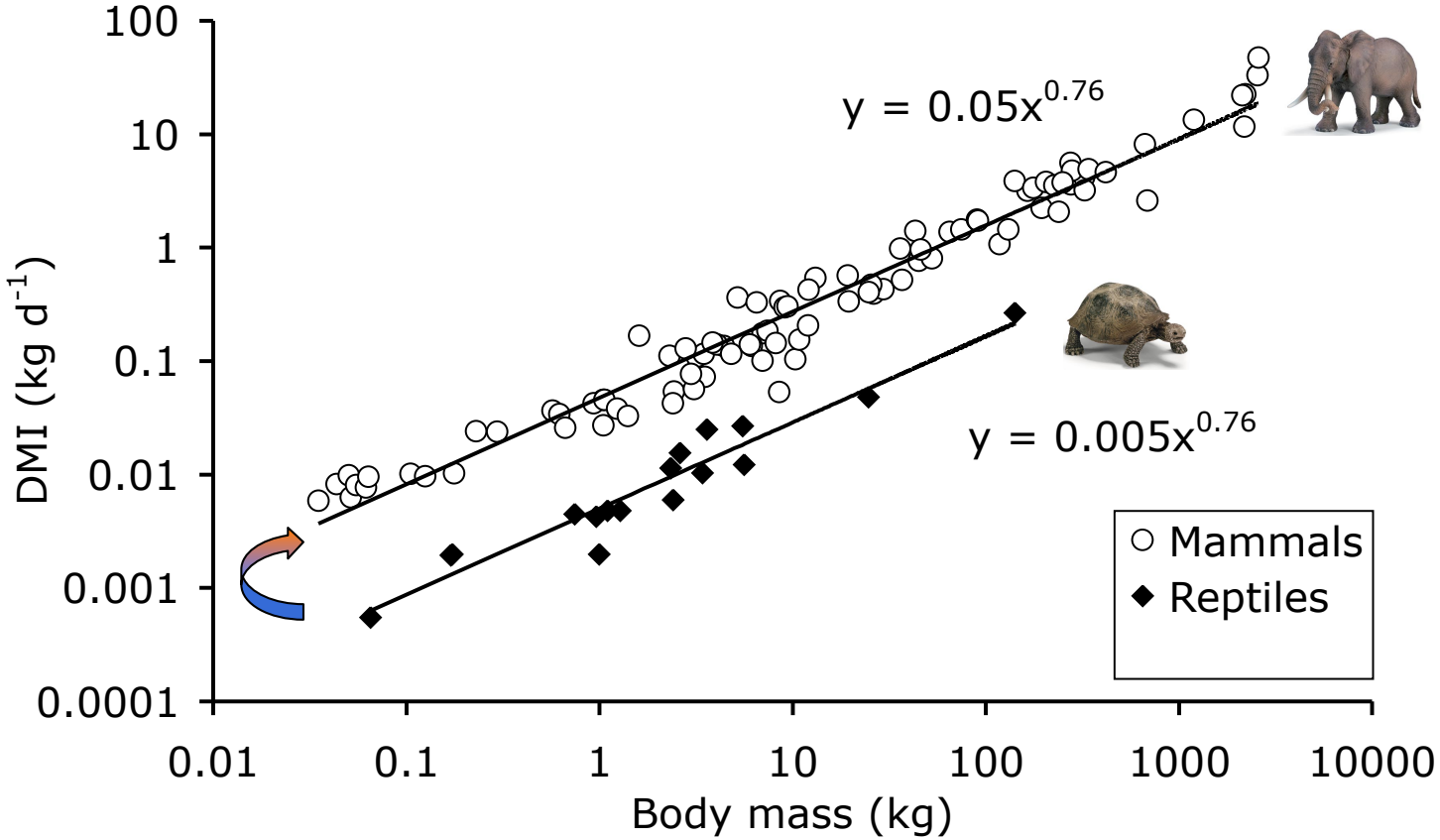

mammal data collection Clauss et al. (2007), reptile from Franz et al. (2009

Using allometries

Differences in allometric relationships ***between animal groups*** can explain different ecological scenarios.

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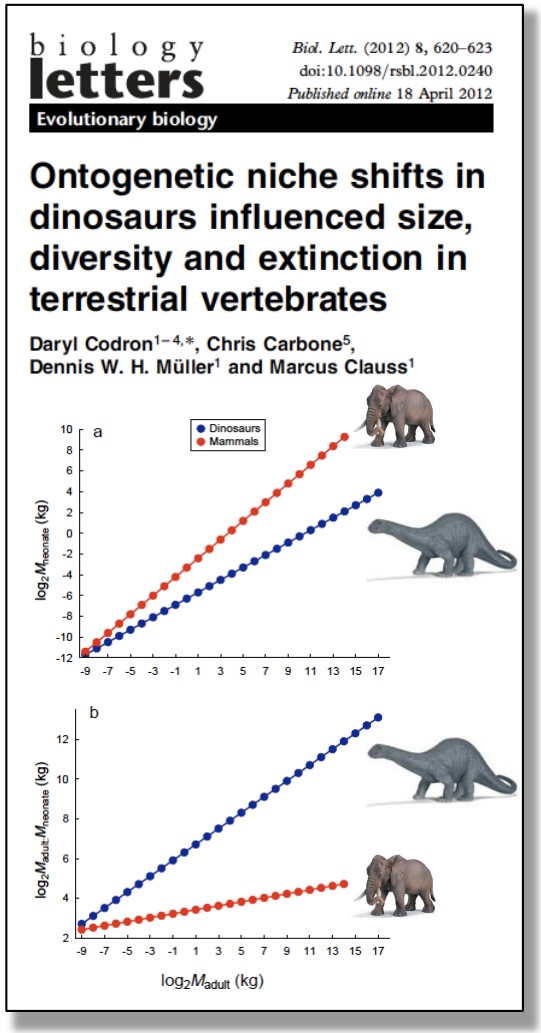

biology letters

Biol. Lett. (2012) **8**, 620–623
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Evolutionary biology

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

Daryl Codron[1–4,*], Chris Carbone[5], Dennis W. H. Müller[1] and Marcus Clauss[1]

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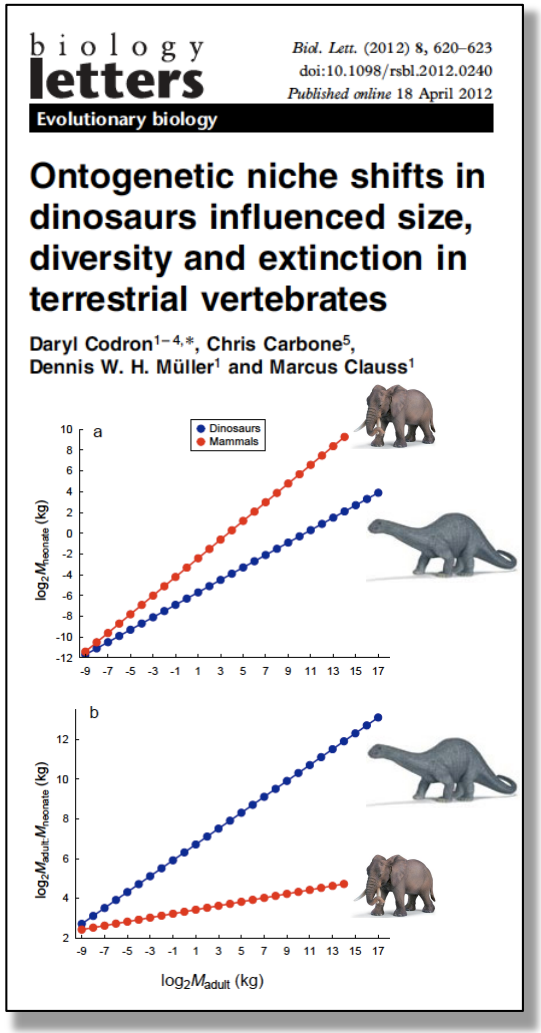

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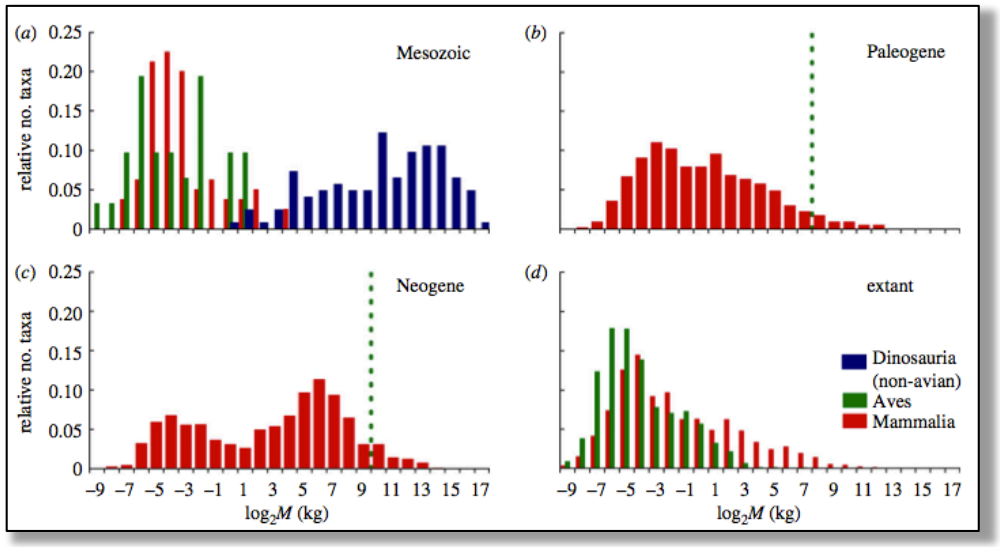

Allometry fallacies

Using allometries: a call for caution

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The probably most-often committed fallacy in ecophysiological manuscripts:

Metabolic rate = requirements

scale to $BM^{0.75}$

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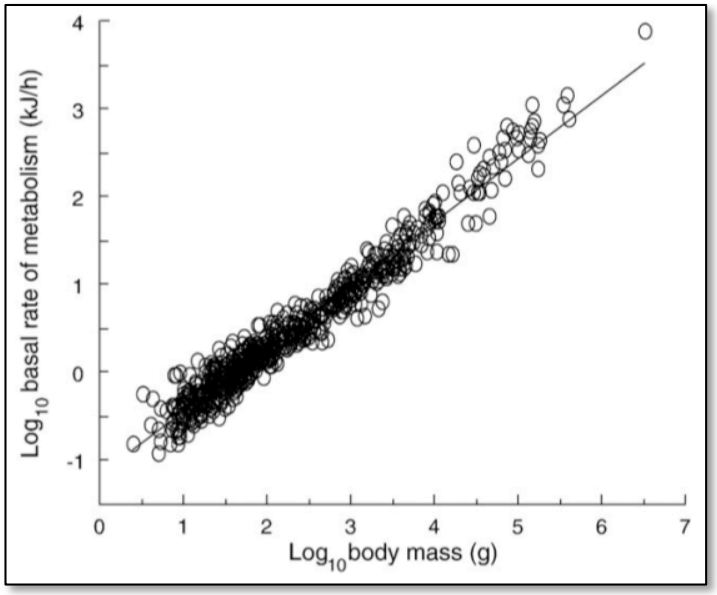
1. larger animals have higher absolute requirements (in joules (per day))



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The probably most-often committed fallacy in ecophysiological manuscripts:
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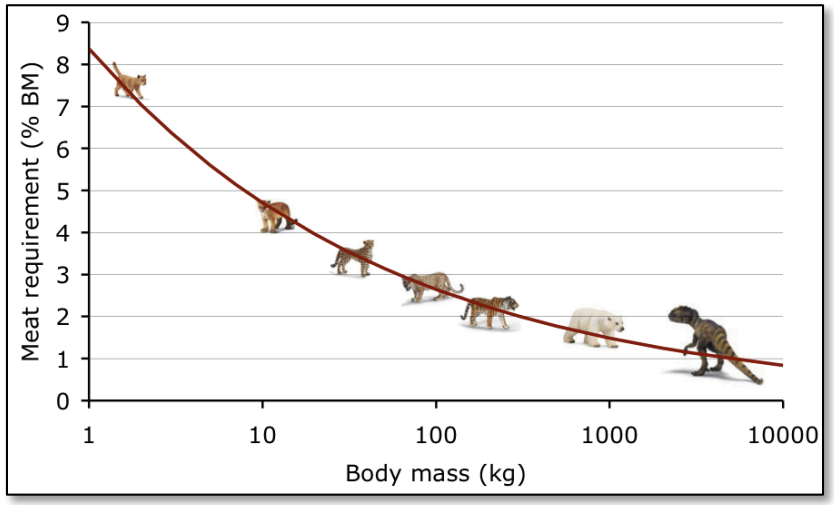
scale to $BM^{0.75}$

This can be expressed in three different ways:

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



Using allometries: a call for caution

The probably most-often committed fallacy in ecophysiological manuscripts:
Metabolic rate = requirements
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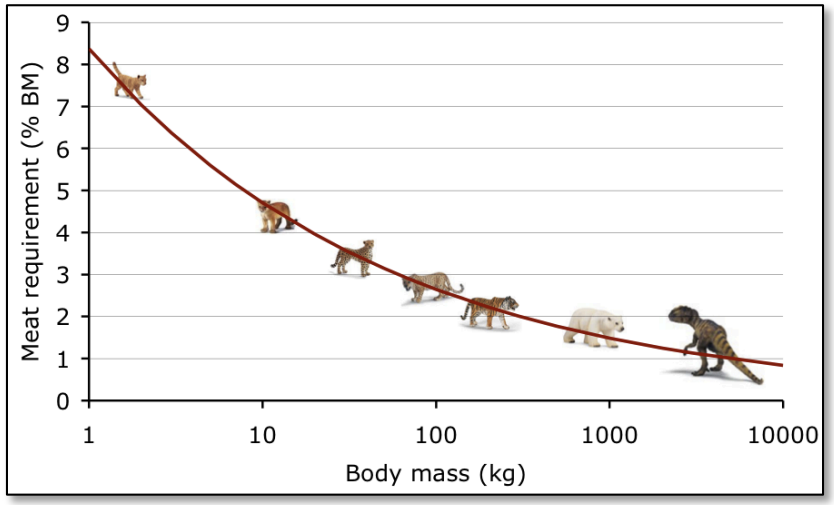
This can be expressed in three different ways:

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



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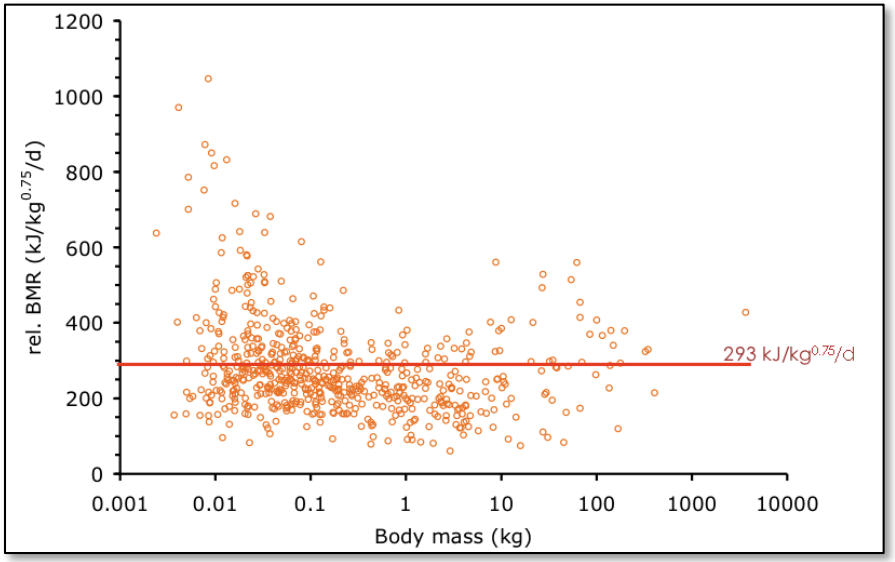
This can be expressed in three different ways:

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



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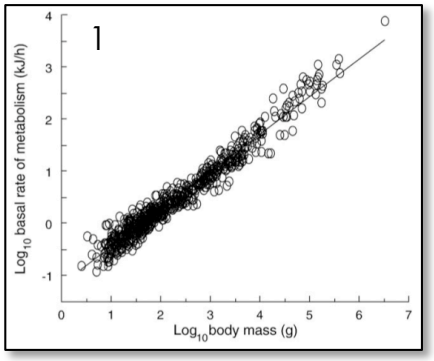

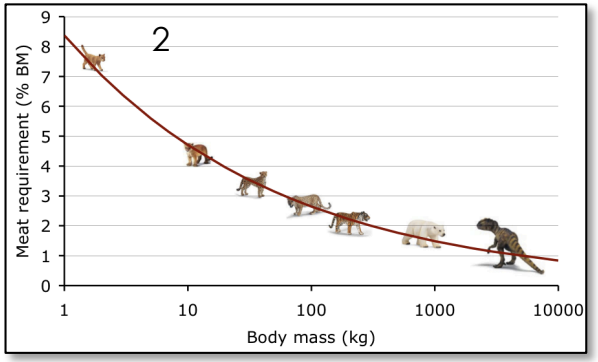

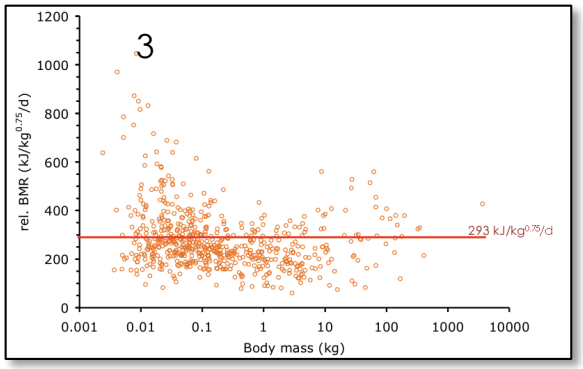

1. larger animals have higher absolute requirements (in joules (per day))
2. larger animals have lower 'mass-specific' requirements (in joules per kg (per day))
3. all animals have the same requirements (in joules per $kg^{0.75}$ (per day))

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

Using allometries: a call for caution

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

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e.g.

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no comparison to other scaling!

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no comparison to other scaling!

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

Using allometries: a call for caution

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

Do not trust one-scaling statements.

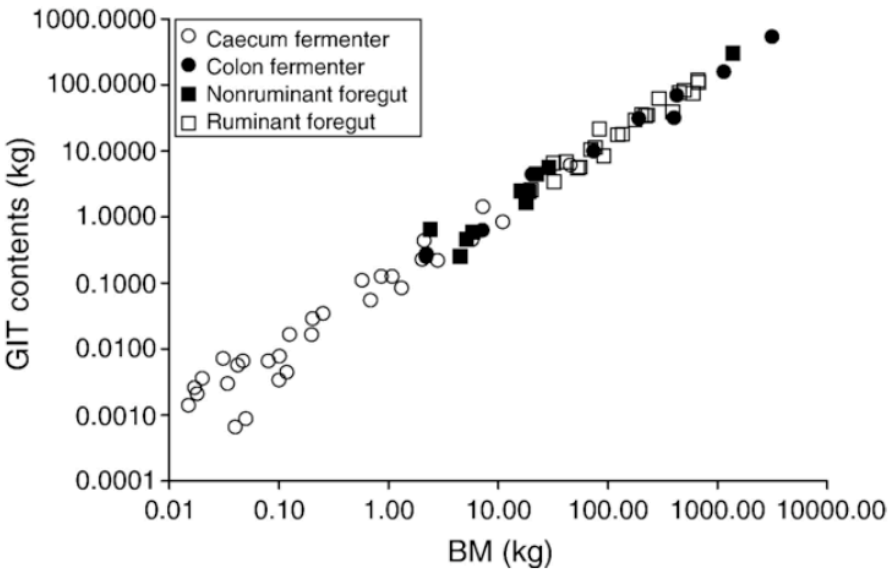
Using allometries: a call for caution

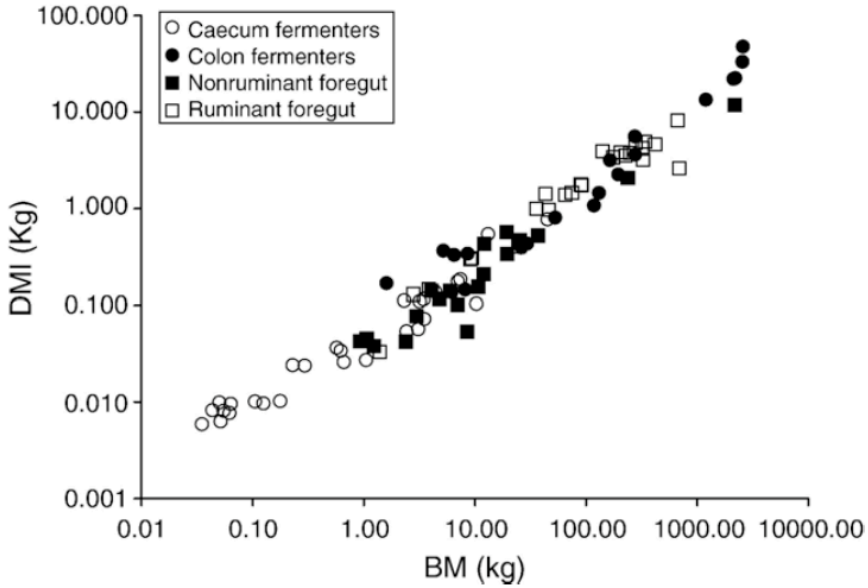
A difference in the scaling of two characteristics has a promising potential to explain diversification and niche differentiation along a body size gradient!

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

Curvature

Straight line ... ?





from Clauss et al. (2007)

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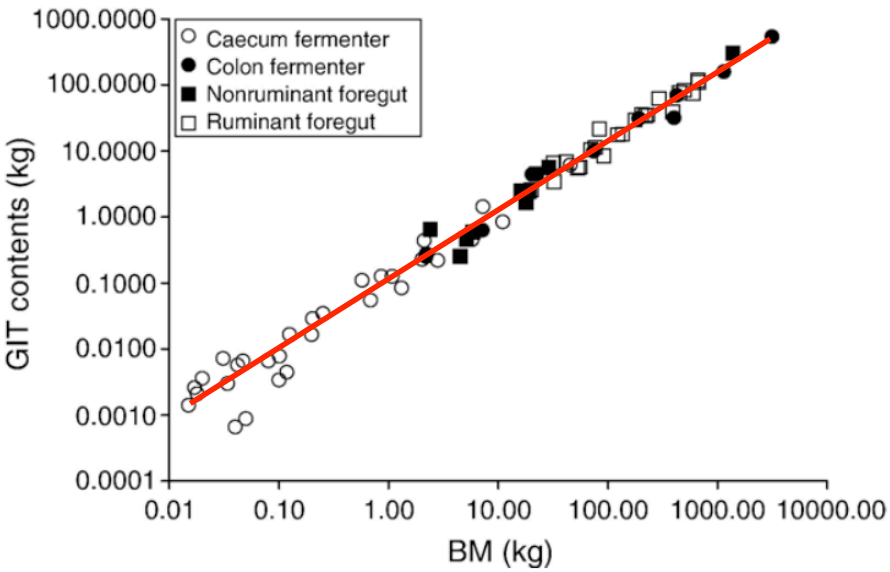

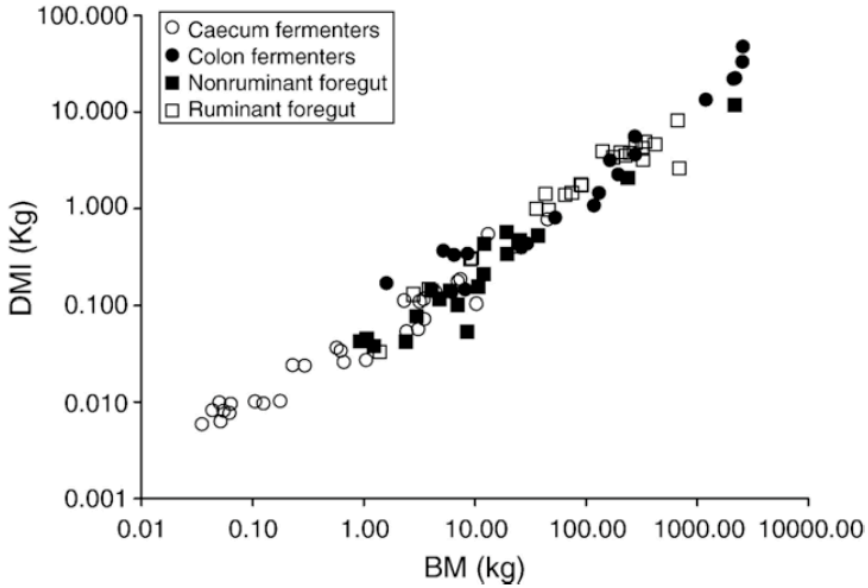

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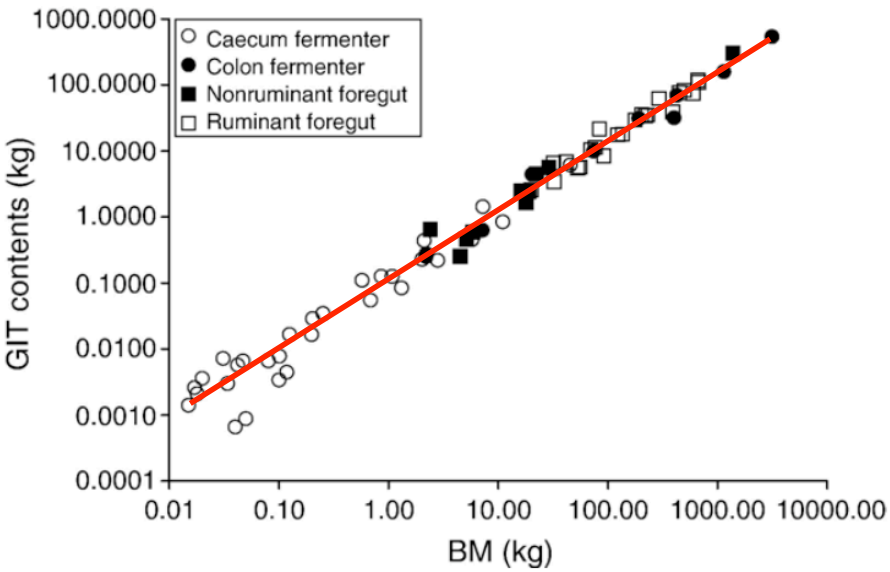
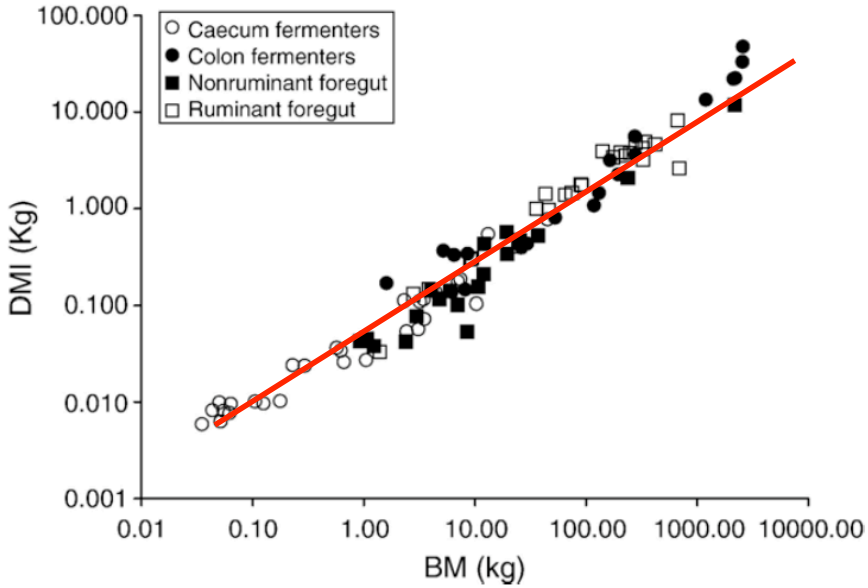
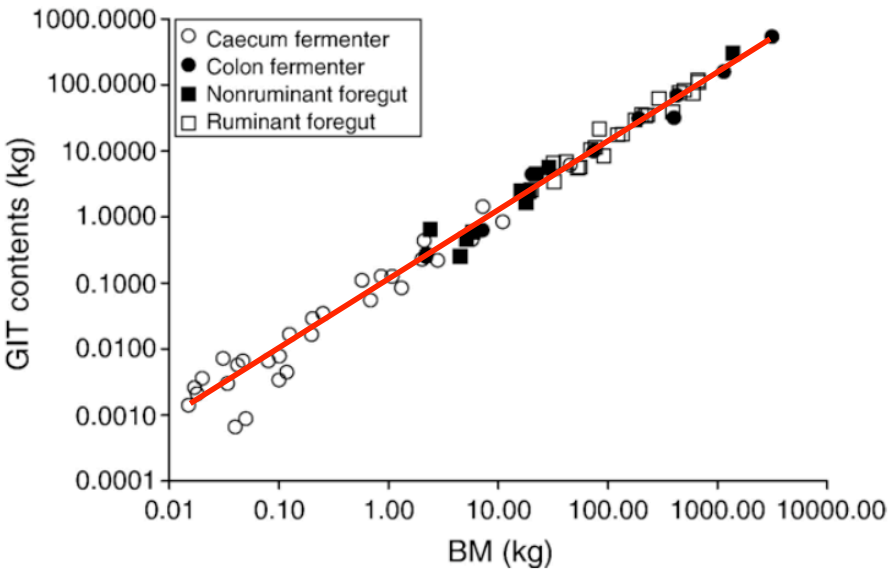
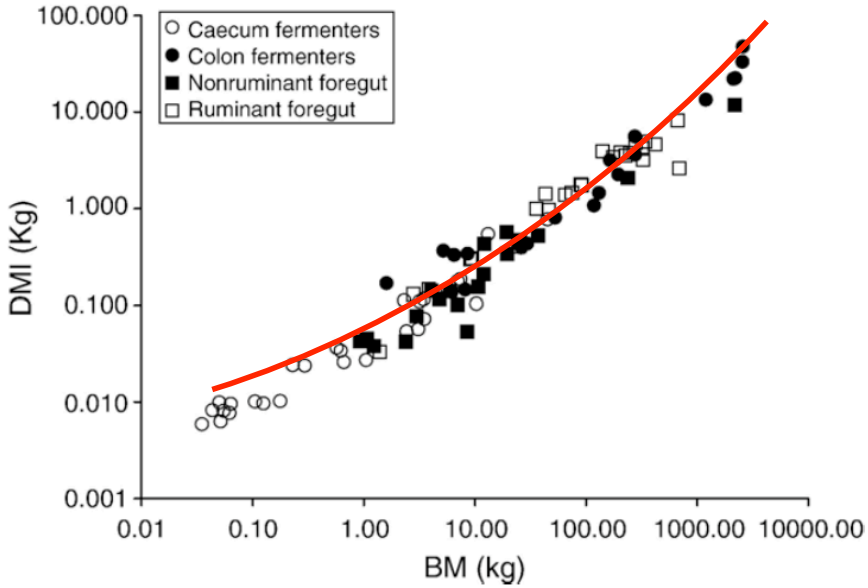




from Clauss et al. (2007)

Straight line ... *or curvature?*





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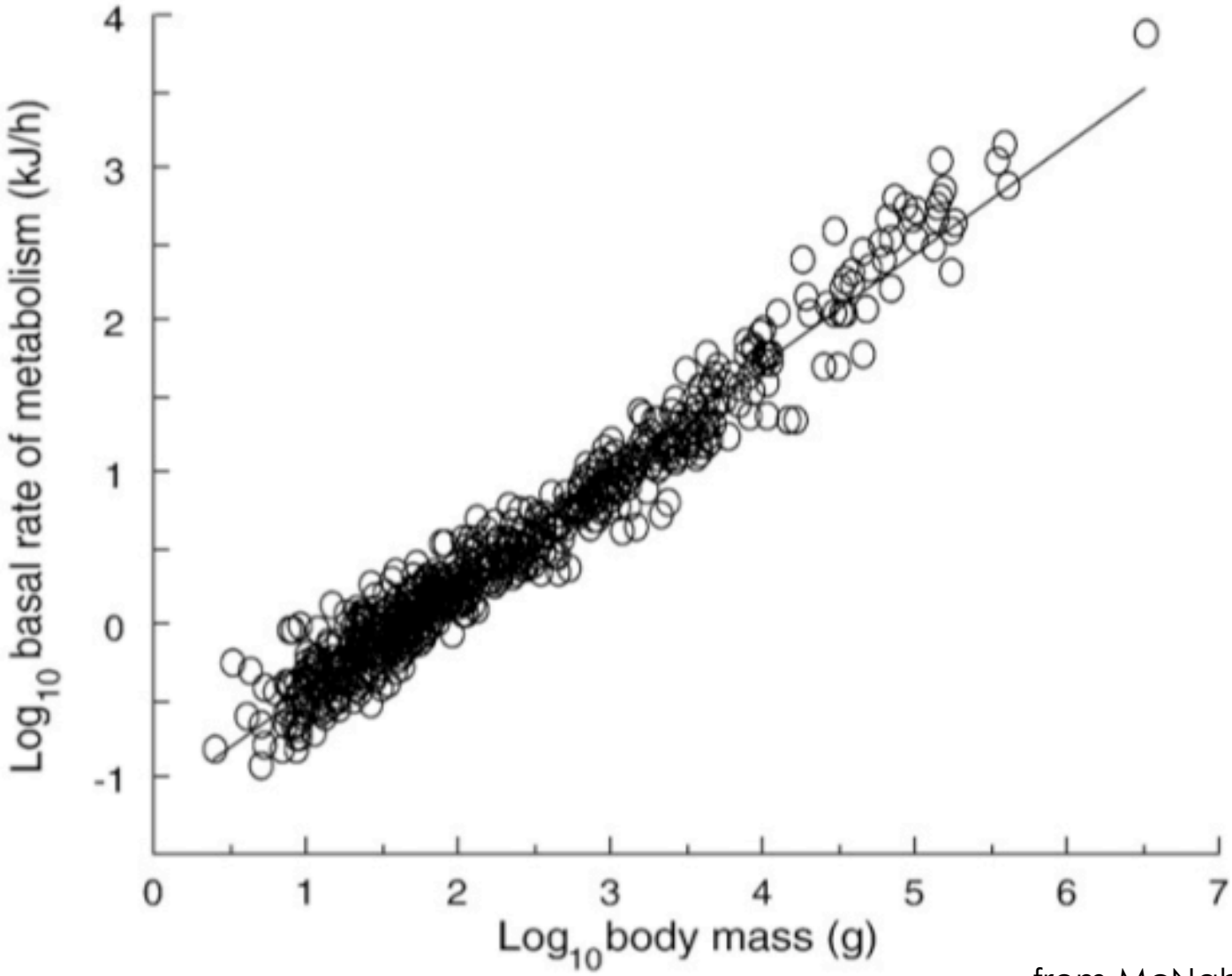

from McNab (2008)

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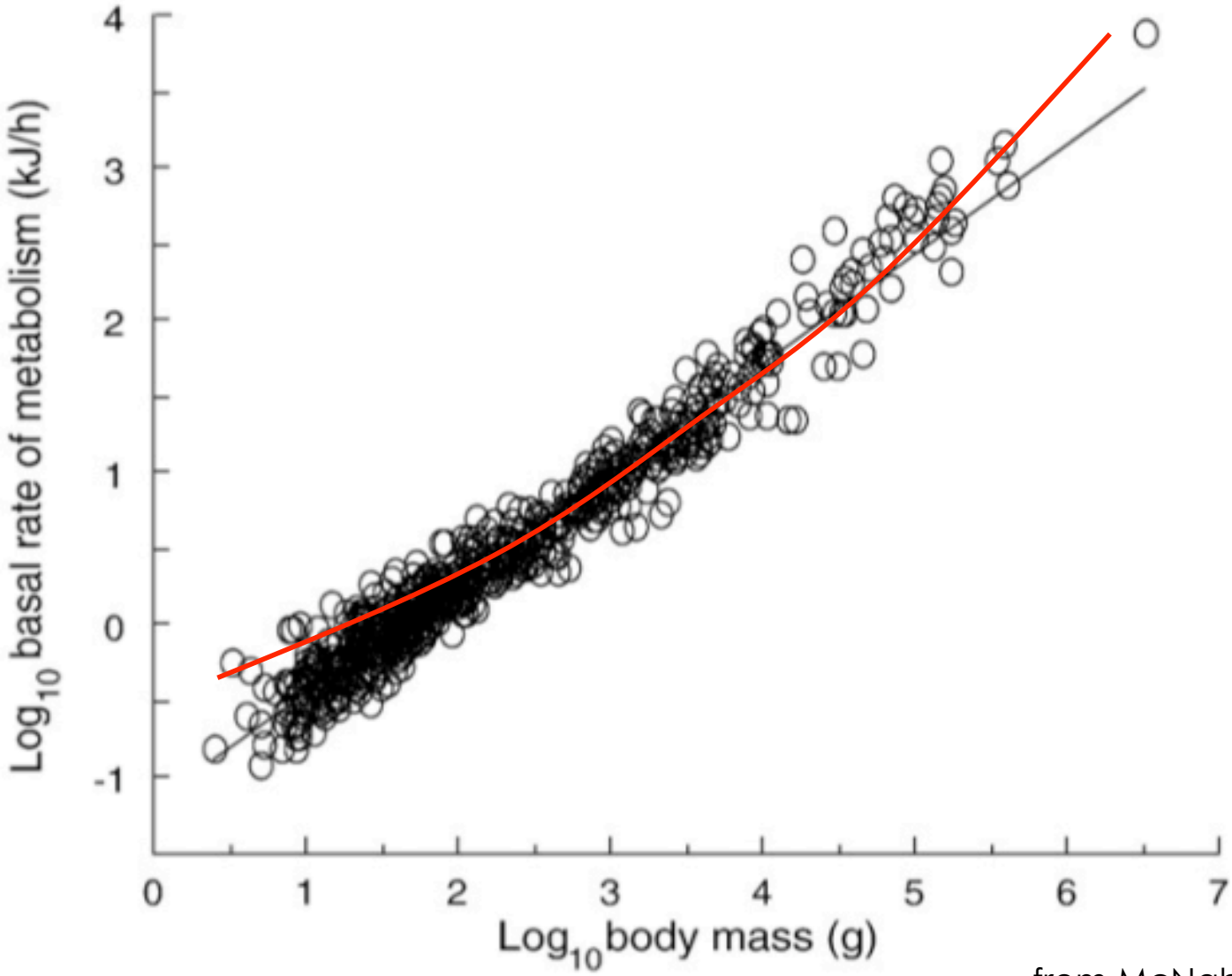


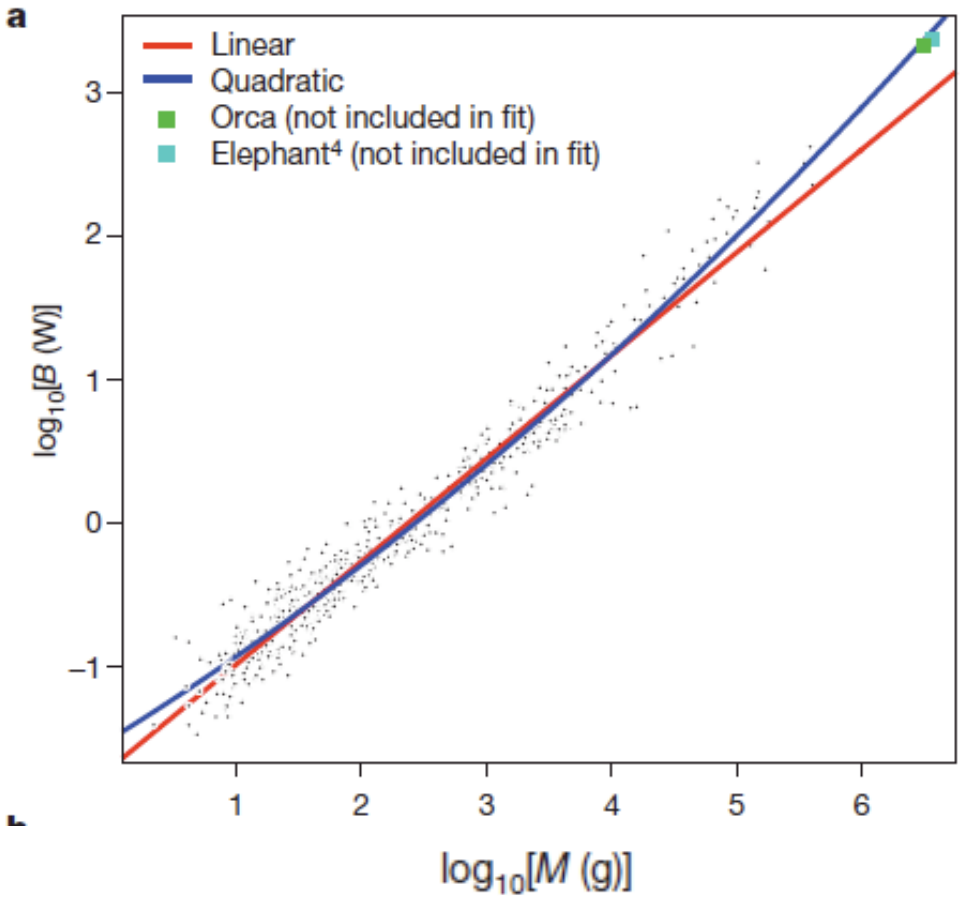
from McNab (2008)

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

LETTERS

Curvature in metabolic scaling

Tom Kolokotrones[1], Van Savage[2], Eric J. Deeds[1] & Walter Fontana[1]



Why the curvature?

Oikos 121: 102–115, 2012
doi: 10.1111/j.1600-0706.2011.19505.x

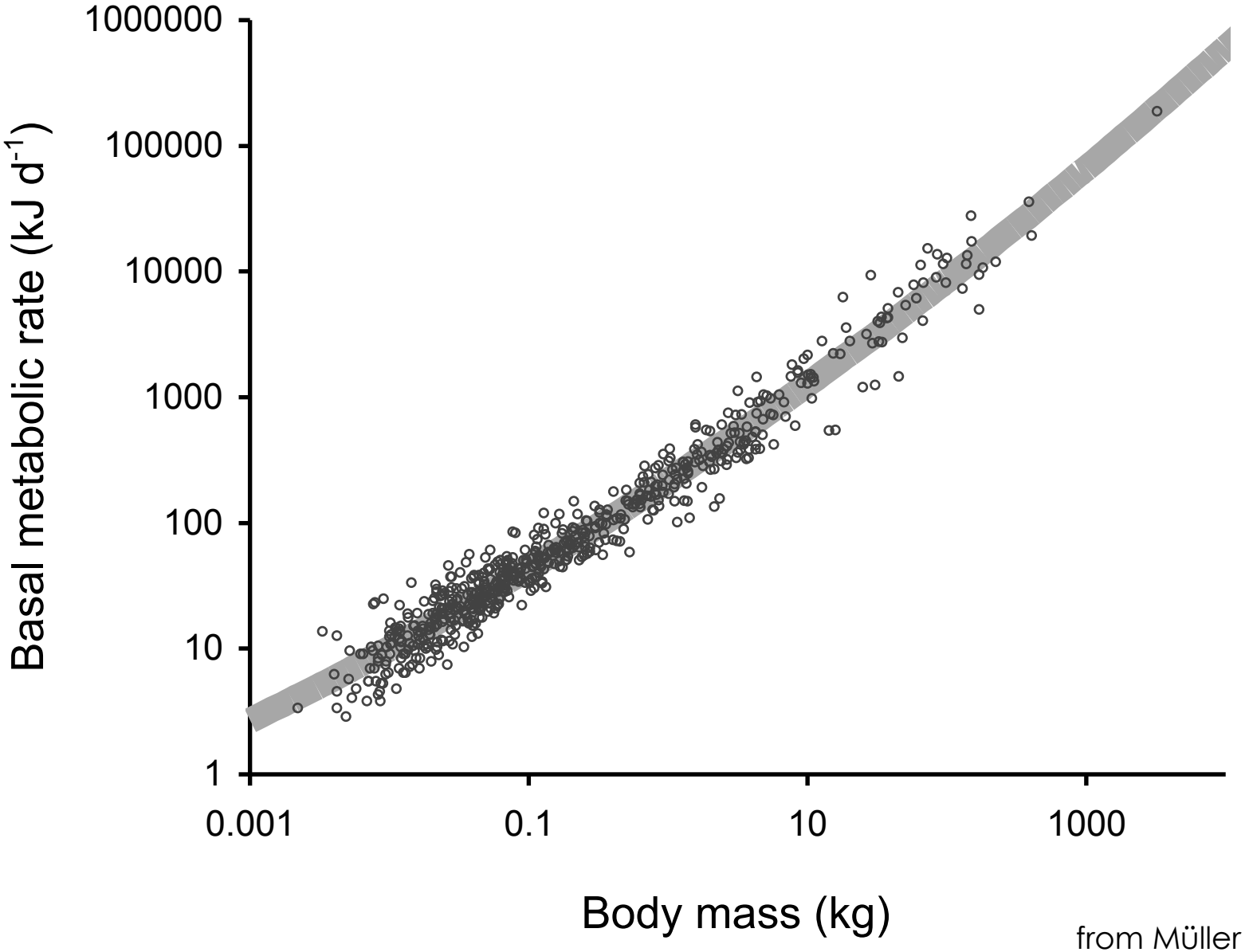
Subject Editor: Dustin Marshall. Accepted 4 April 2011

Dichotomy of eutherian reproduction and metabolism

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

D. W. H. Müller, D. Codron and M. Clauss (mclauss@vetclinics.uzh.ch), Clinic for Zoo Animals, Exotic Pets and Wildlife, 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.

Mode of reproduction?



from Müller et al. (2012)

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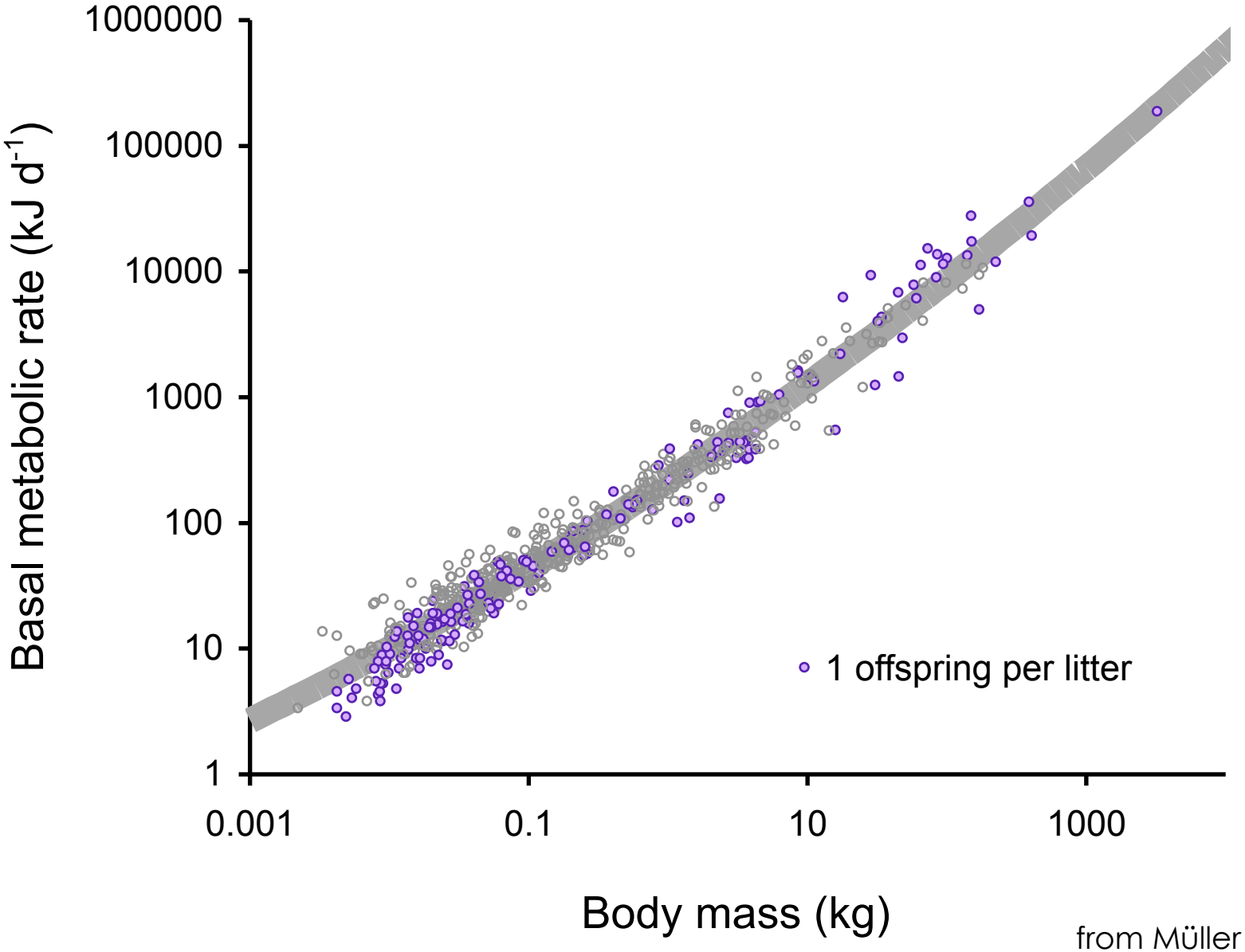

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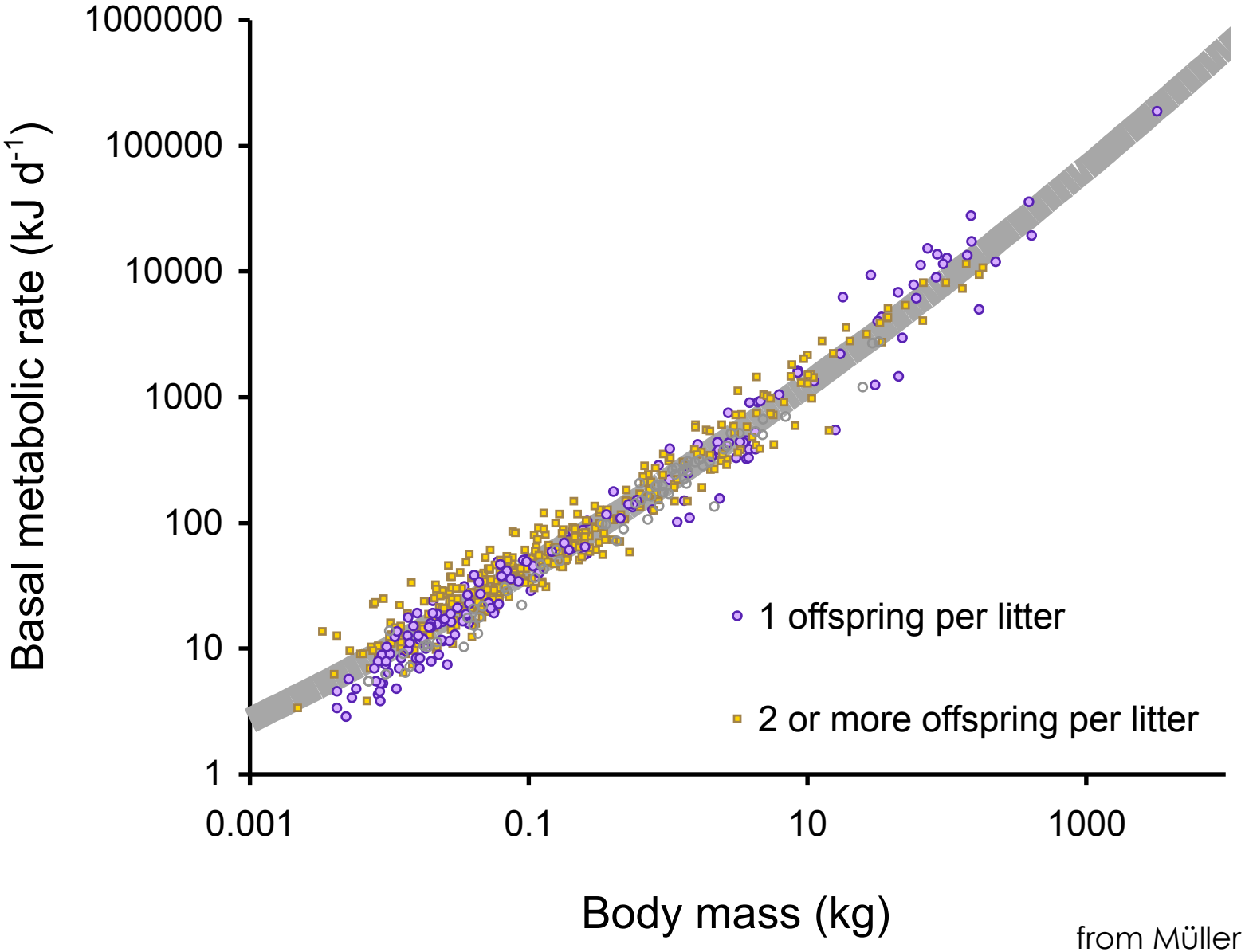

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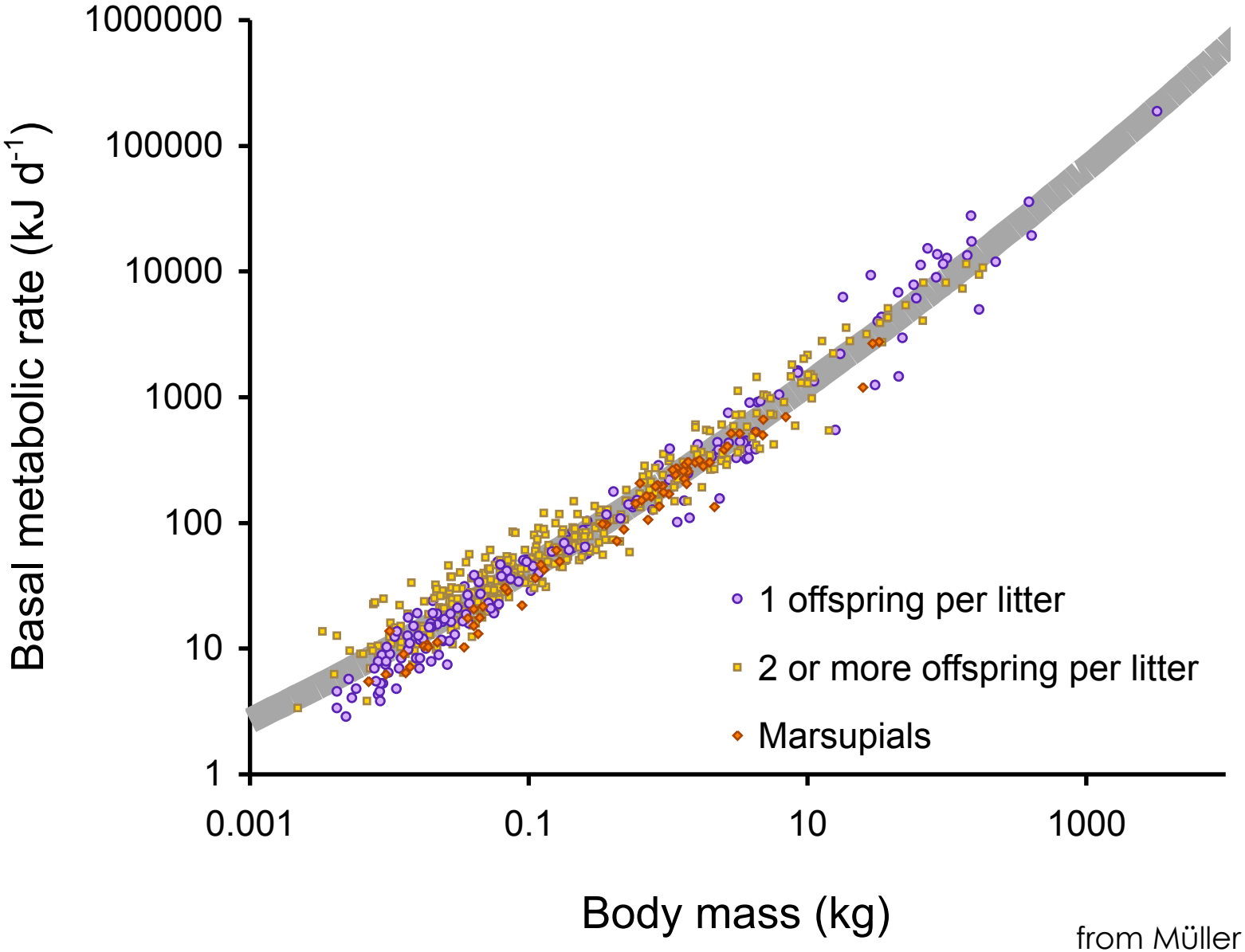

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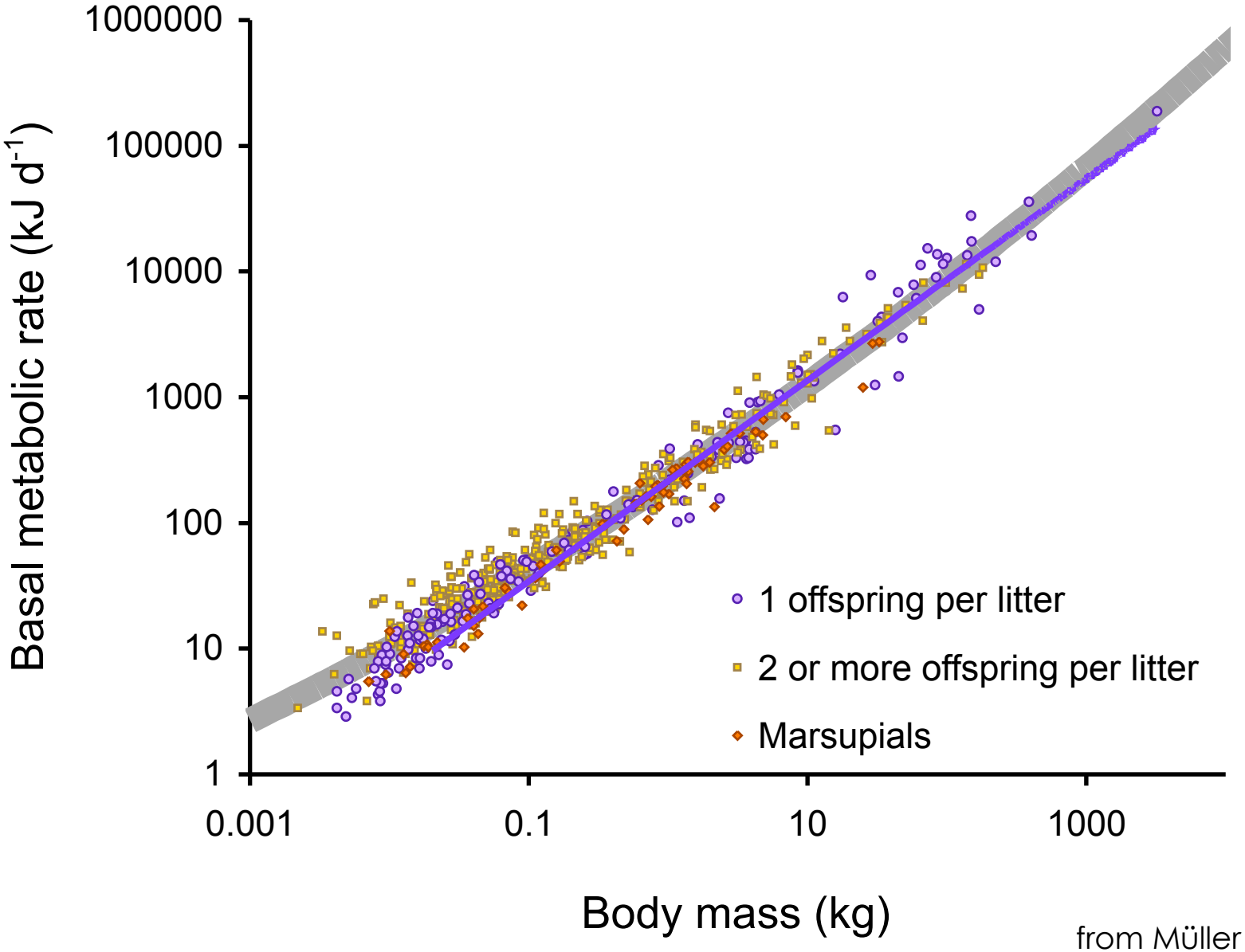

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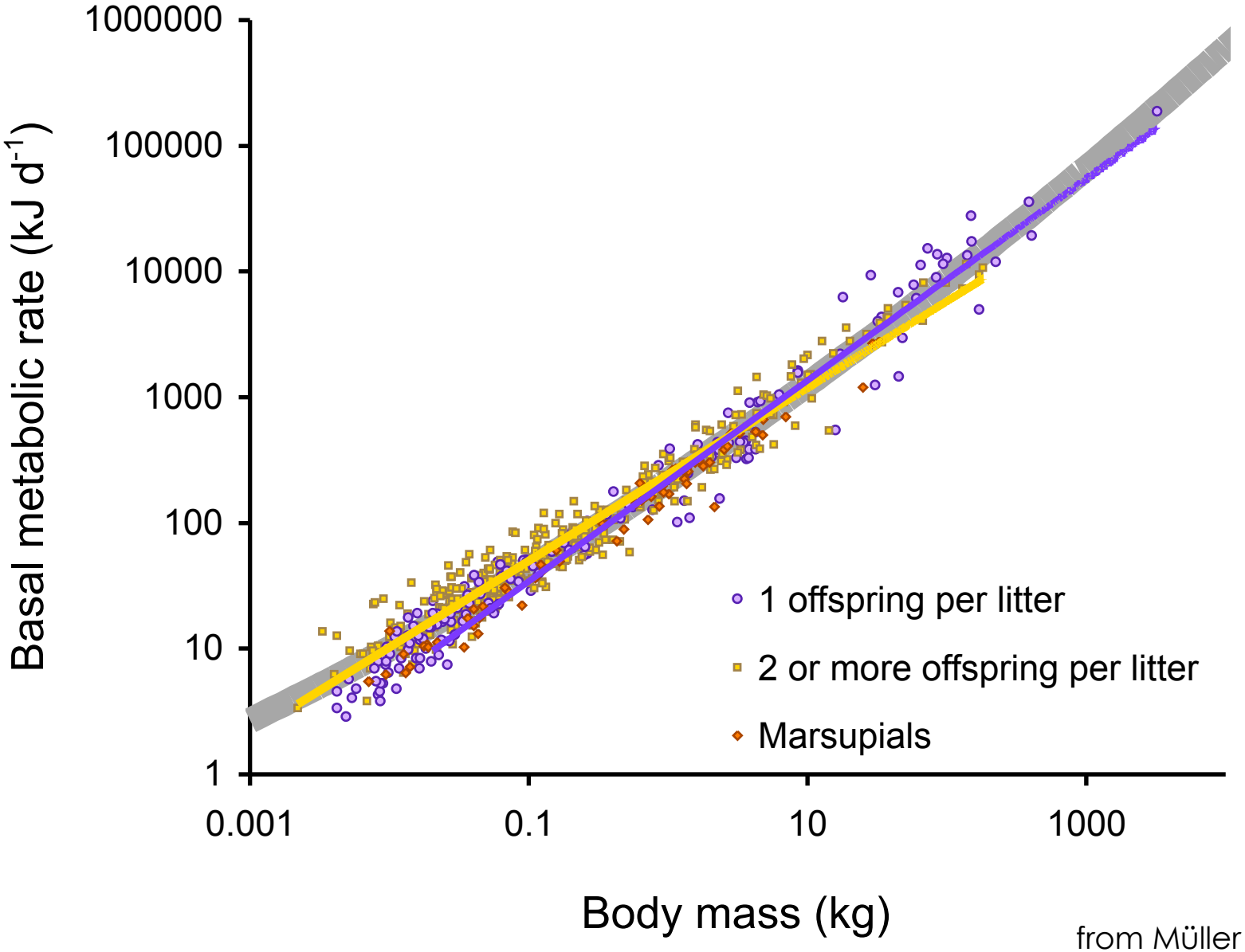

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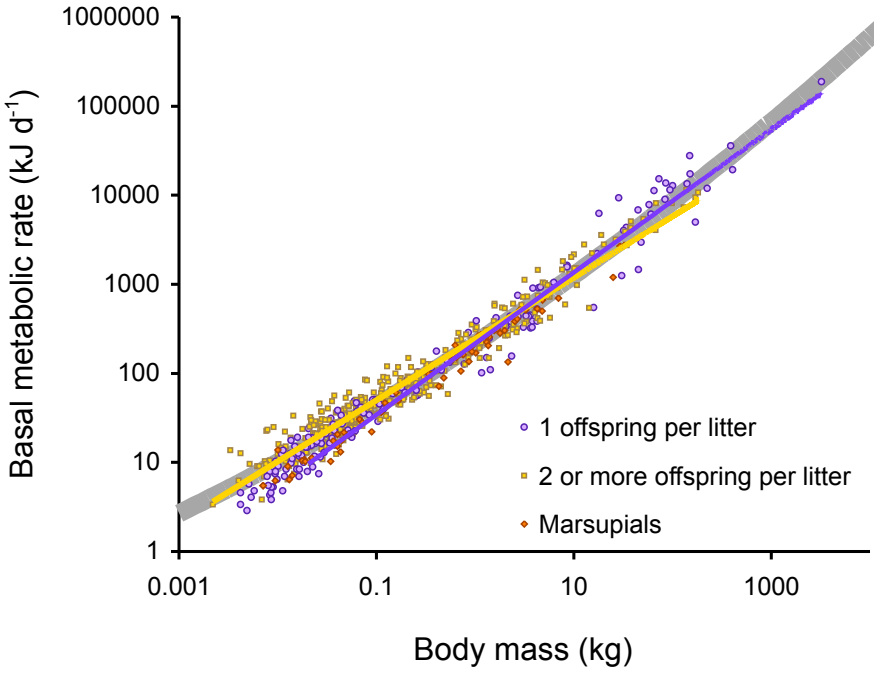

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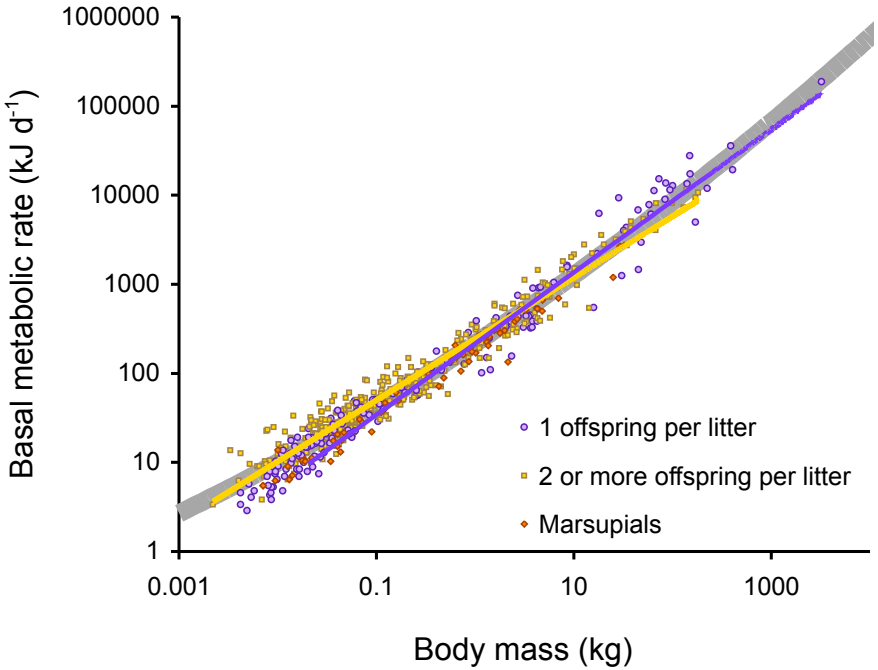
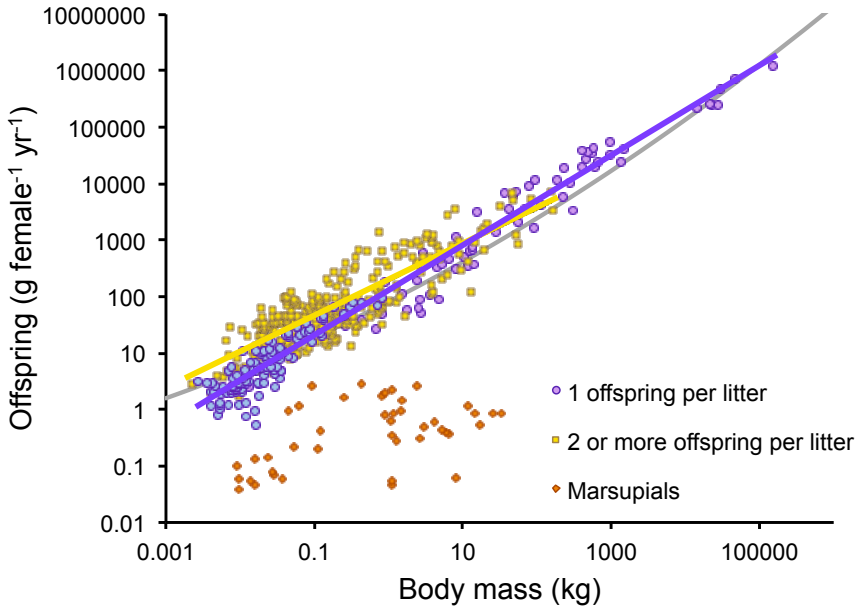




from Müller et al. (2012)

The ‘Jarman-Bell-principle’:

Larger herbivores have a digestive advantage

because of allometric principles

Using allometries

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

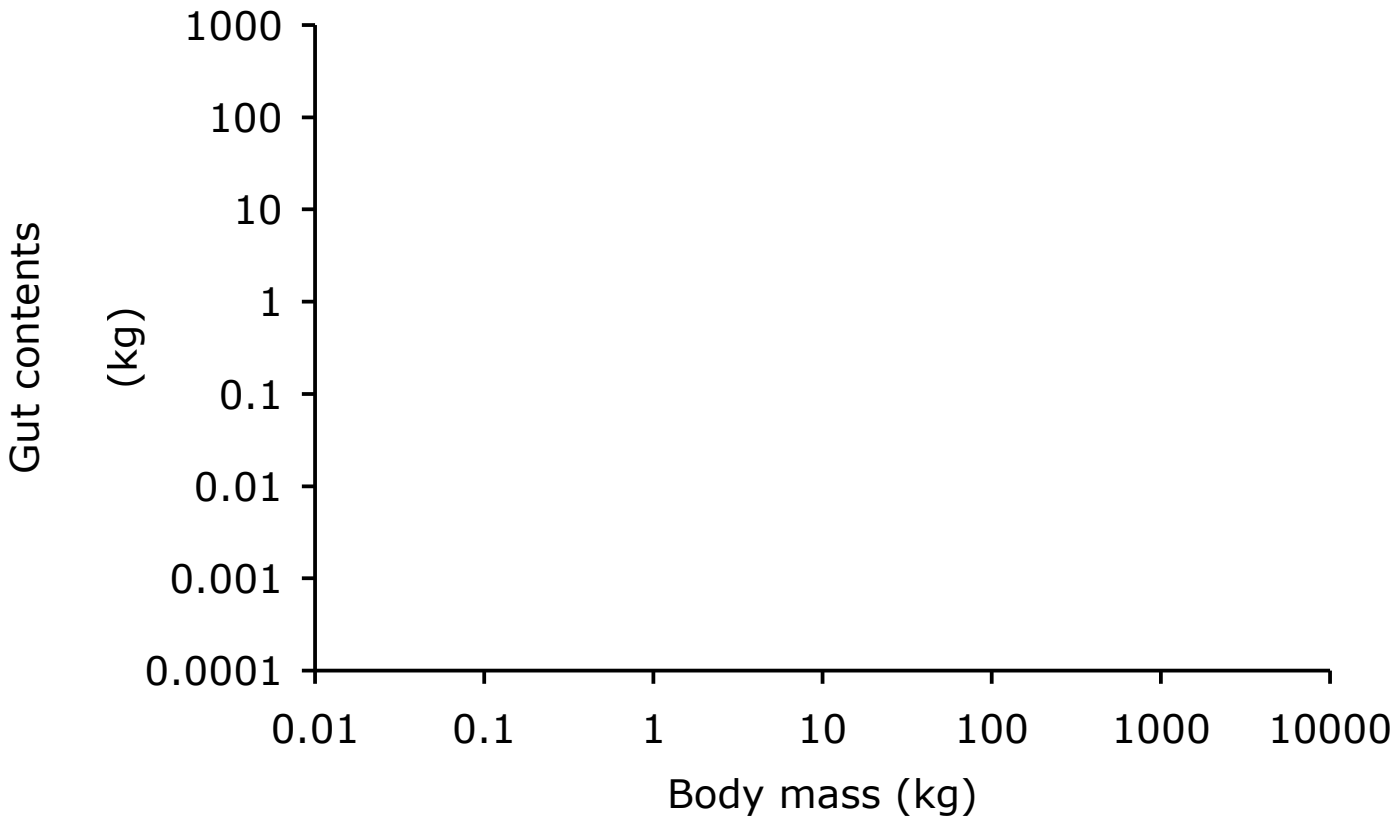
Using allometries

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

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

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

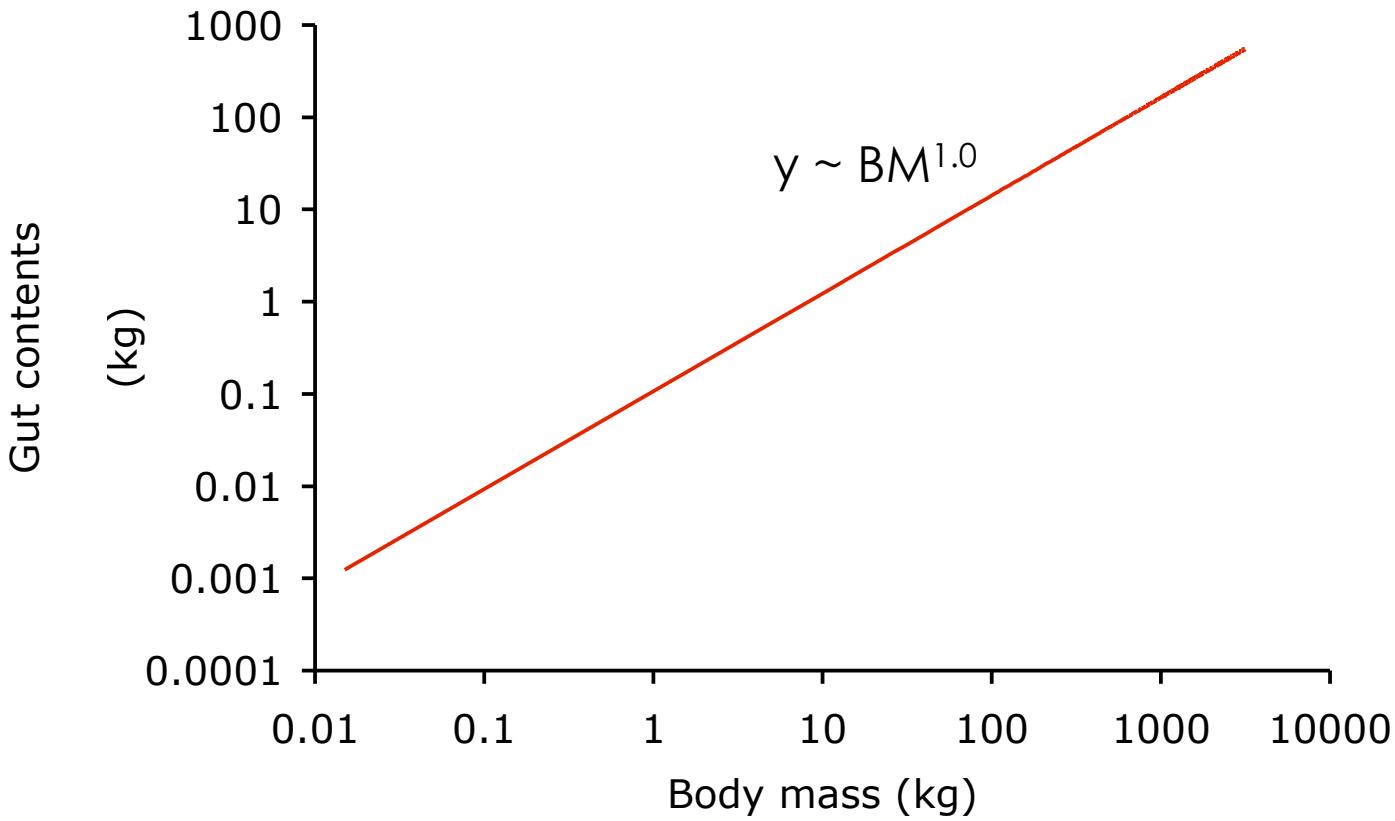
General allometric considerations



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

General allometric considerations

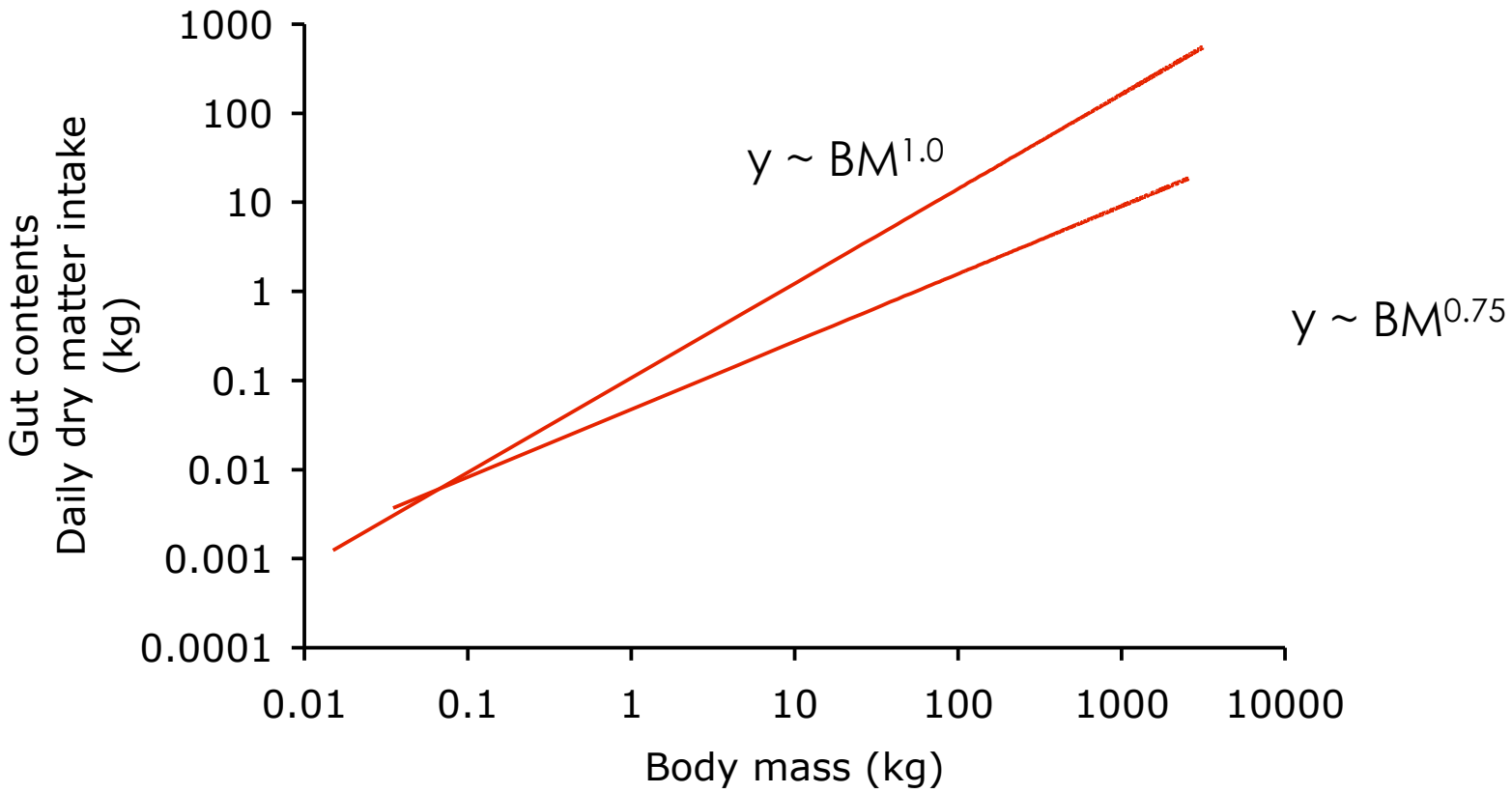
Gut capacity (measured as gut contents) scales linearly with body mass.



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

General allometric considerations

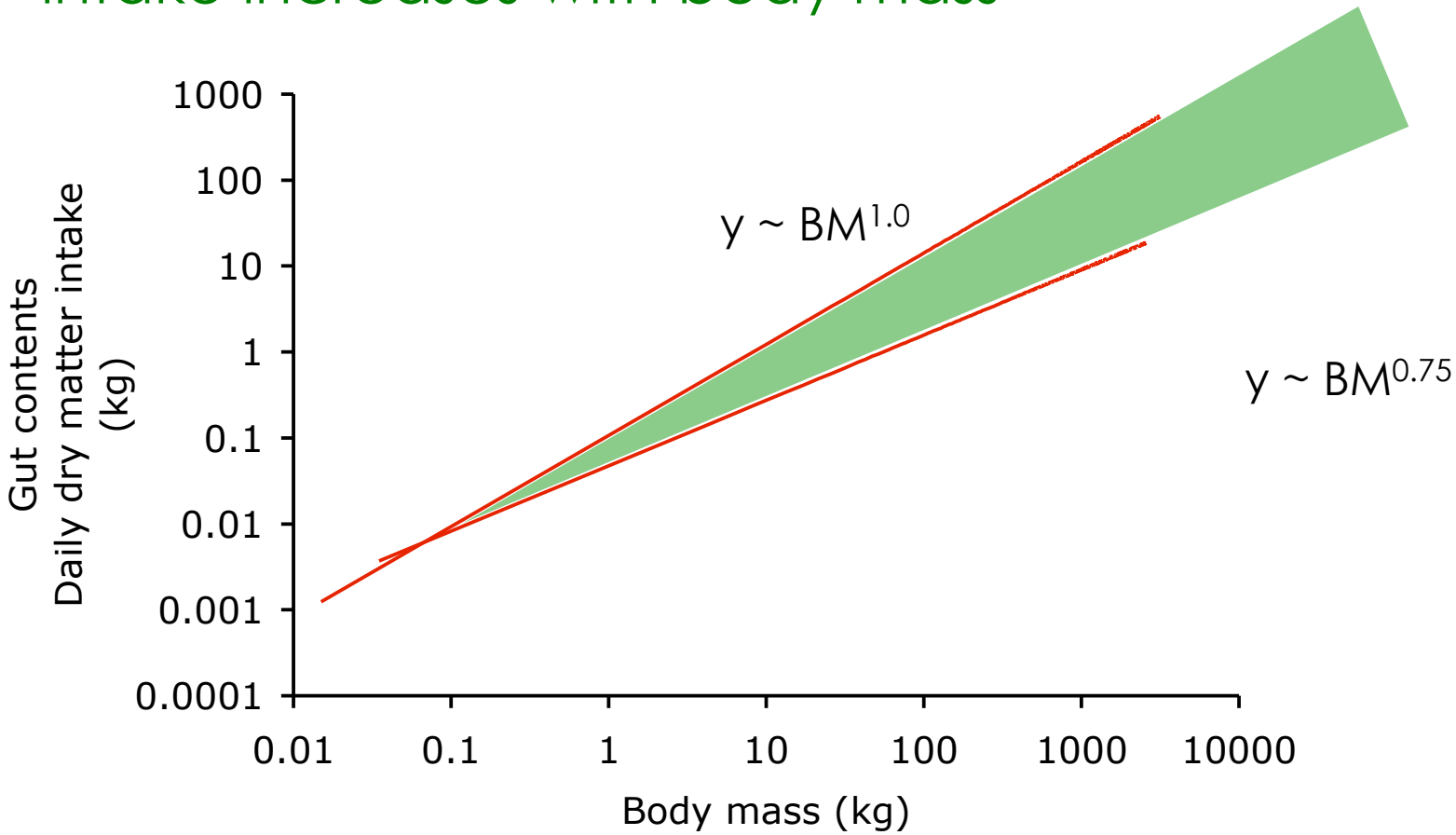
Food intake (relating to energy requirements) scales to metabolic body mass (body mass$^{0.75}$)



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

General allometric considerations

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

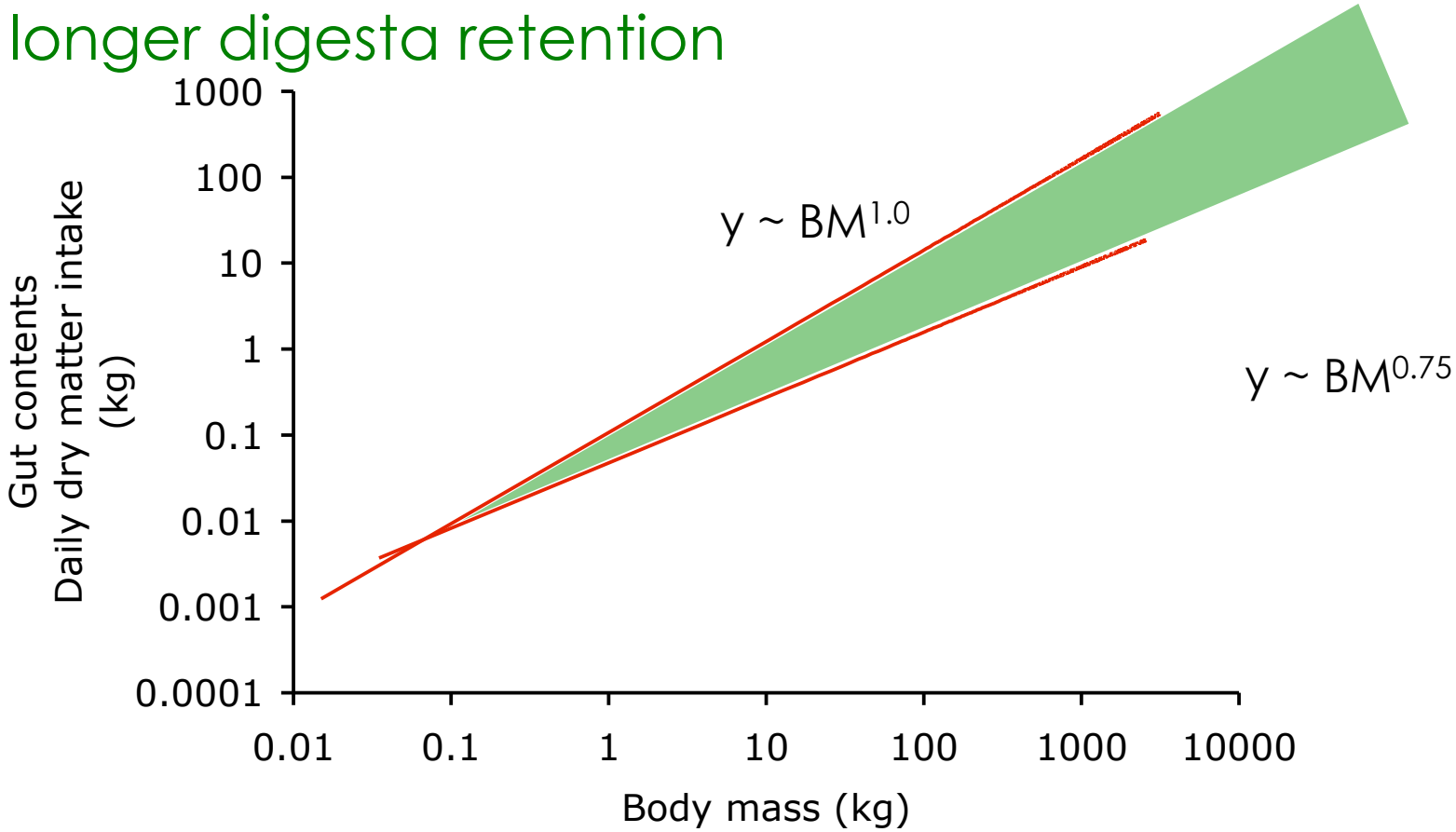


from Parra (1978), Demment & Van Soest (1985), Illius & Gordon (1992); McNab (2002)

General allometric considerations

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

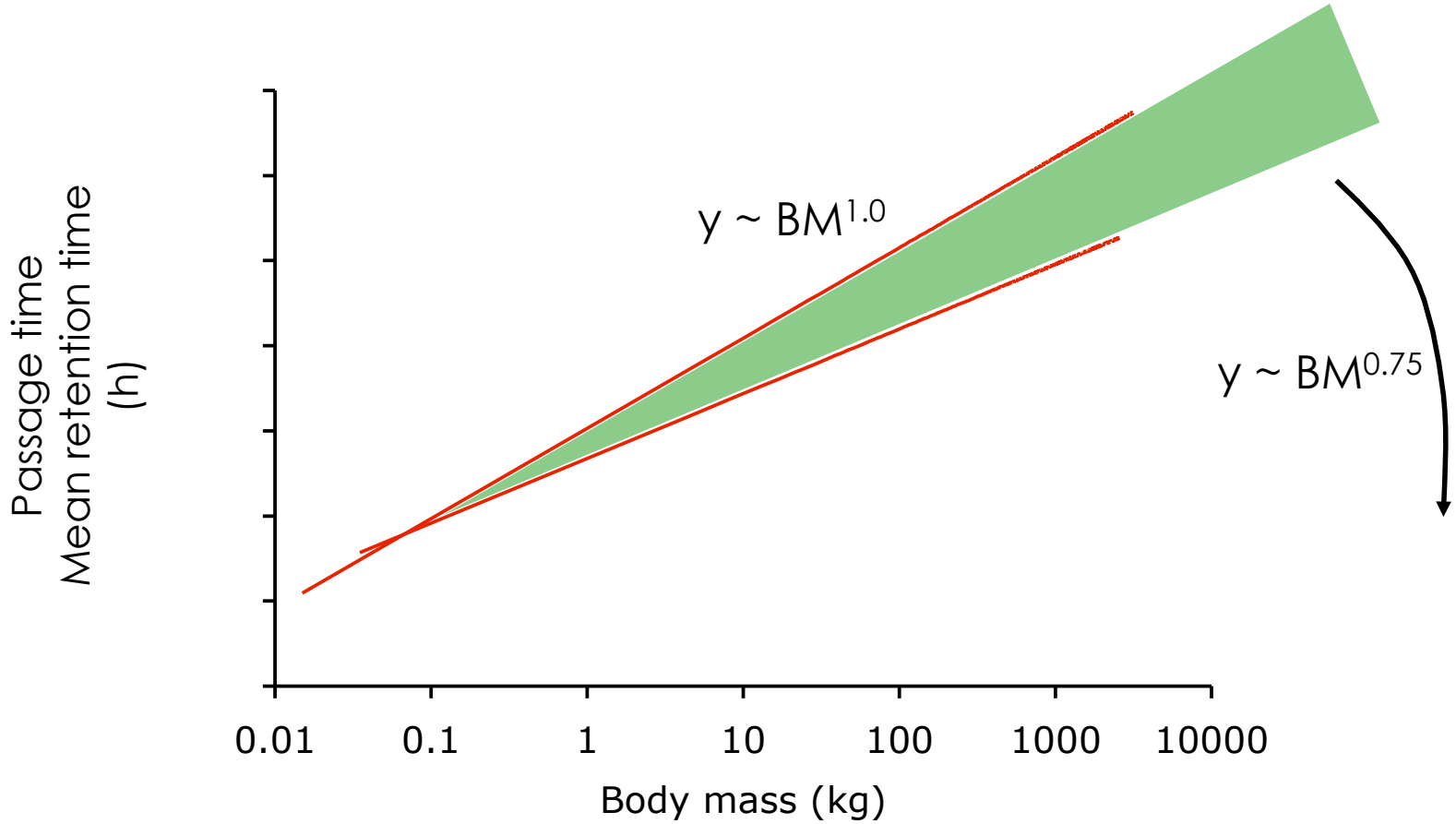
=> longer digesta retention



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

General allometric considerations

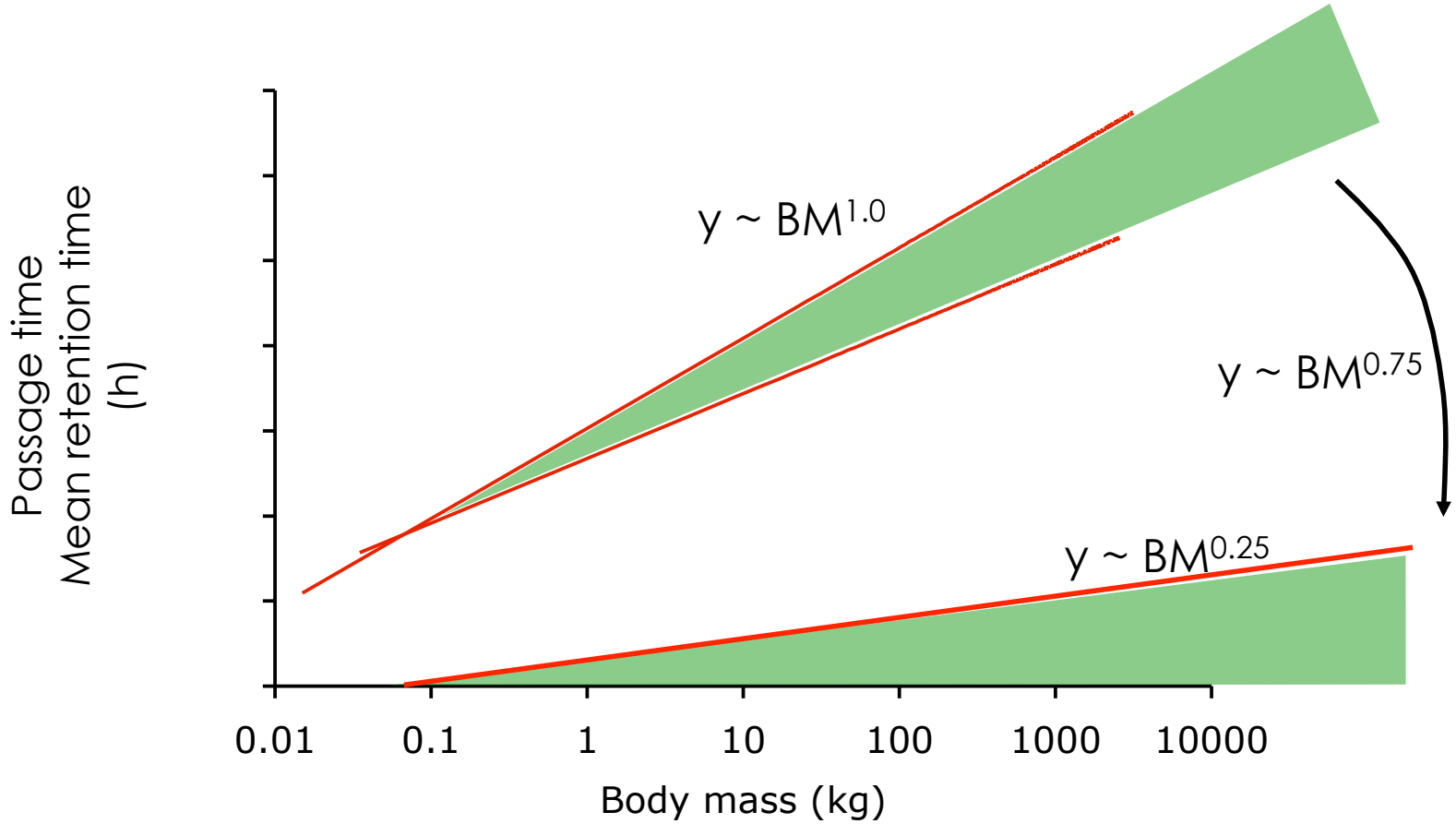
Digesta retention scales to body mass ...



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

General allometric considerations

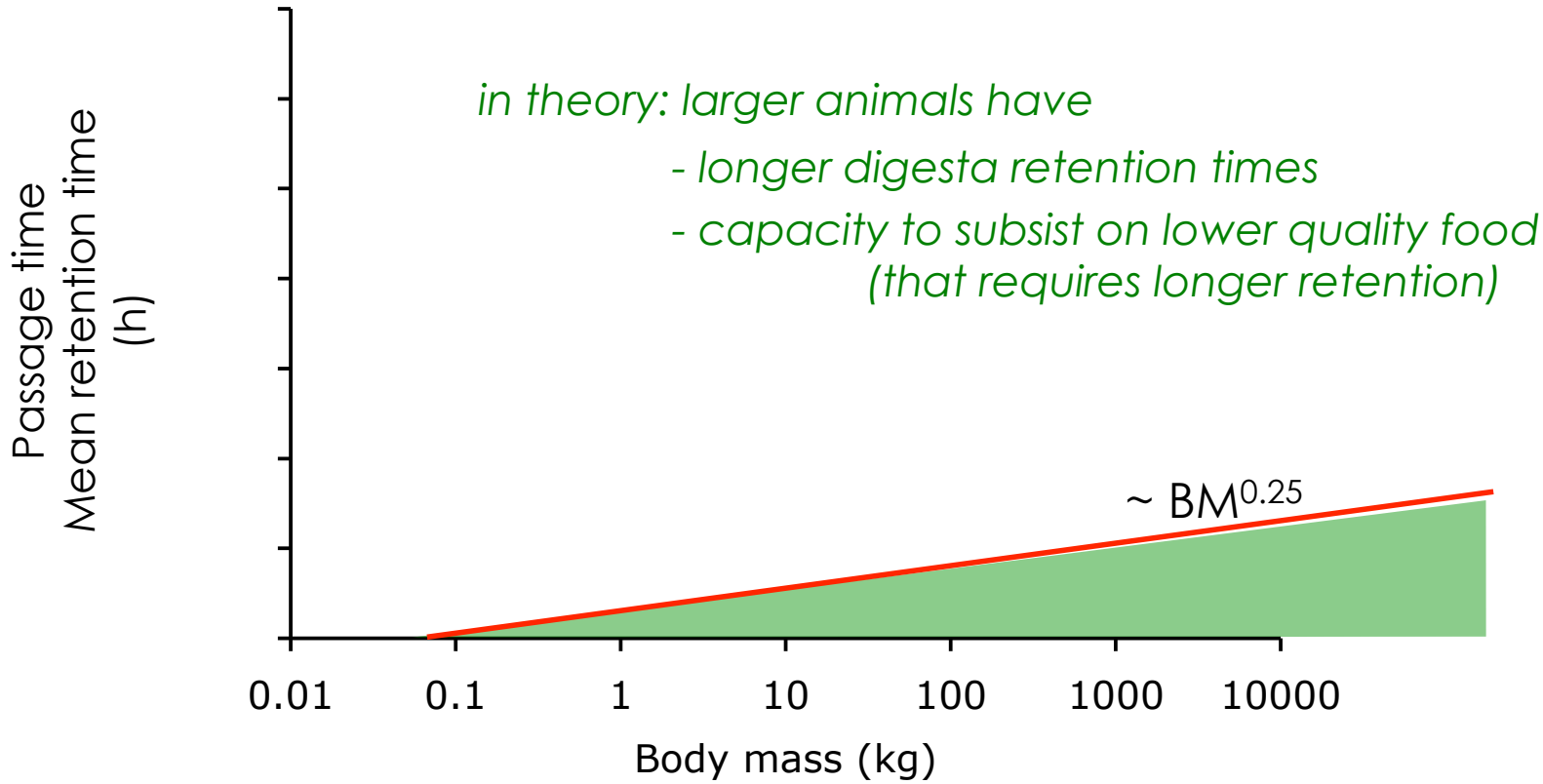
... to the power of 0.25



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

General allometric considerations

"Therefore, larger herbivores can achieve higher digestive efficiencies"



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

The **'Jarman-Bell Principle'**

is used widely to infer (herbivore) niche differentiation along a body size gradient

(incl. e.g. sexual segregation in dimorphic species)

Checking the validity of a concept

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

(vary sequence to suit your preference or intellectual capacity)

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1. **Check if empirical data matches the hypothesis**
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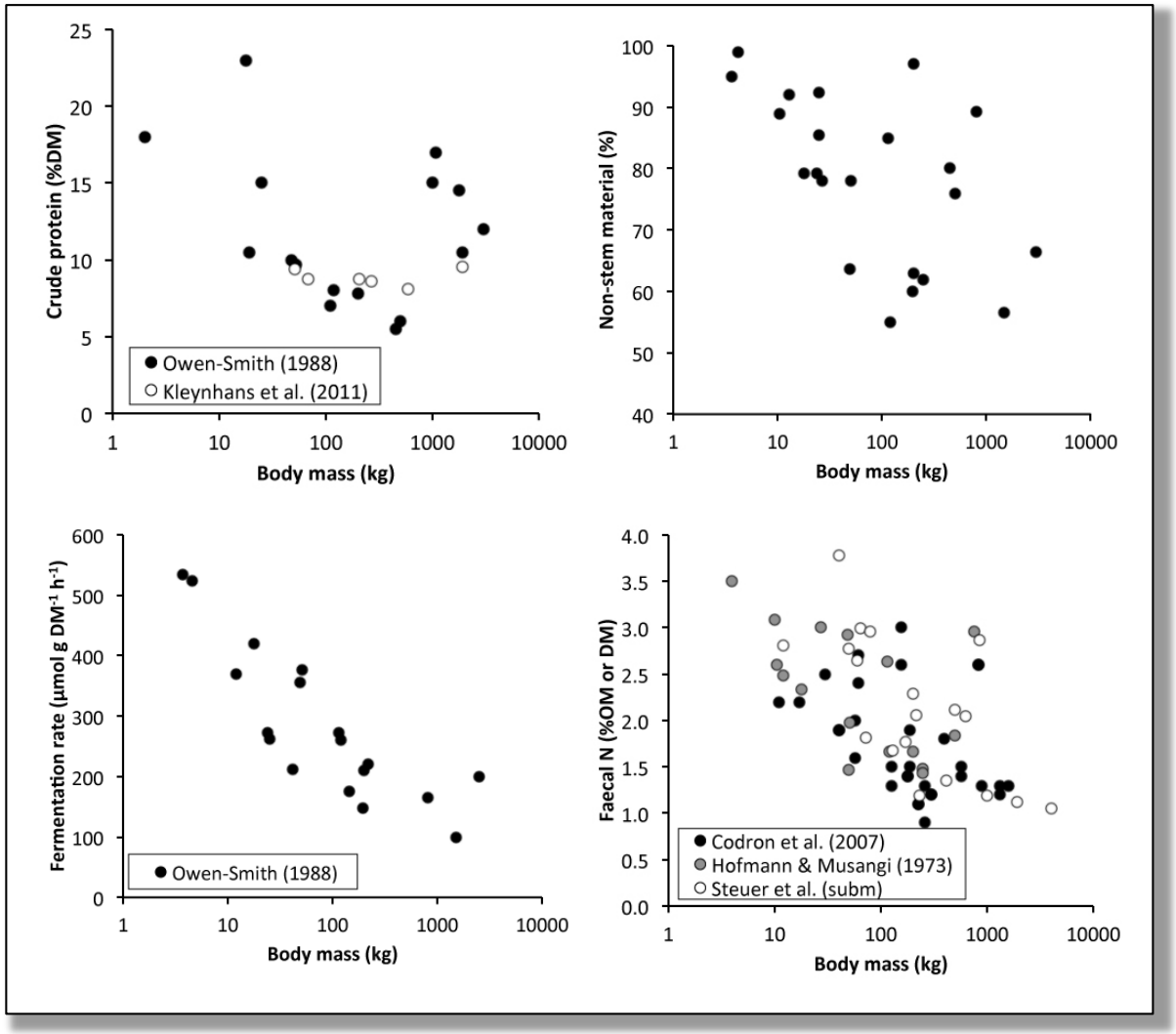
Diet quality

Larger herbivores eat lower-quality diets

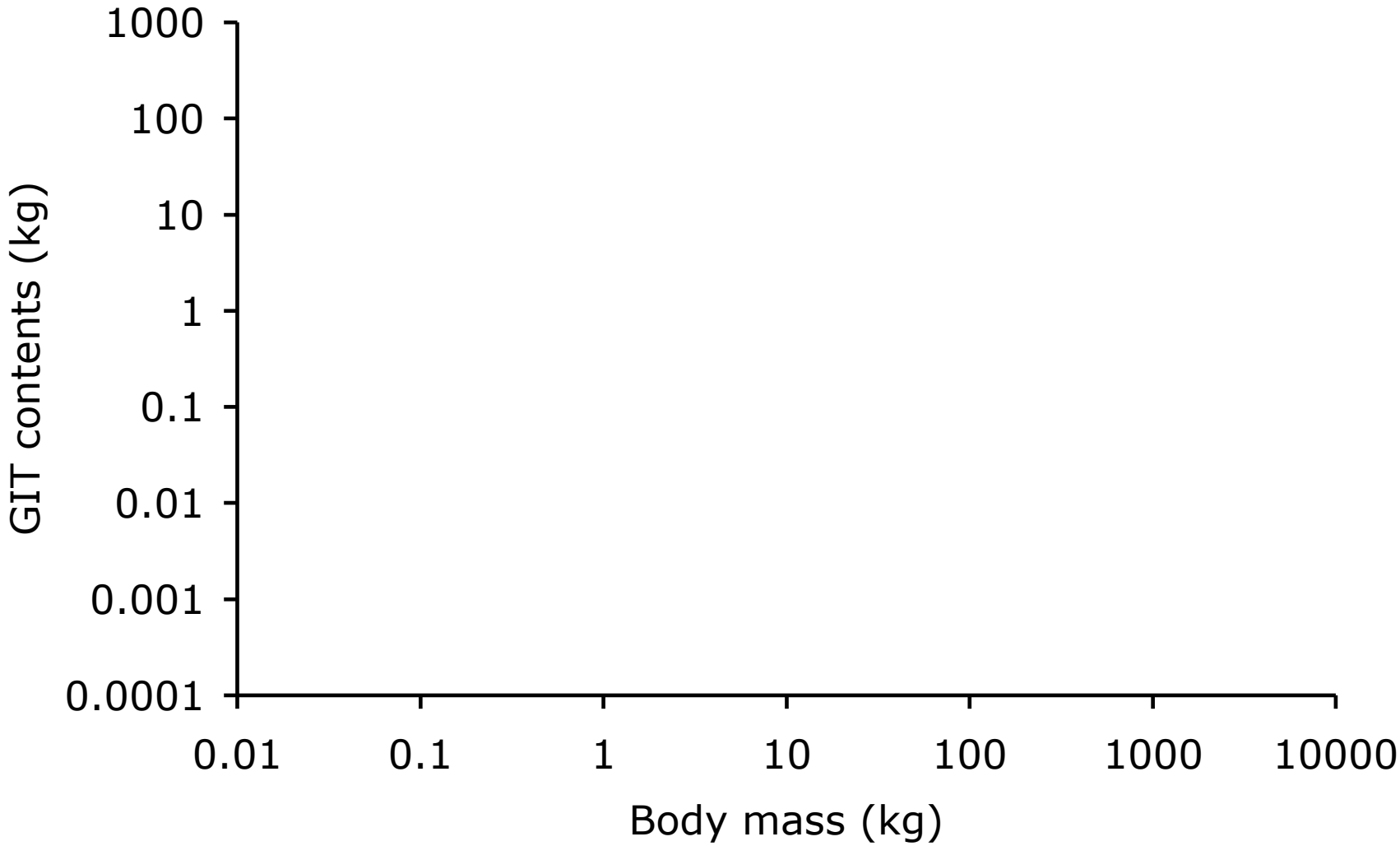


from Clauss et al. (2013)

Gut capacity

Wet gut content mass

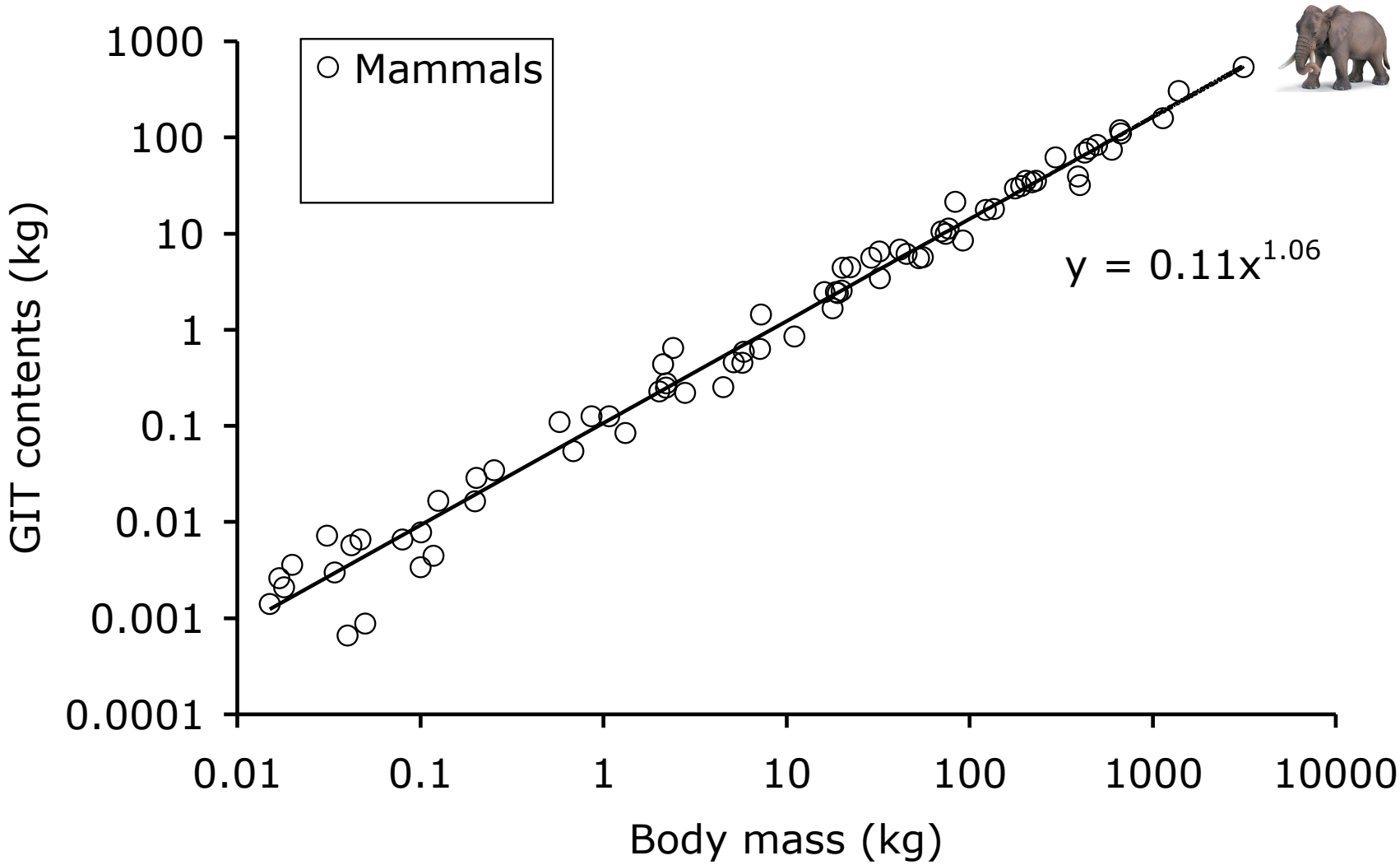
(measured by slaughtering)



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

Wet gut content mass

(measured by slaughtering)



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Wet gut content mass

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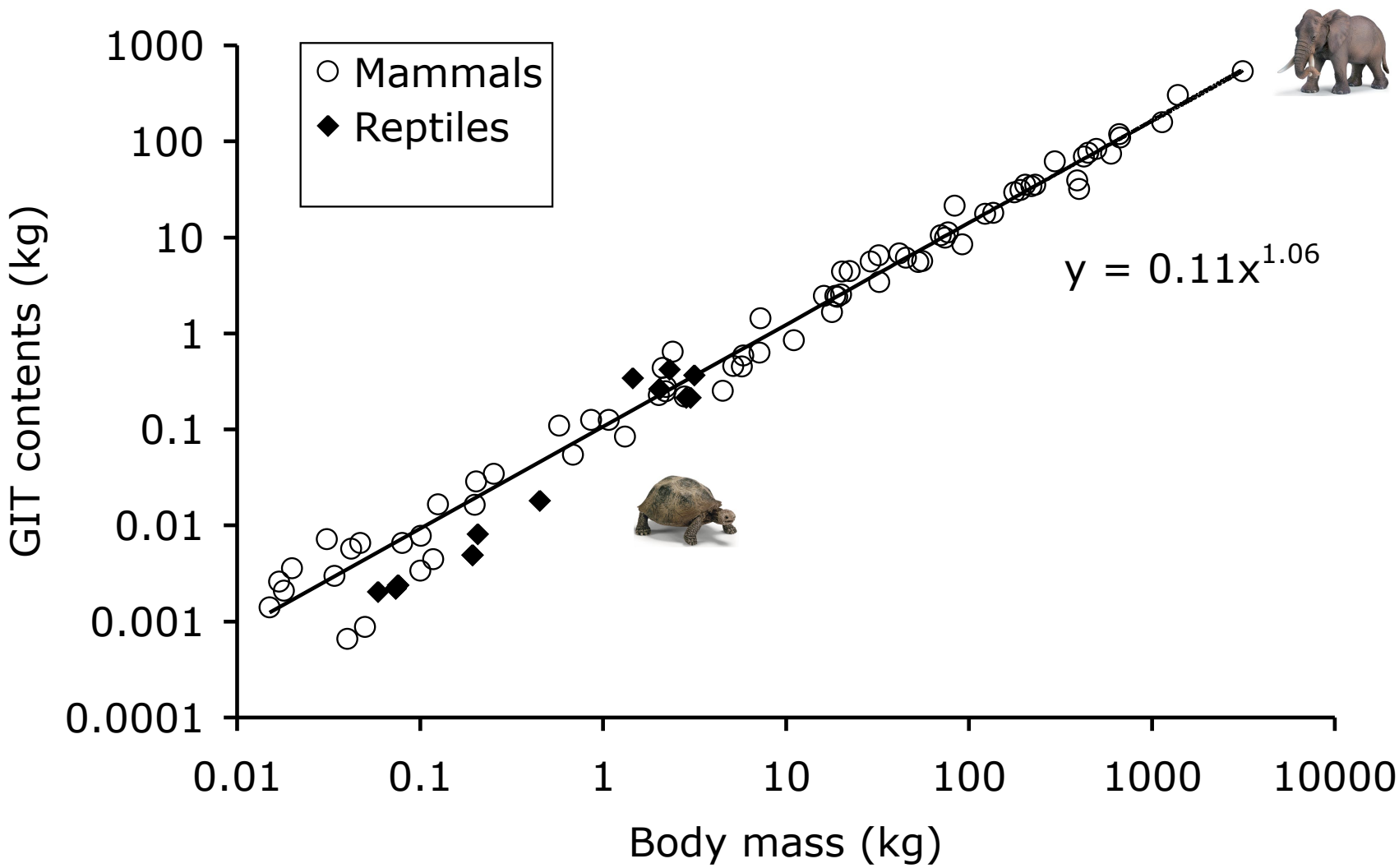

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Wet gut content mass

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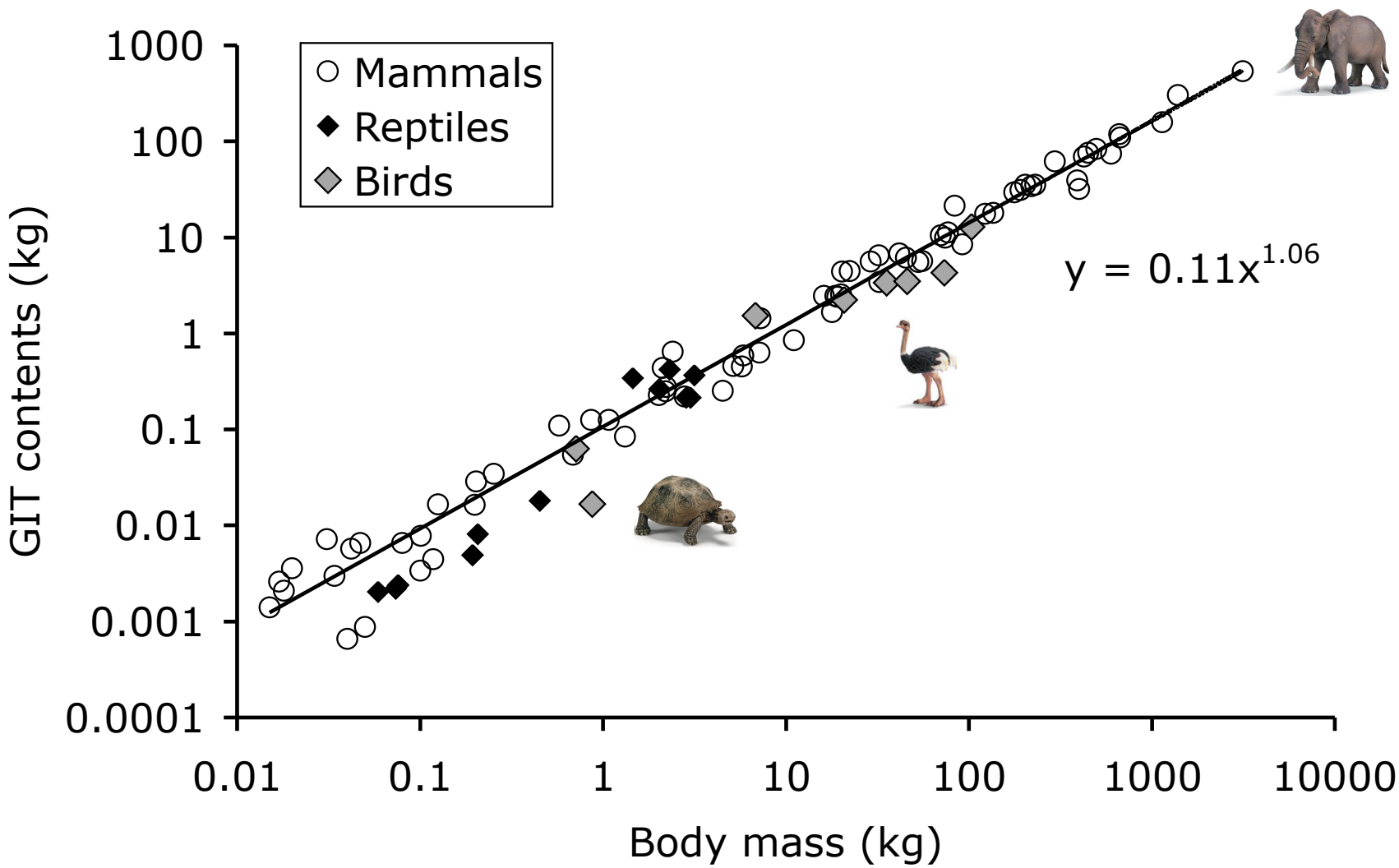

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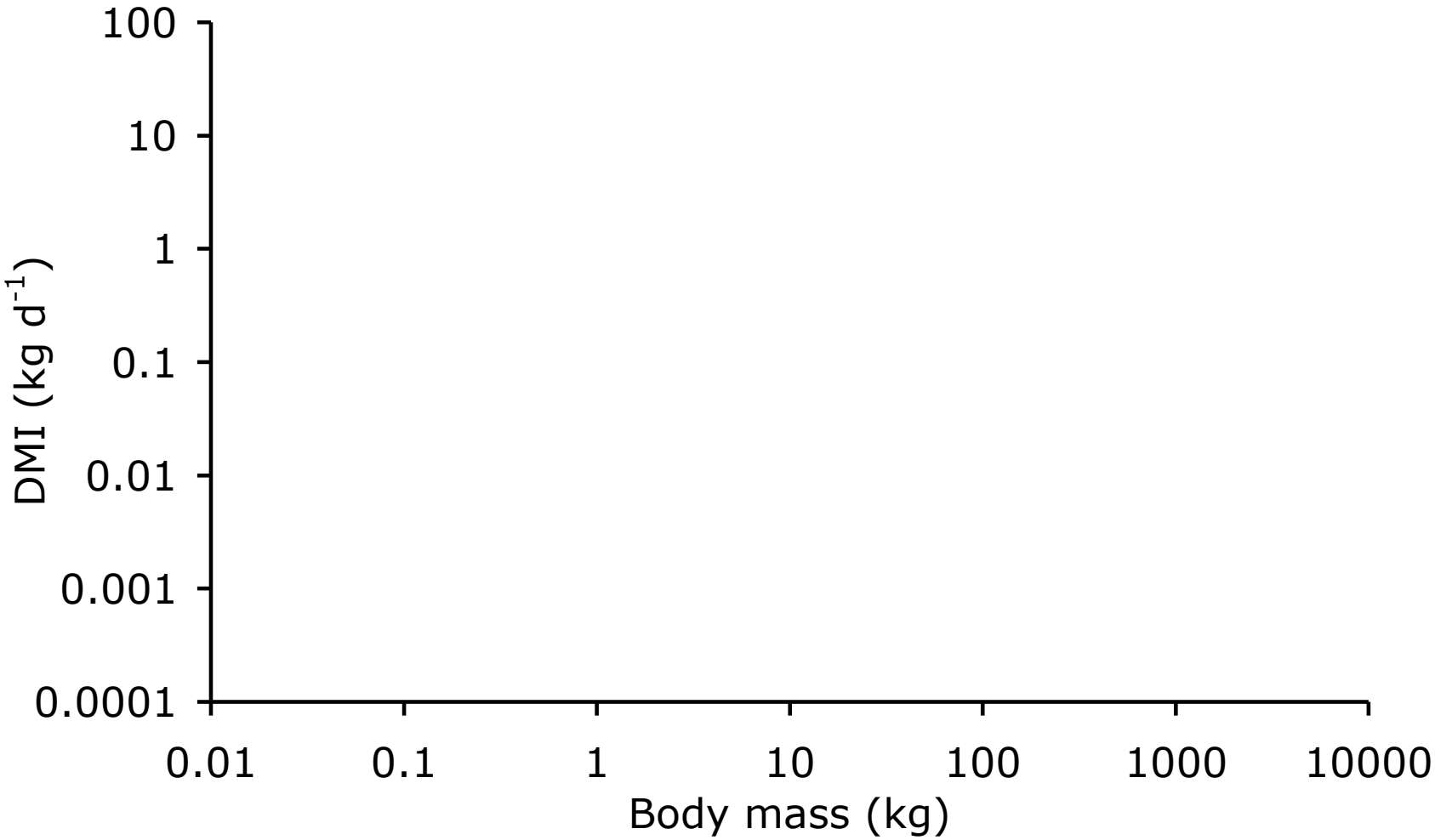
Food intake

Food intake



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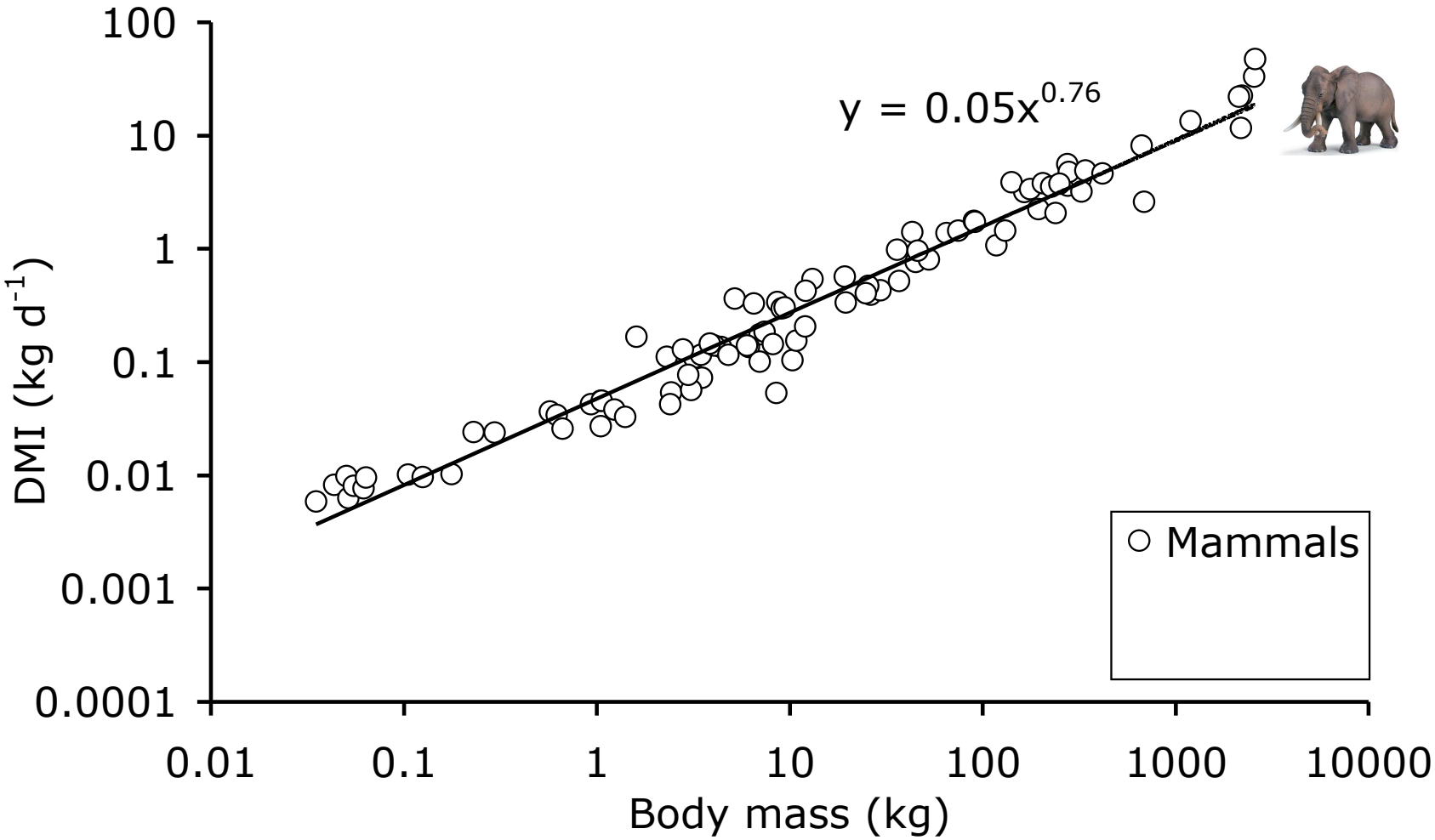
Food intake



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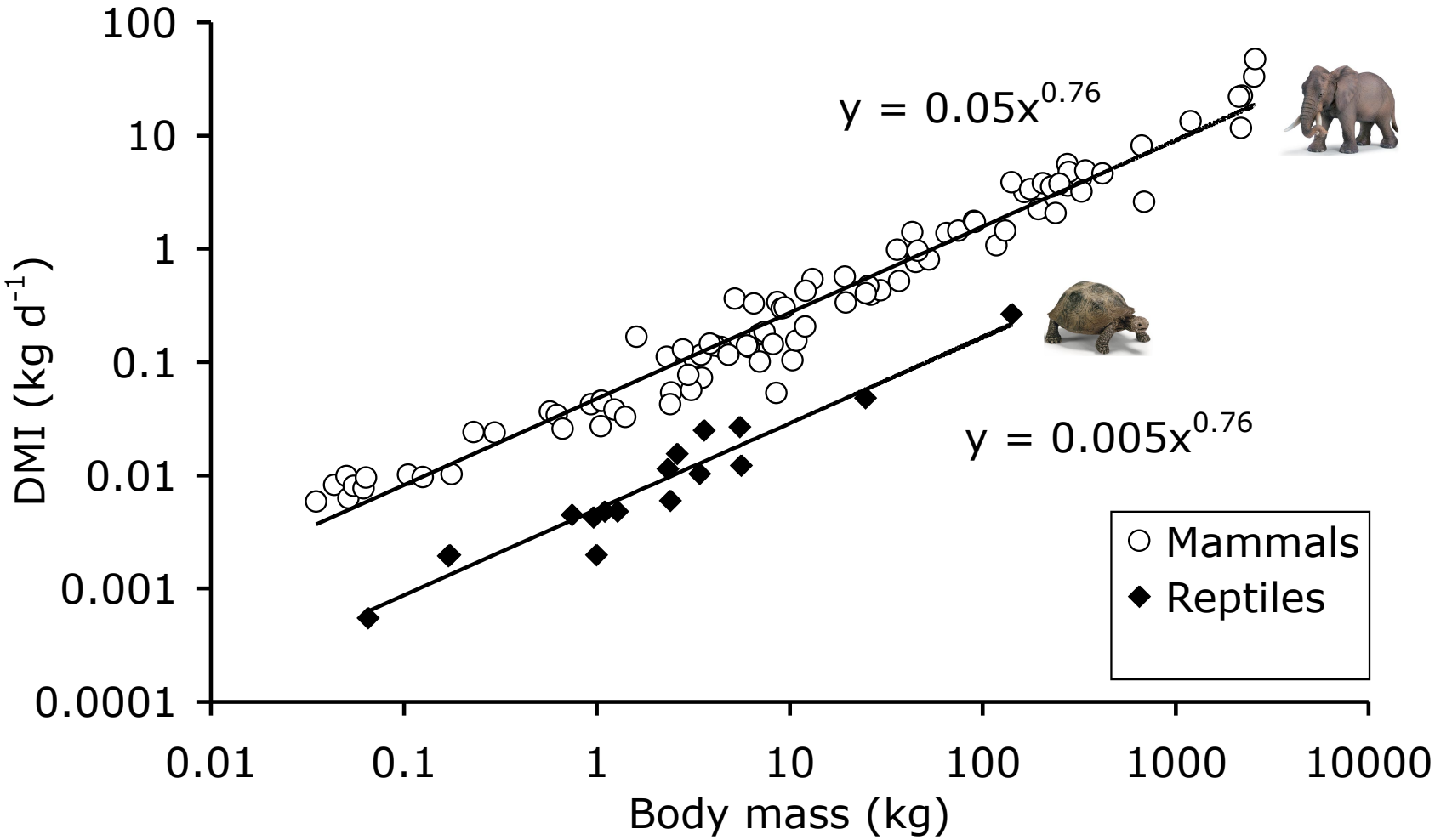
Food intake



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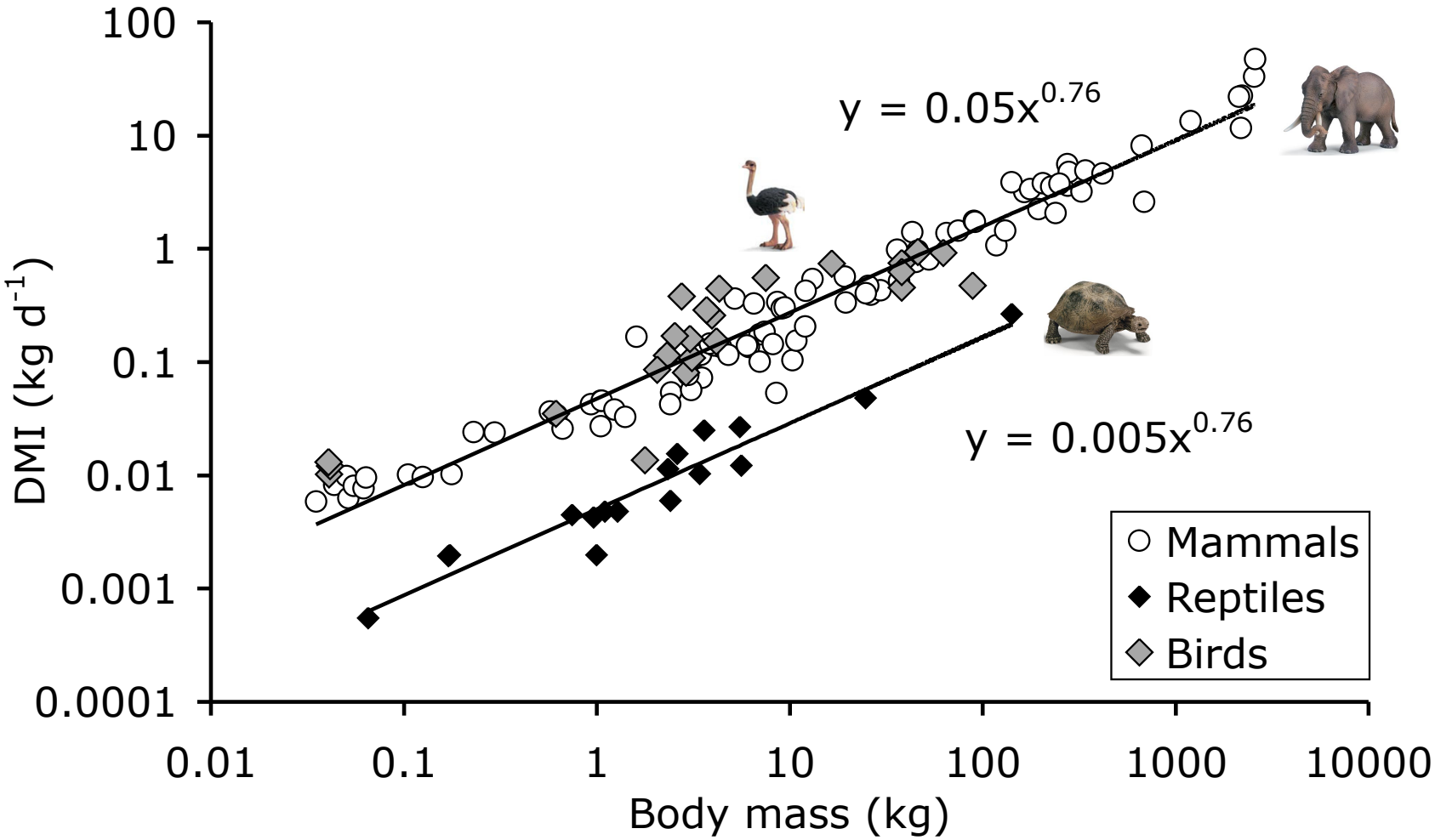
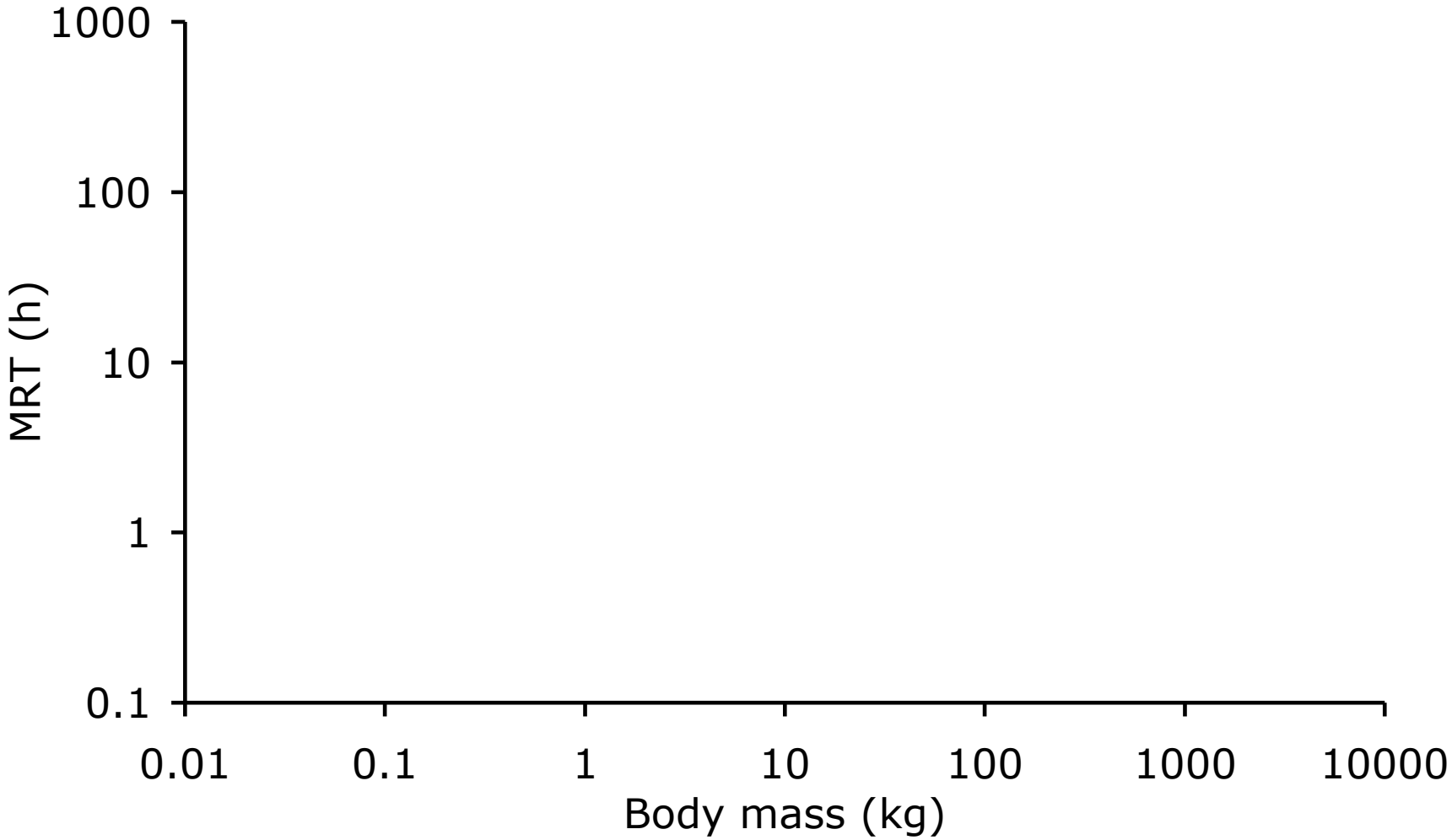


mammal data collection Clauss et al. (2007), reptile from Franz et al. (2009), bird from Fritz et al. (2012)

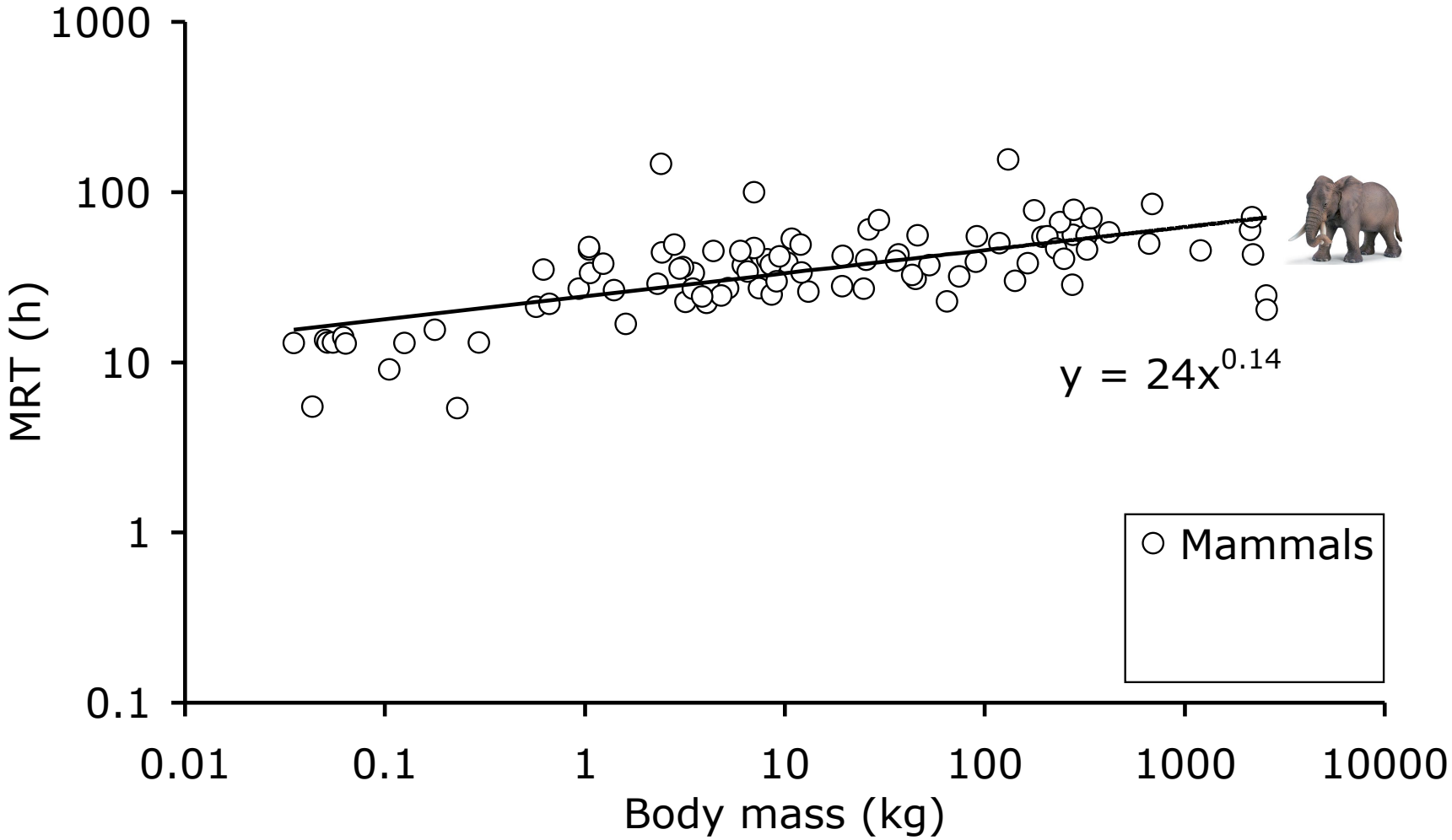
Digesta retention

Mean retention time



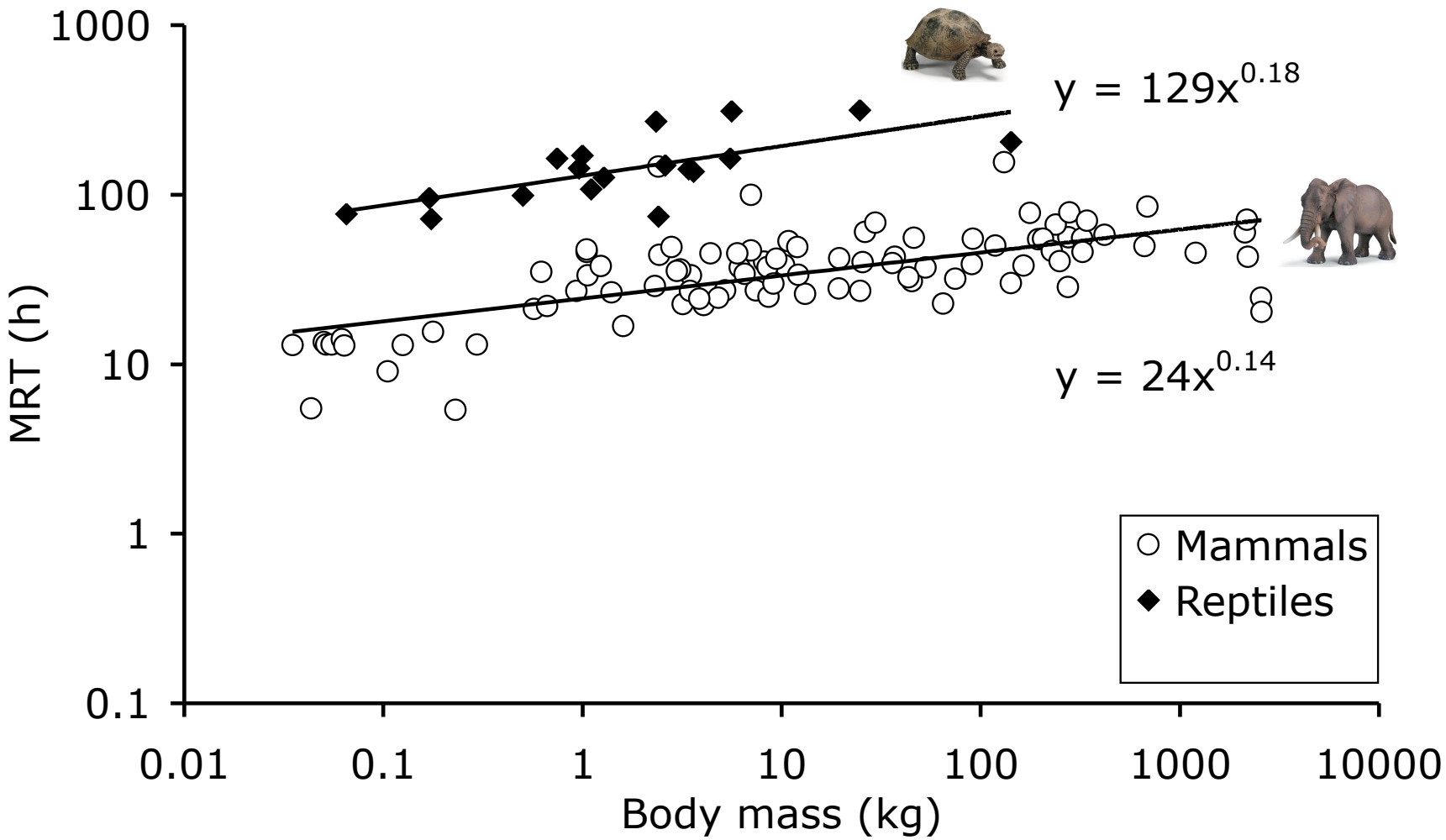
mammal data collection Clauss et al. (2007), reptile from Franz et al. (2009), bird from Fritz et al. (2012)

Mean retention time



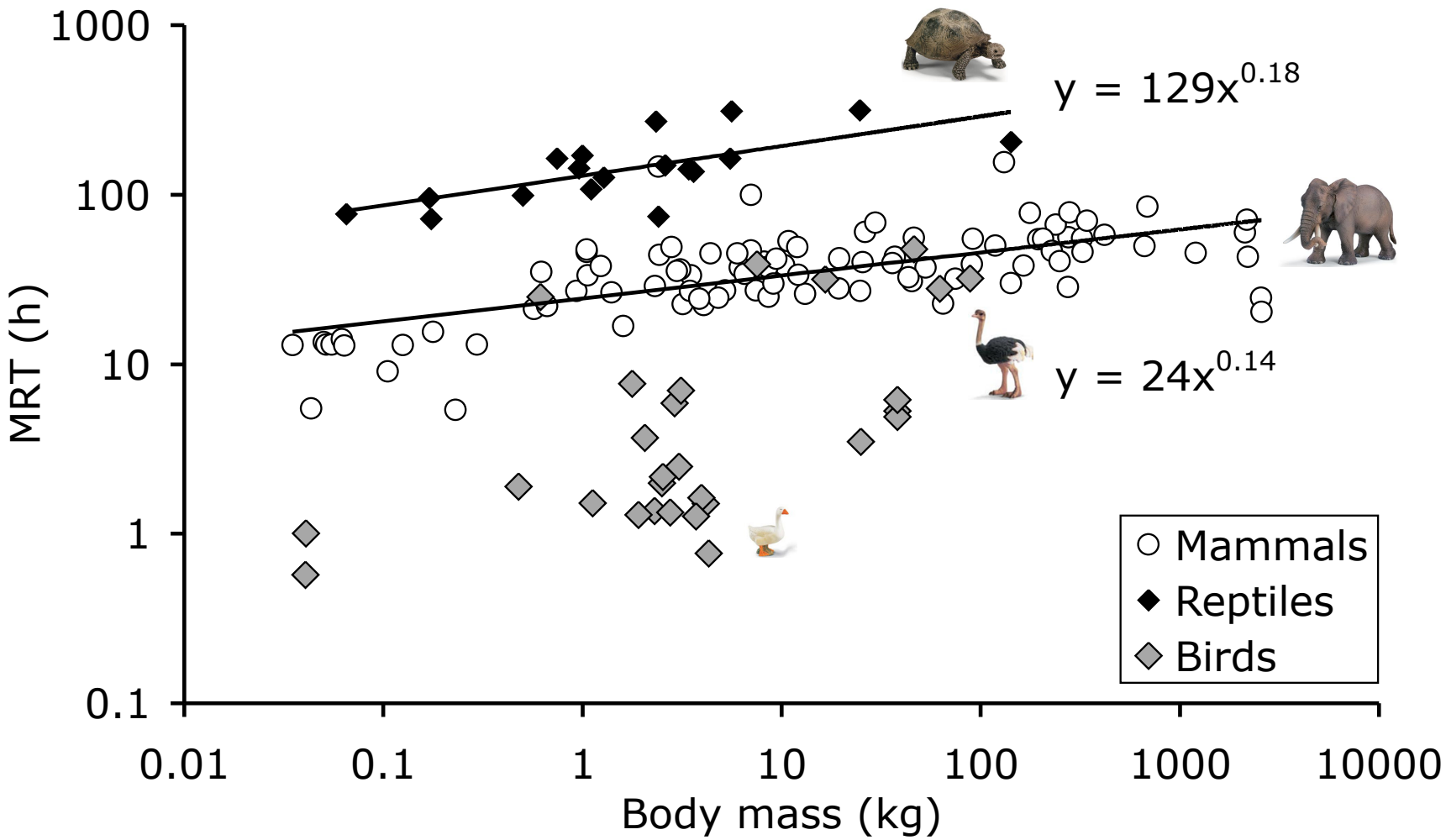
mammal data collection Clauss et al. (2007), reptile from Franz et al. (2009), bird from Fritz et al. (2012)

Mean retention time



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

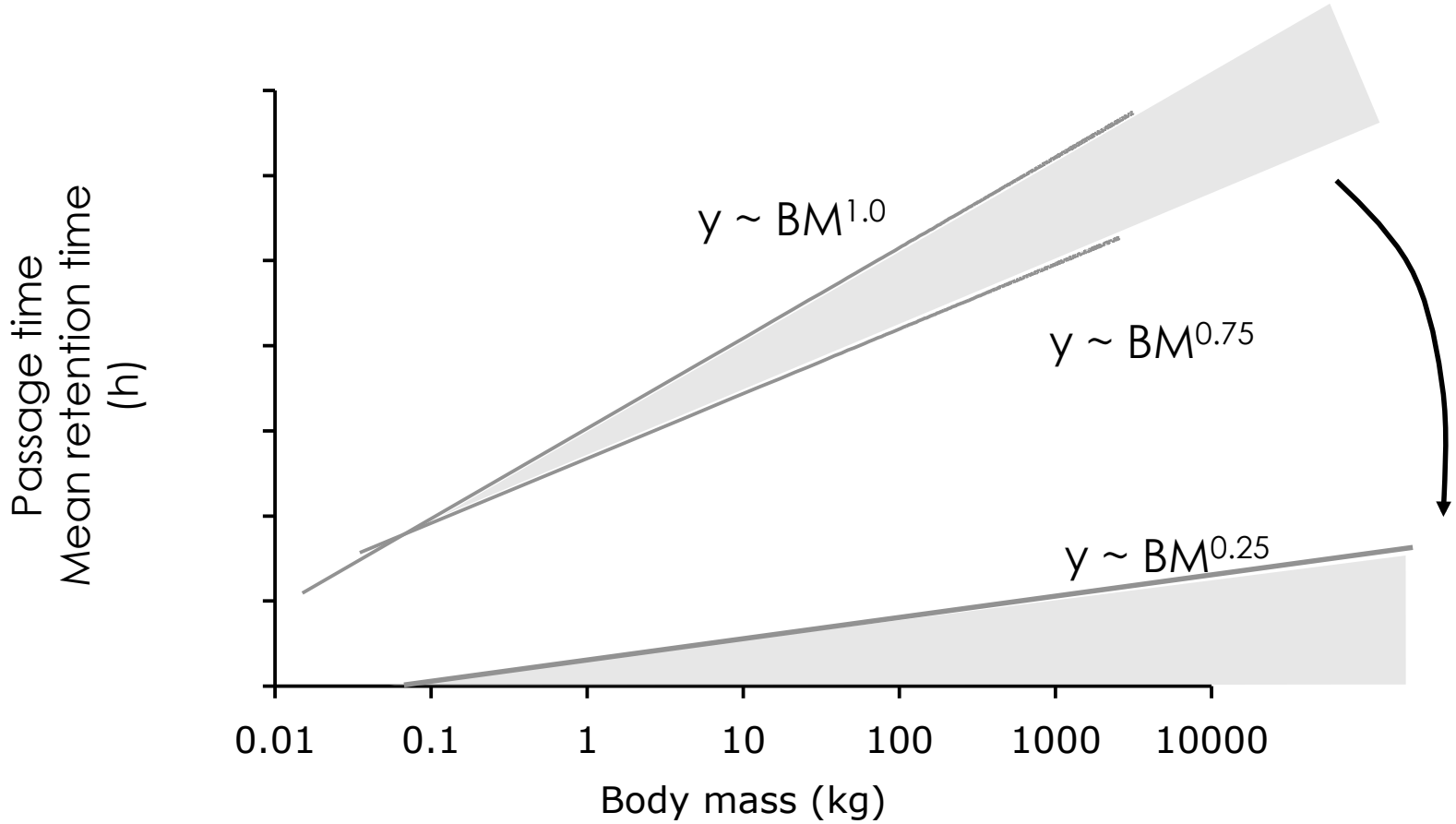
Mean retention time



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

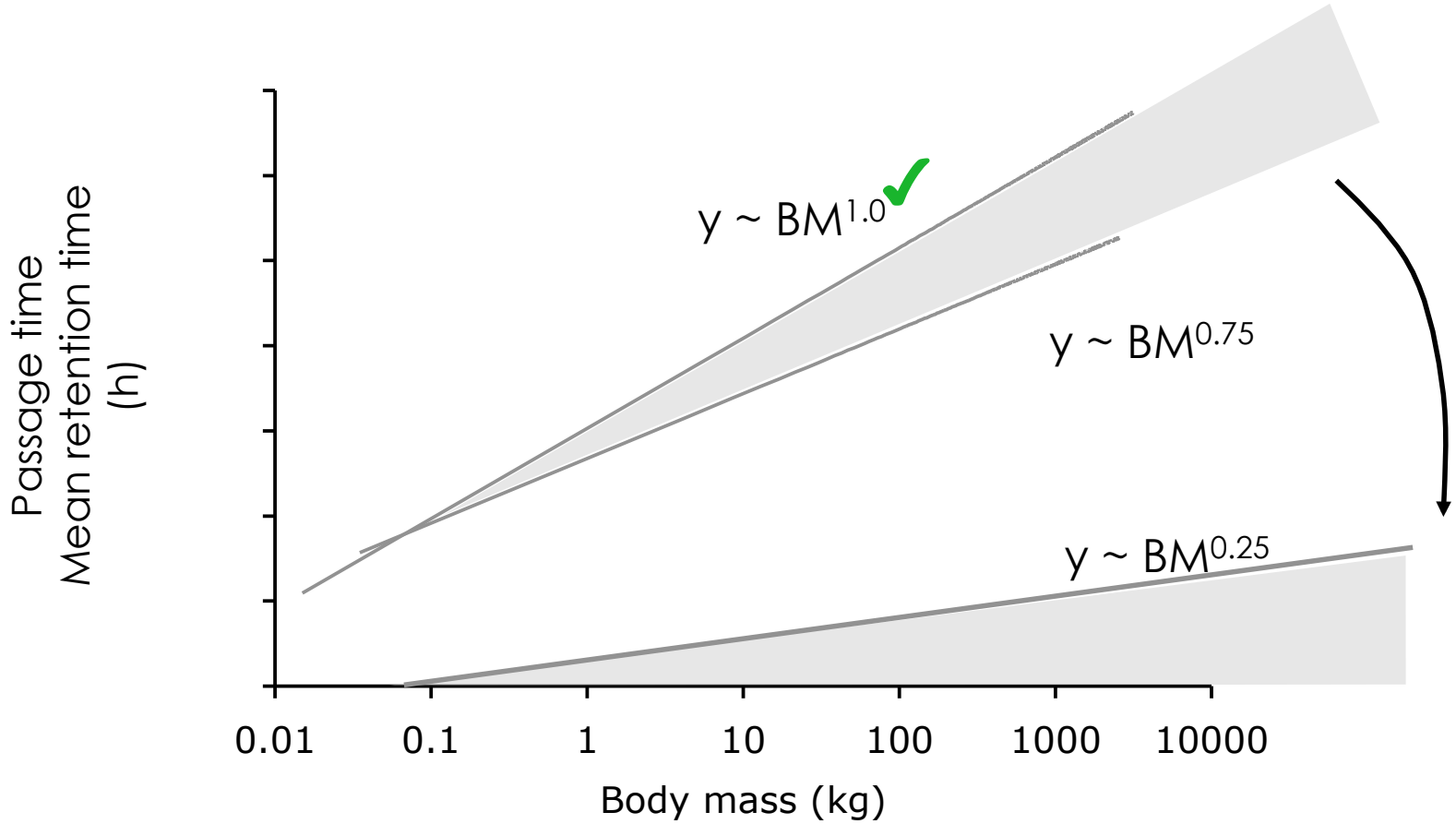
So what now?

General allometric considerations



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

General allometric considerations



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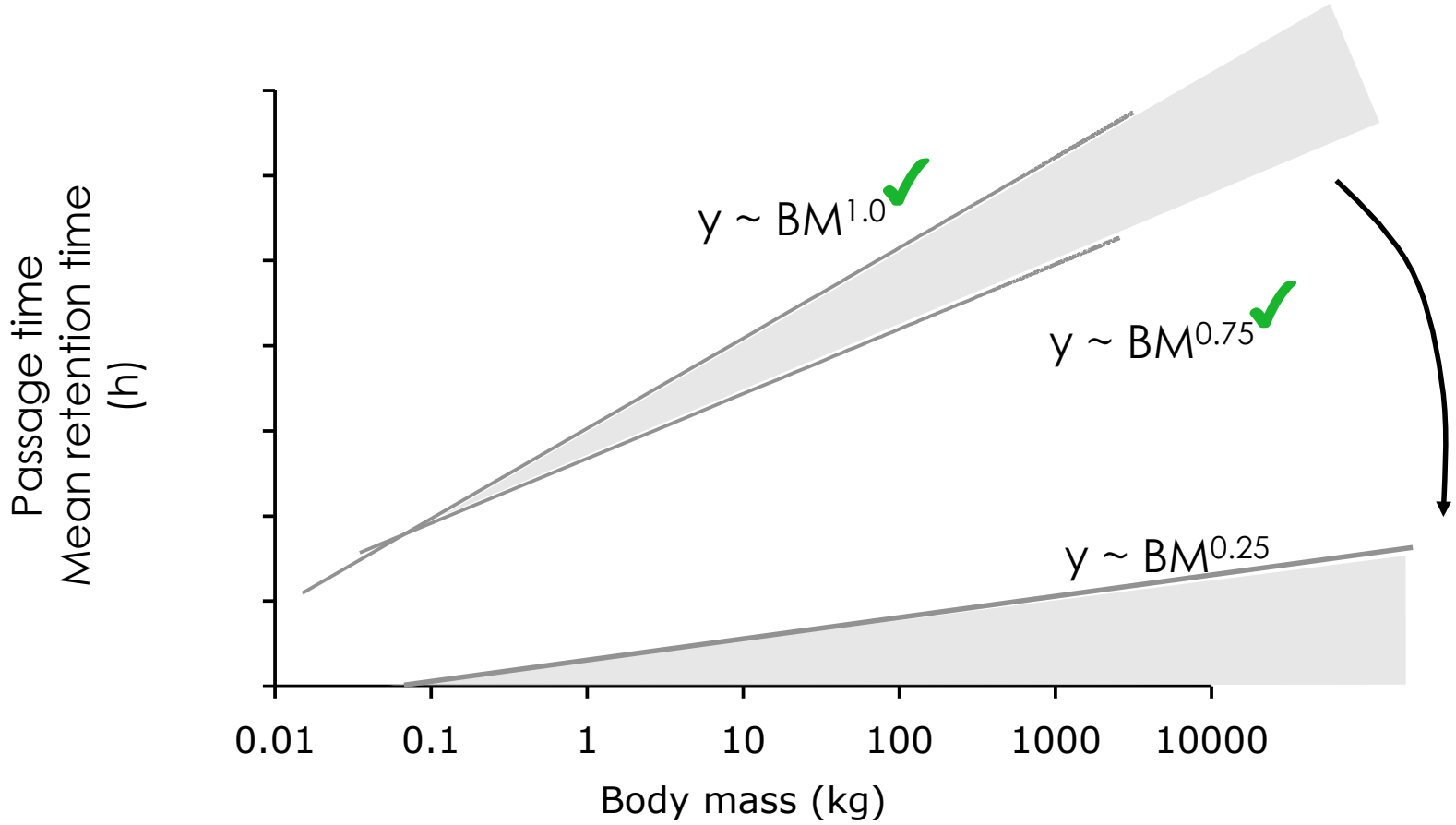
General allometric considerations



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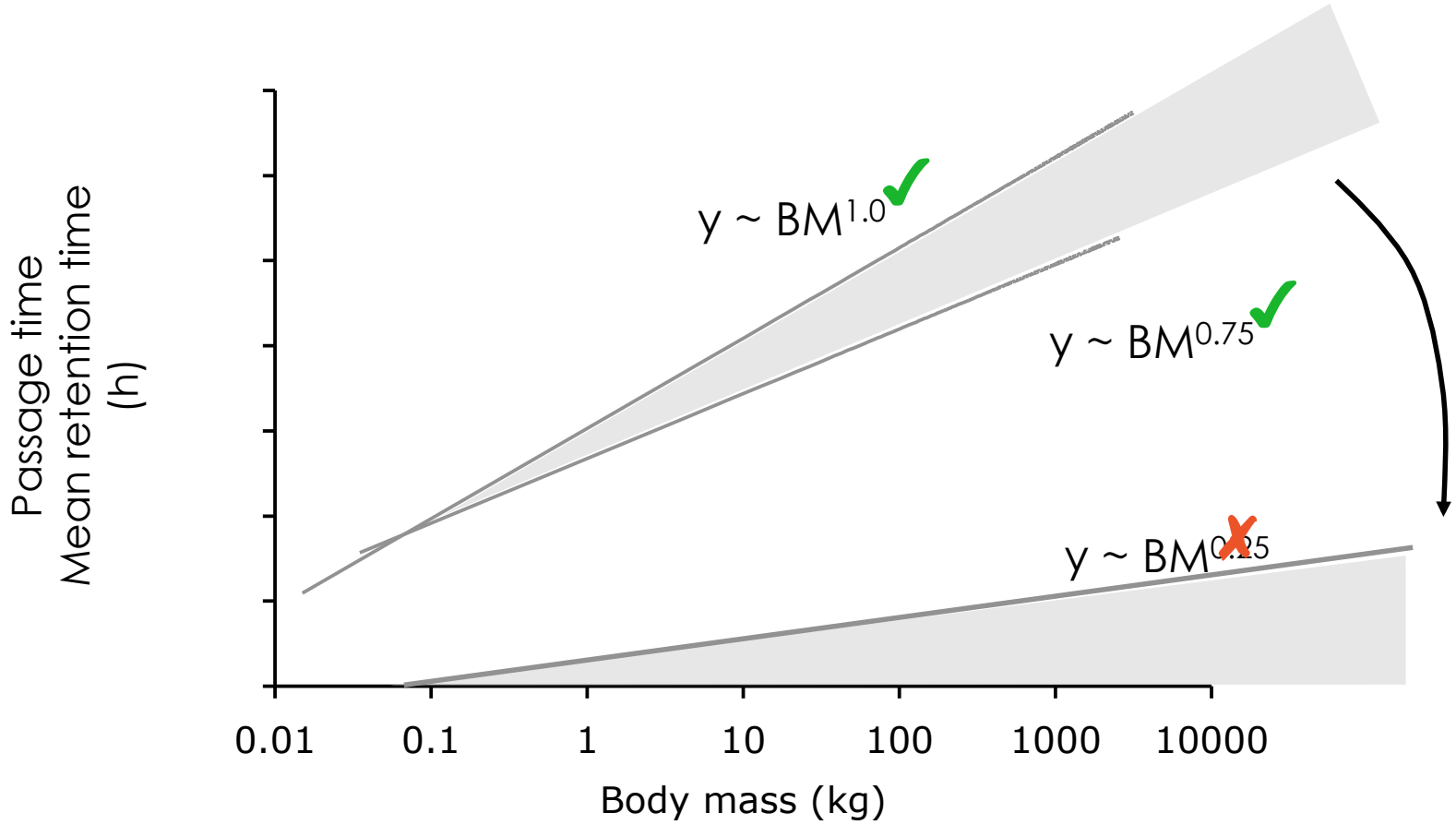
General allometric considerations



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

A serious problem

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

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

Using a single dataset

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

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

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

D. F. HOLLEMAN AND R. G. WHITE

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

Received May 11, 1987

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

A method is given for analyzing particulate digestive marker data in terms of digesta fill, fecal output, and digesta passage times. The method applies the Stewart–Hamilton Principle to data obtained from a single marker dosing followed by feces sampling; it assumes steady-state conditions for the digesta, but makes no assumptions concerning compartmentalization of digesta. Data analyses are presented for an experiment with sheep in which a particle phase marker, cerium-141 chloride, was used. The estimate of fecal output obtained was 1.8 ± 2.2% (mean percent difference ± SE) greater than the actual fecal output; the *in vivo* estimate of total digesta fill was 3.3 ± 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.

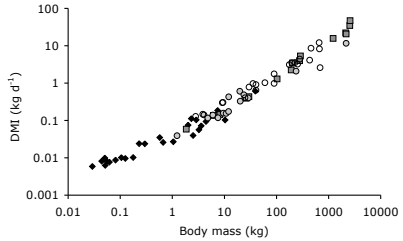
Using a single dataset

Measurement	Scaling (95%CI)

from Müller et al. (2013)

Using a single dataset

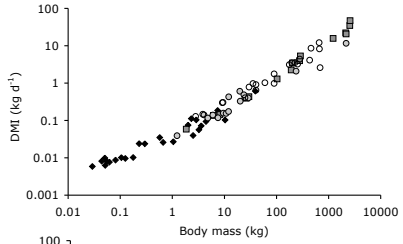
Measurement	Scaling (95%CI)
Dry matter intake	0.76 (0.73-0.79)

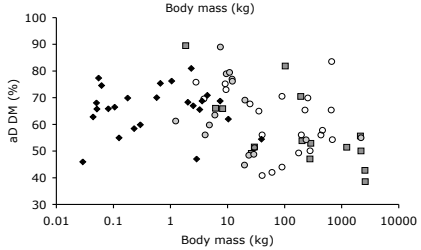


from Müller et al. (2013)

Using a single dataset

Measurement	Scaling (95%CI)
Dry matter intake	0.76 (0.73-0.79)
Digestibility	-0.03 (-0.04--0.01)





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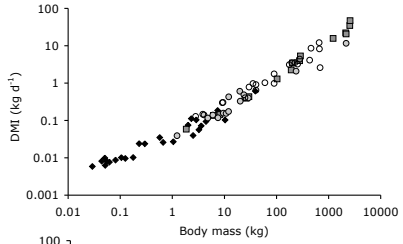
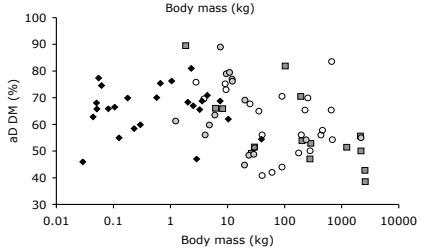
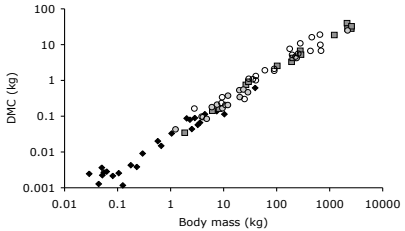
Using a single dataset

Measurement	Scaling (95%CI)
Dry matter intake	0.76 (0.73-0.79)
Digestibility	-0.03 (-0.04--0.01)
Dry matter gut fill	0.93 (0.90-0.96)







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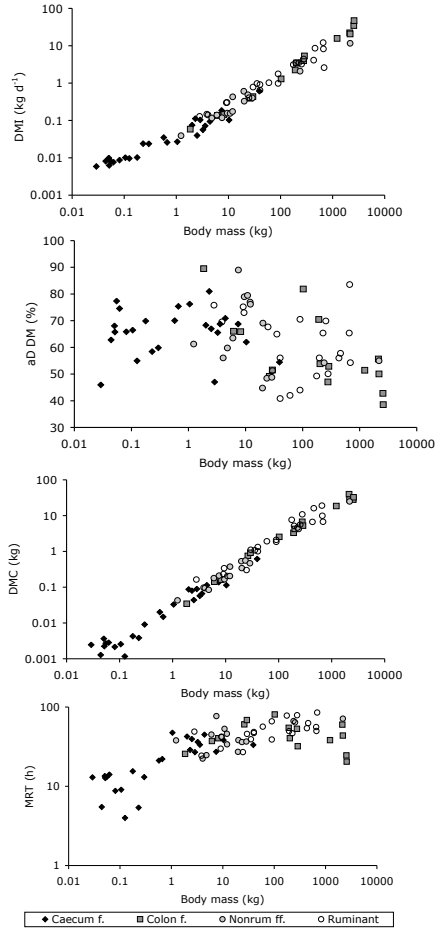
Using a single dataset

Measurement	Scaling (95%CI)
Dry matter intake	0.76 (0.73-0.79)
Digestibility	-0.03 (-0.04--0.01)
Dry matter gut fill	0.93 (0.90-0.96)
Particle retention time	0.16 (0.12-0.19)

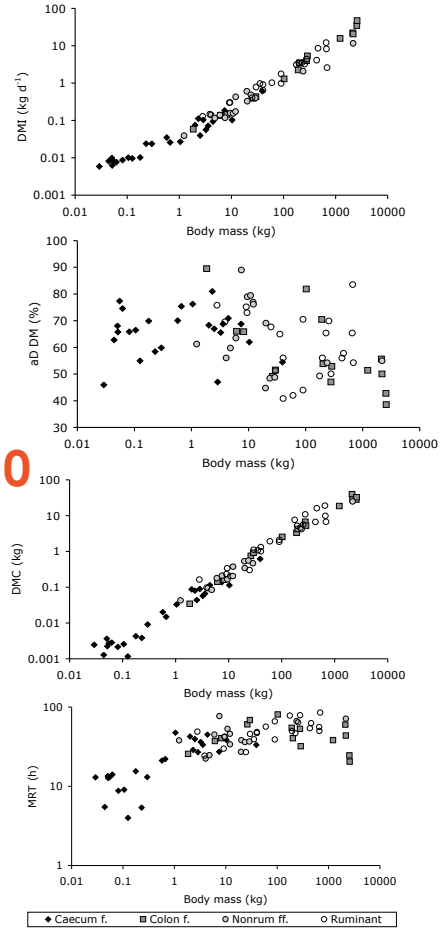


from Müller et al. (2013)

The *really real* exponents

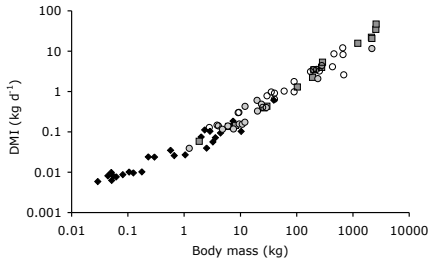
Measurement	Scaling (95%CI)
Dry matter intake	0.76 (0.73-0.79)
Digestibility	-0.03 (-0.04--0.01)
Dry matter gut fill	0.93 (0.90-0.96)
Particle retention time	0.16 (0.12-0.19)

not 1.0

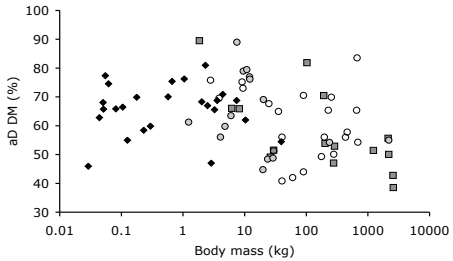


from Müller et al. (2013)

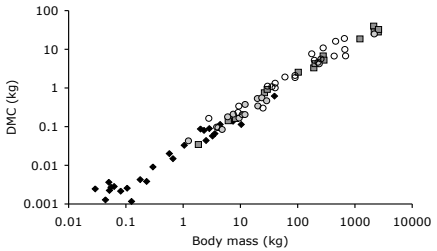
The curvature in herbivore digestive physiology



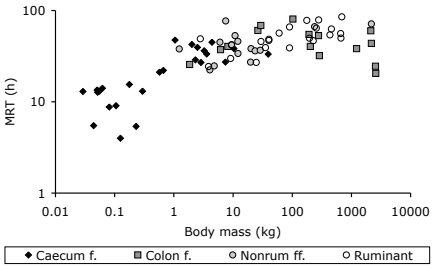
Dry matter intake



Digestibility



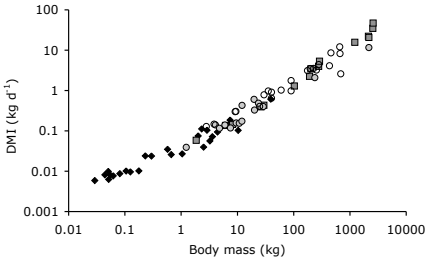
Dry matter gut content



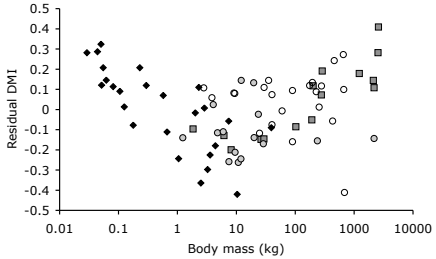
Particle retention time

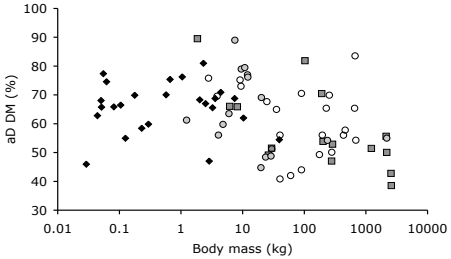
from Müller et al. (2013)

The curvature in herbivore digestive physiology - plotting residuals

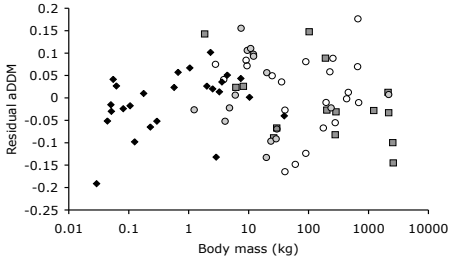


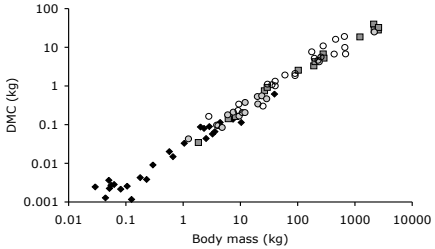
Dry matter intake



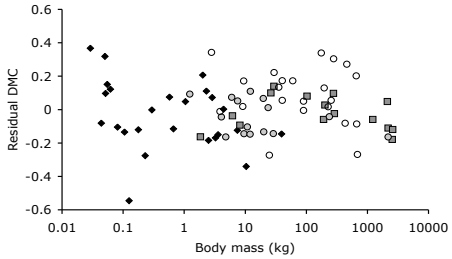


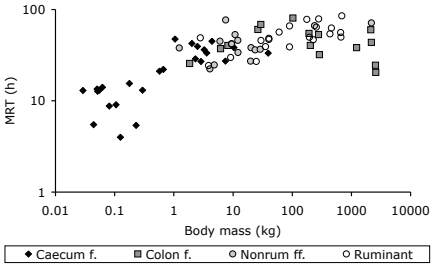
Digestibility



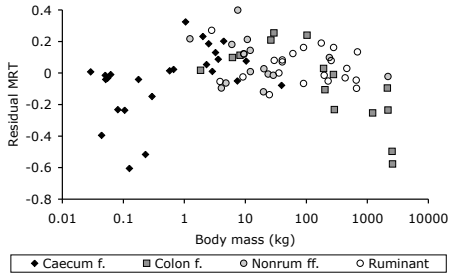


Dry matter gut content





Particle retention time



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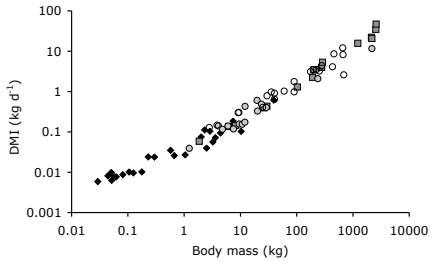
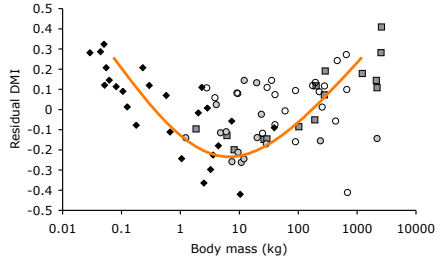
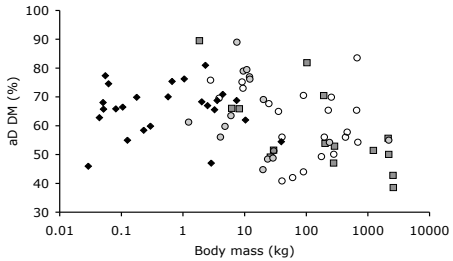
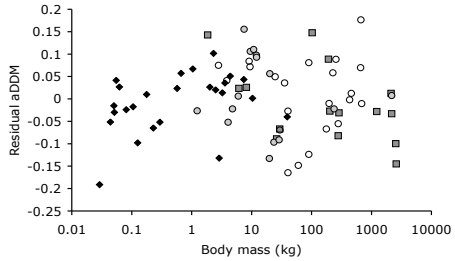


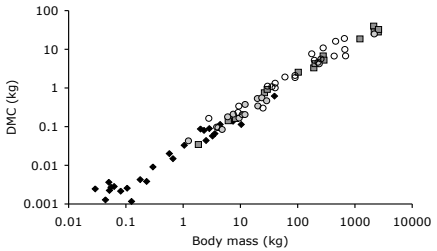
Dry matter intake



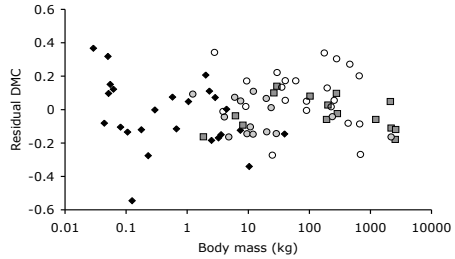


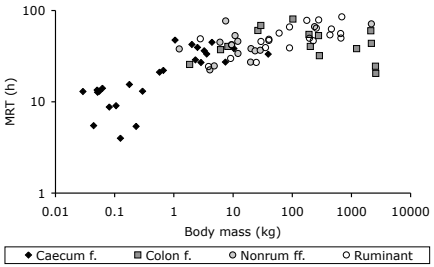
Digestibility



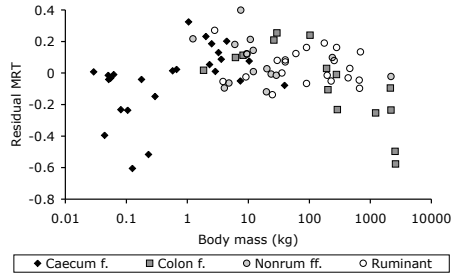


Dry matter gut content





Particle retention time



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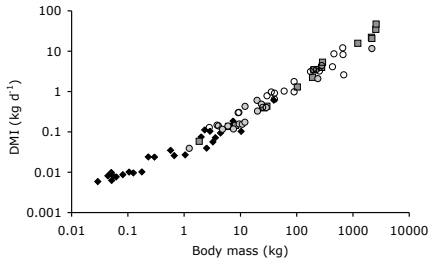

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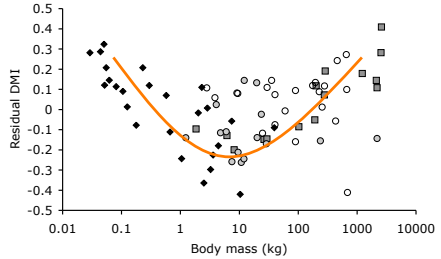

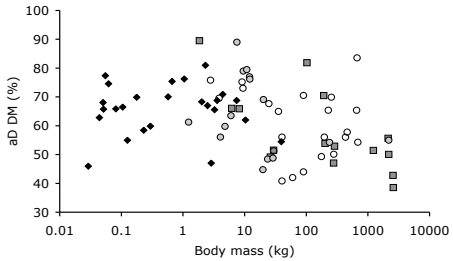

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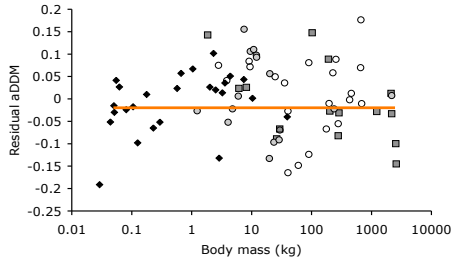

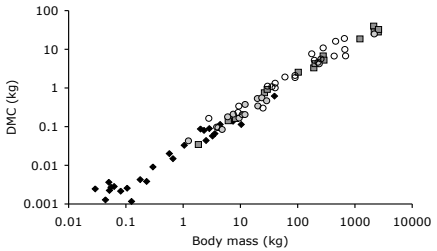

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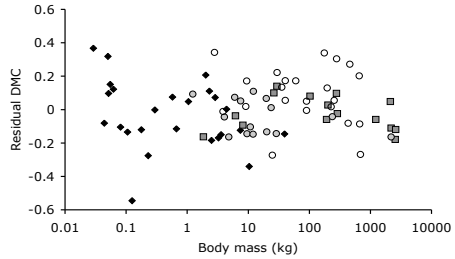

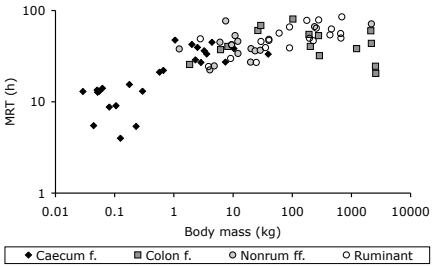

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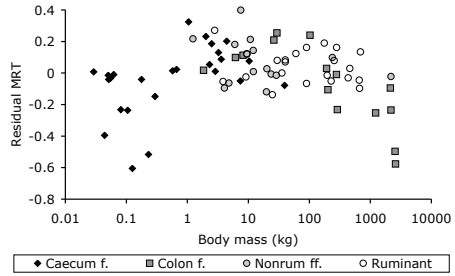

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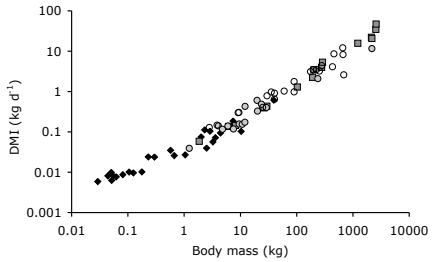

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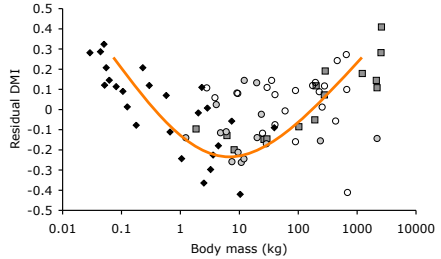

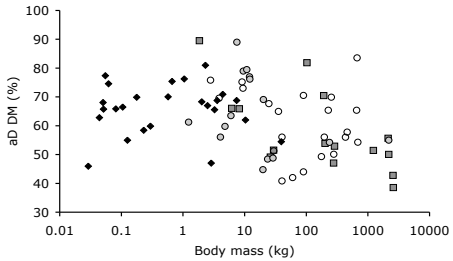

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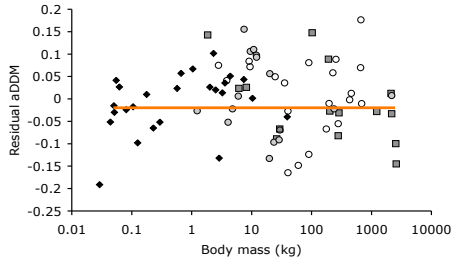

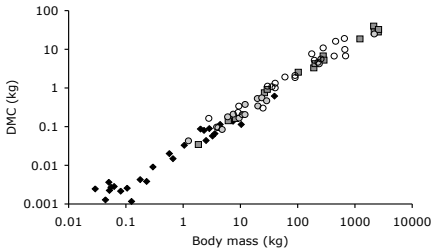

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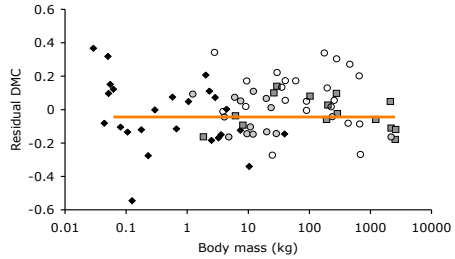
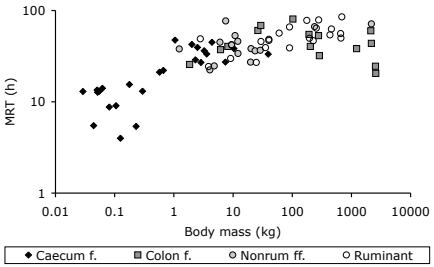
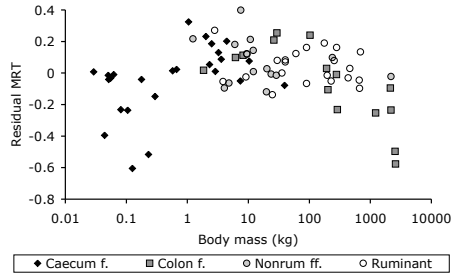




Particle retention time



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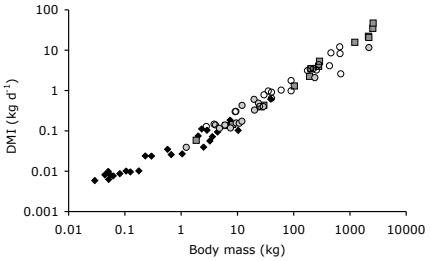
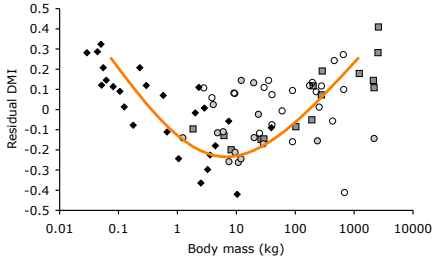
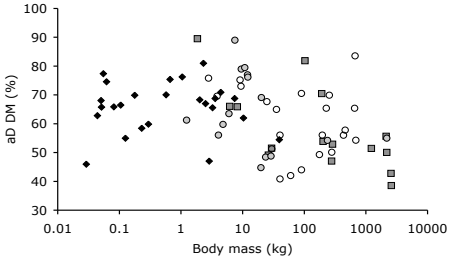
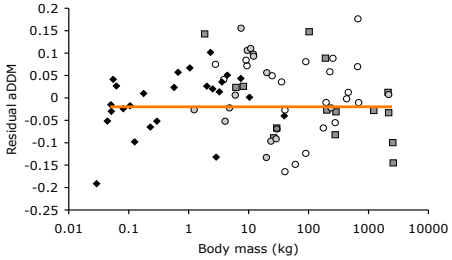


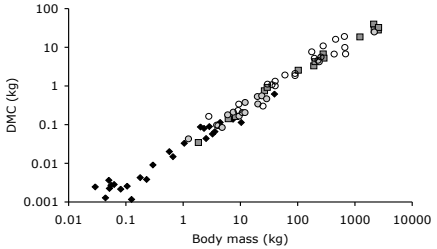
Dry matter intake



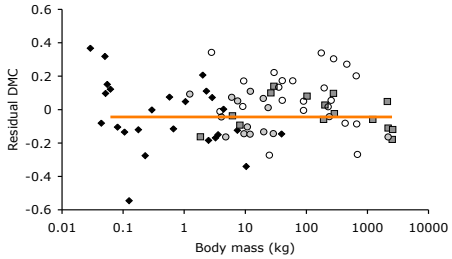


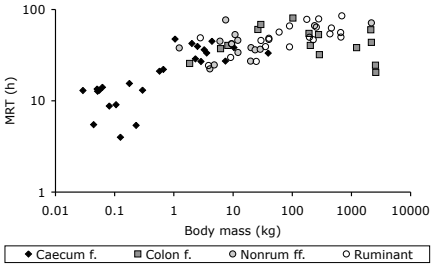
Digestibility



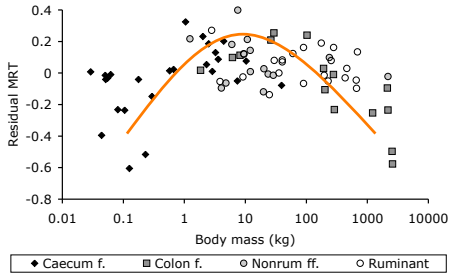


Dry matter gut content





Particle retention time



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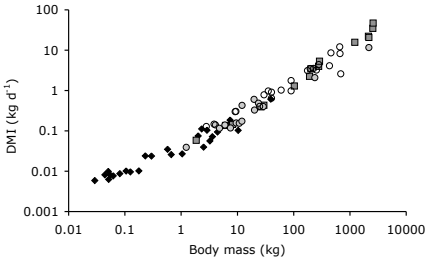
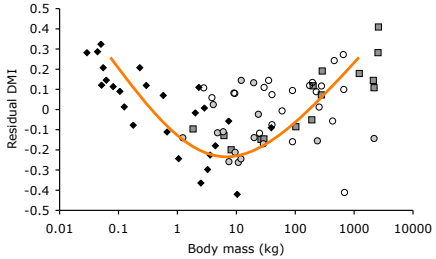
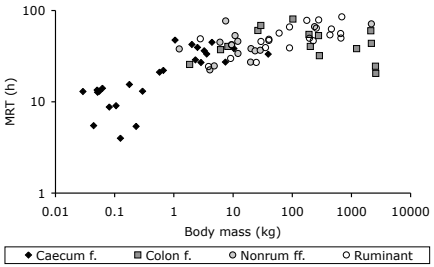


Dry matter intake



corresponding inverse curvatures



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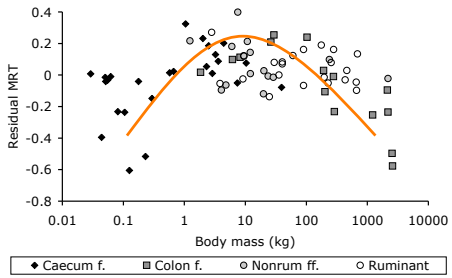

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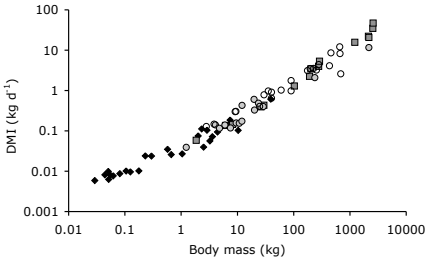

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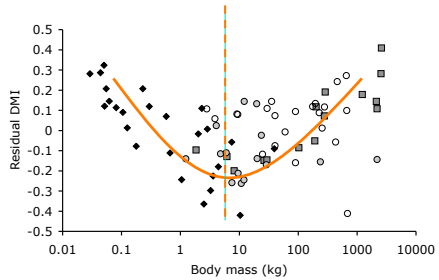

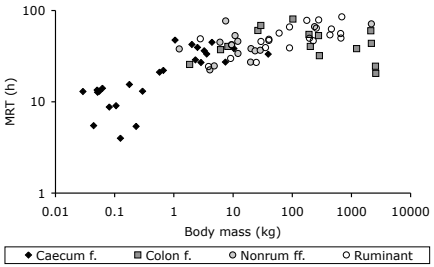

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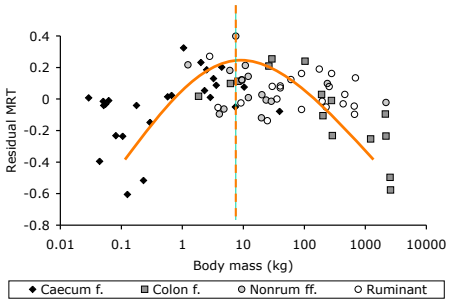

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The *really real* exponents

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)
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Checking the validity of a concept

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

(vary sequence to suit your preference or intellectual capacity)

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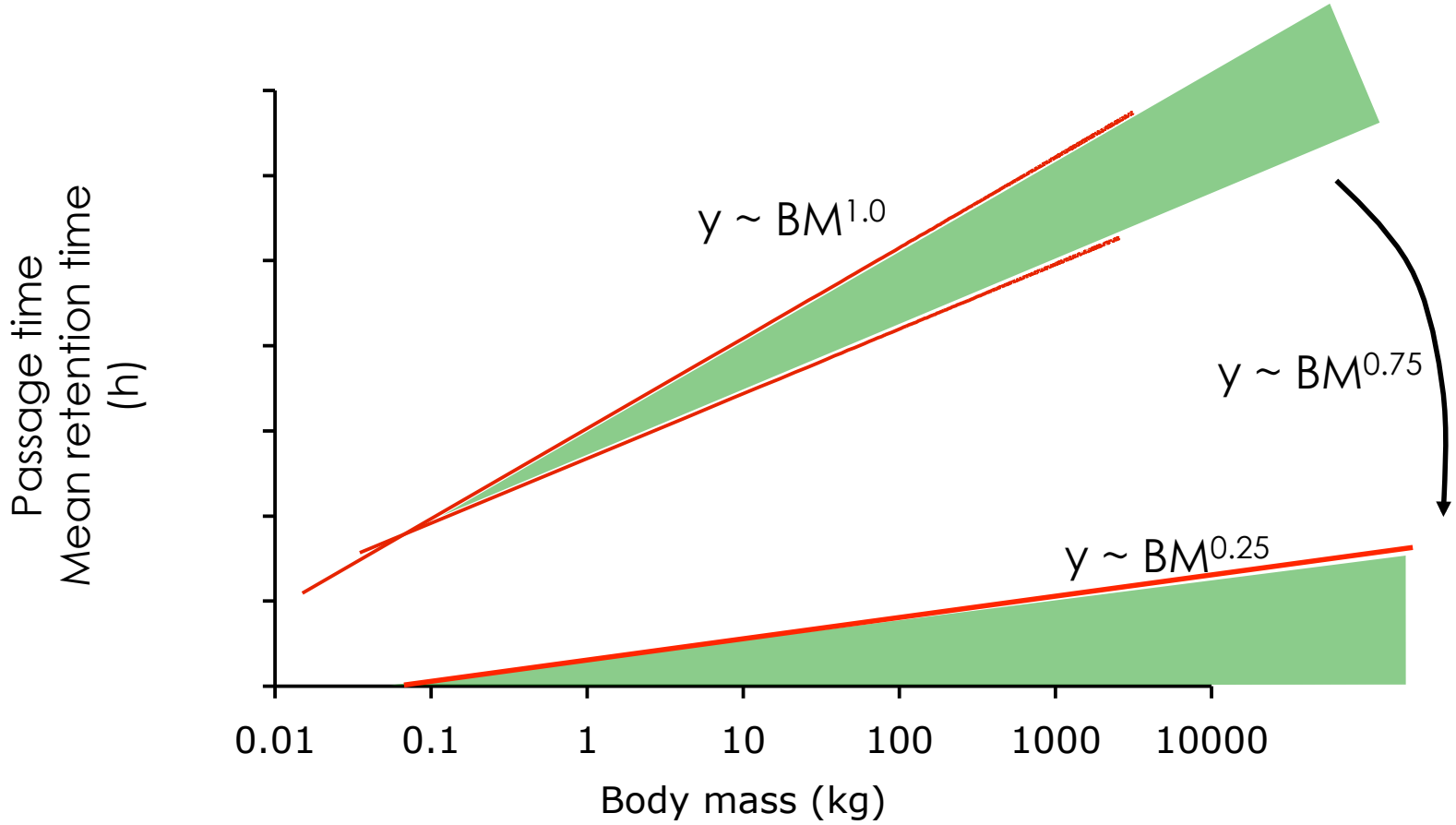
Circular reasoning



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

A logical flaw

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

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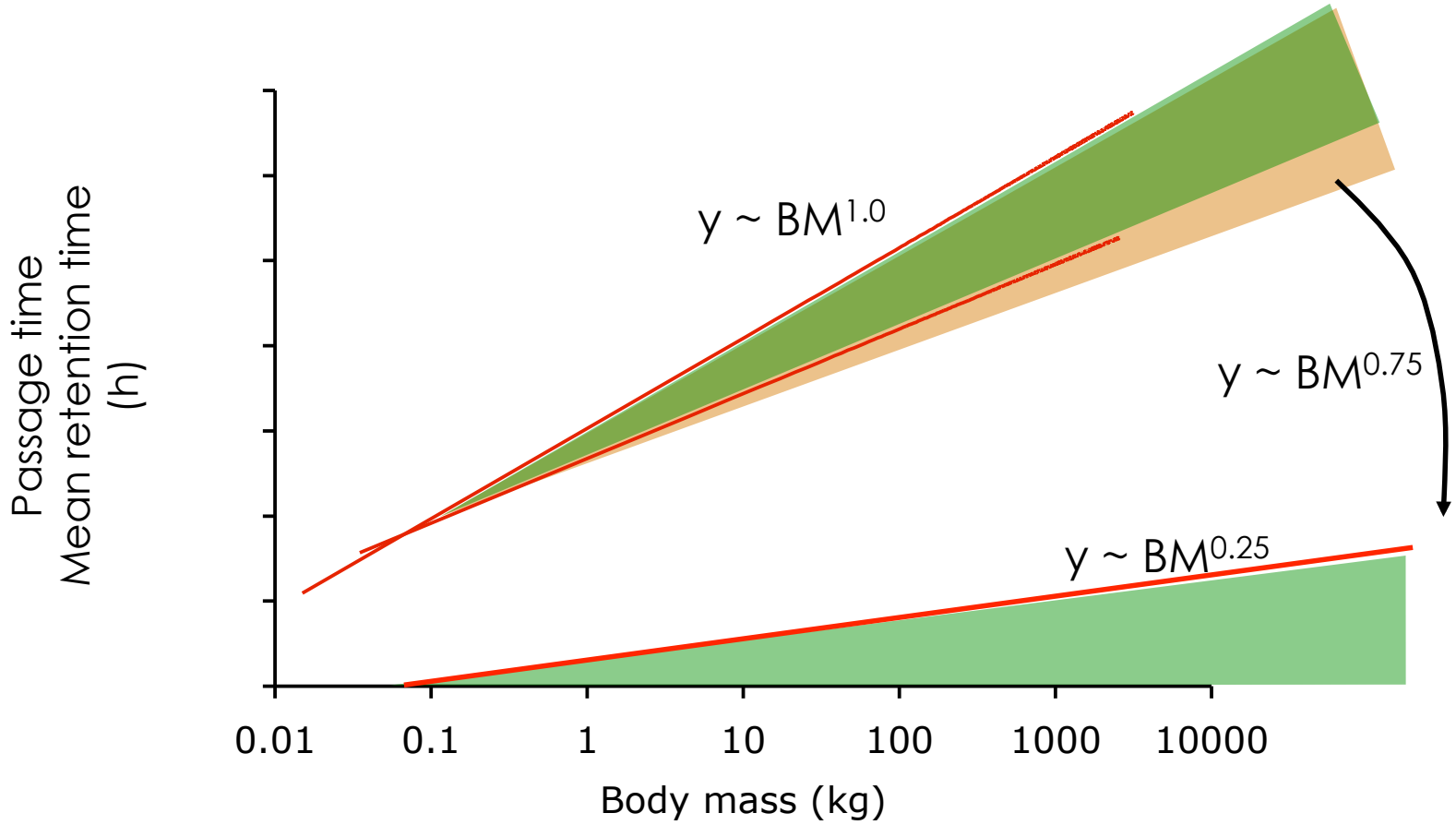
Digesta retention then scales to $BM^d = BM^{(a-b+c)}$

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

Circular reasoning



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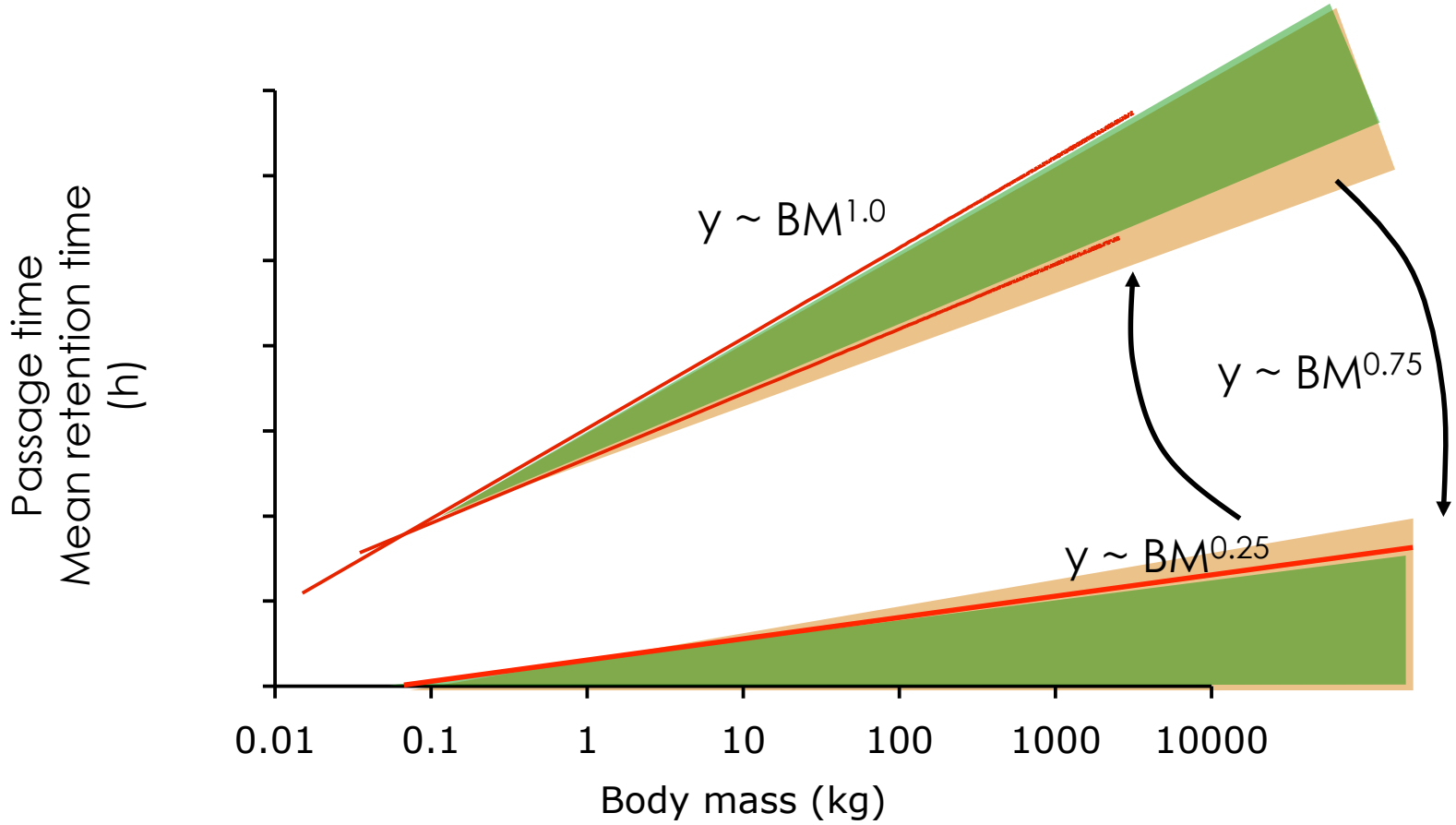

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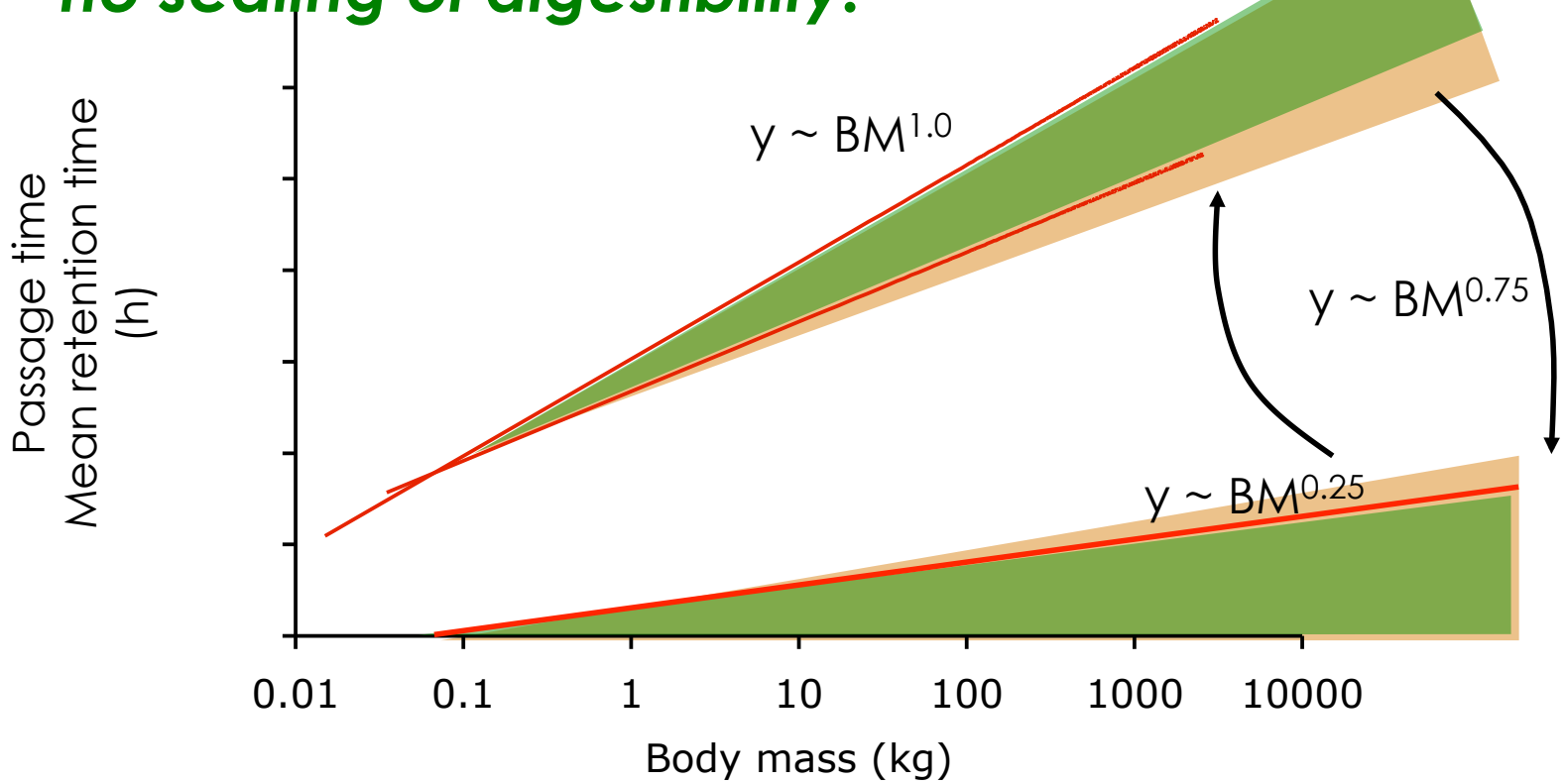
Circular reasoning

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



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

(vary sequence to suit your preference or intellectual capacity)

Checking the validity of a concept

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

(vary sequence to suit your preference or intellectual capacity)

Conceptual problems

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

Conceptual problems

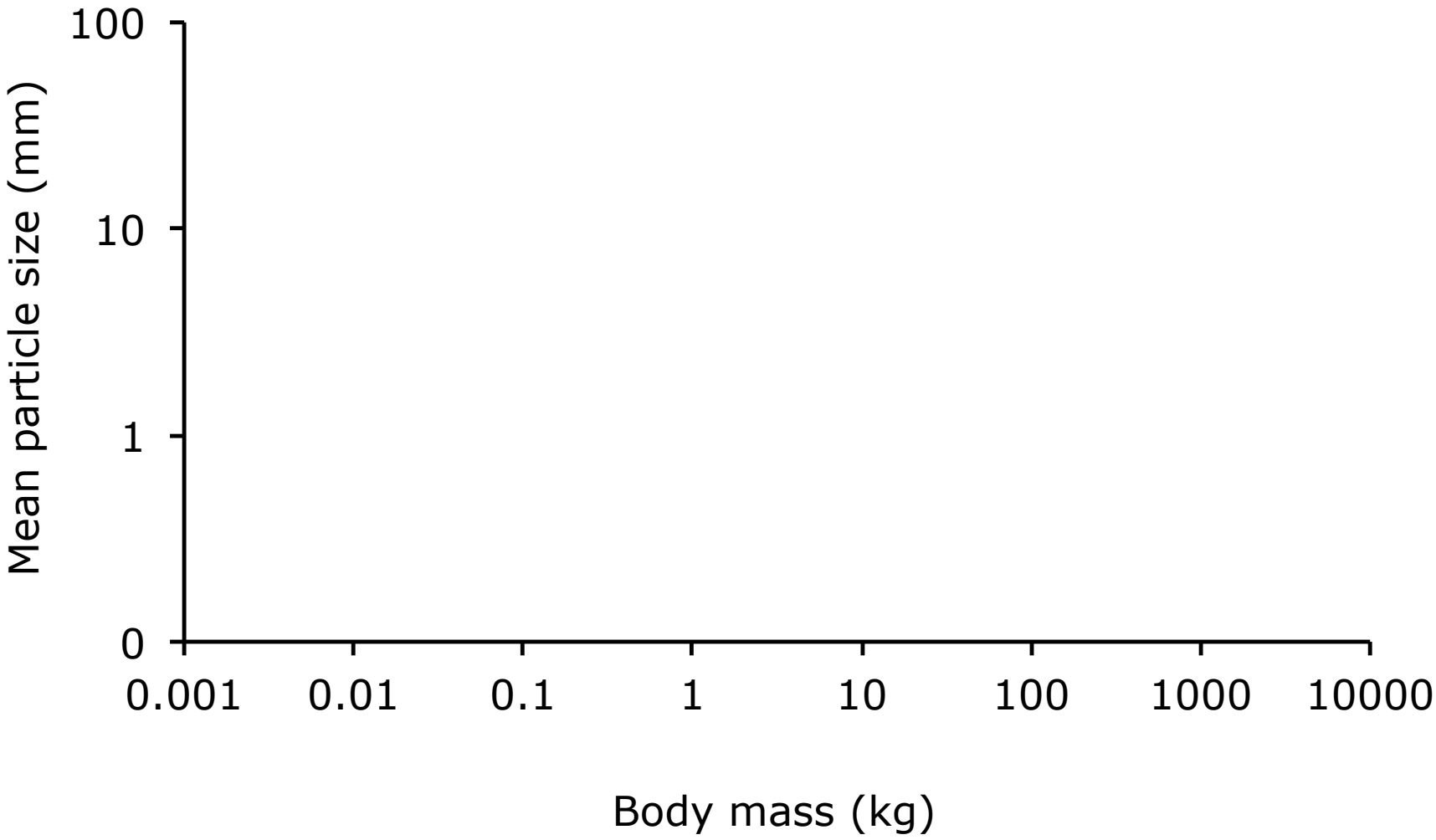
2. What about other, potential digestive ***disadvantages*** linked to larger body size – such as

   - digesta particle size

   - methane losses

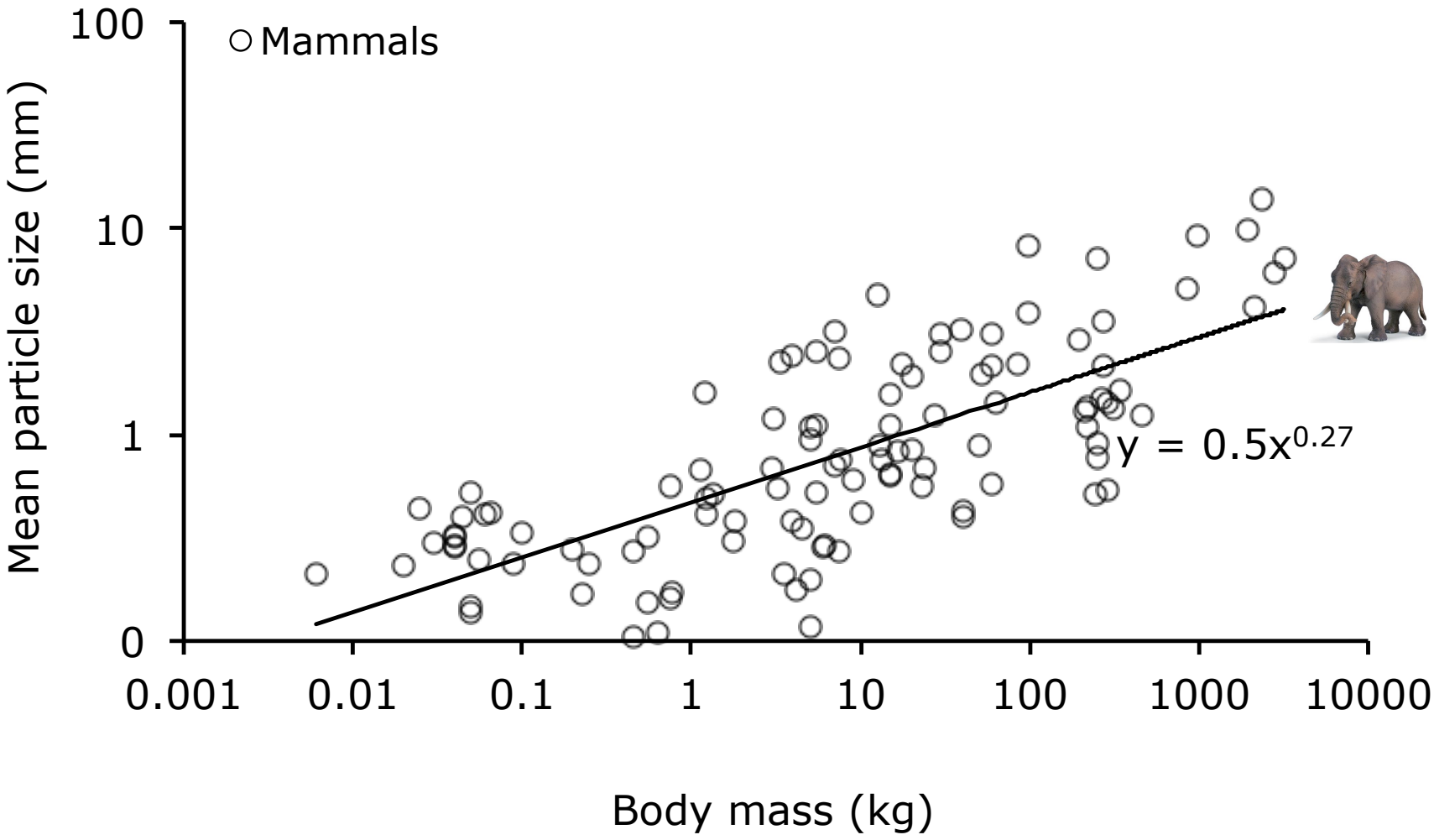
Particle size

Faecal particle size allometry in herbivores



(Fritz et al. 209, 2010, 2011)

Faecal particle size allometry in herbivores



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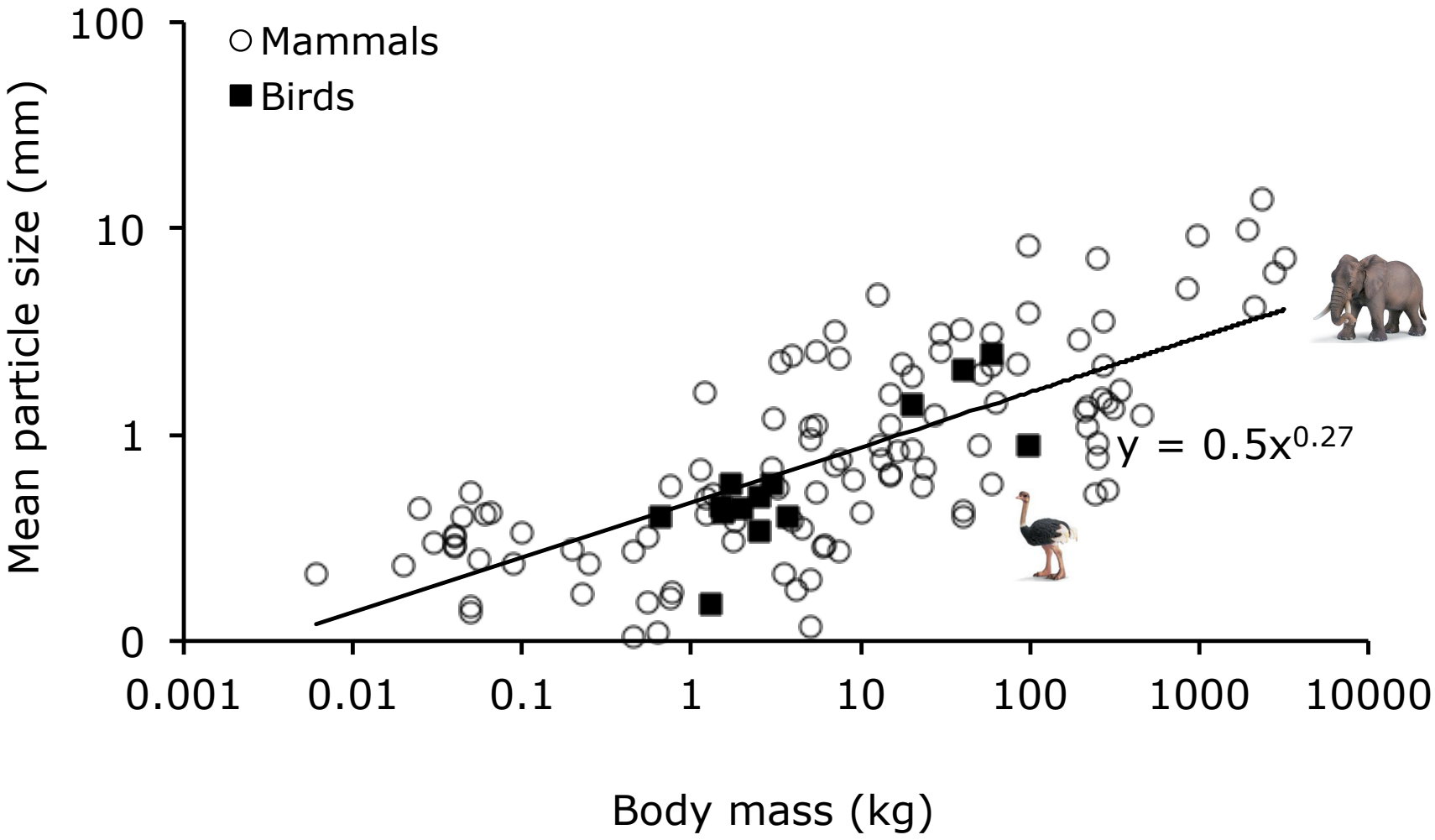

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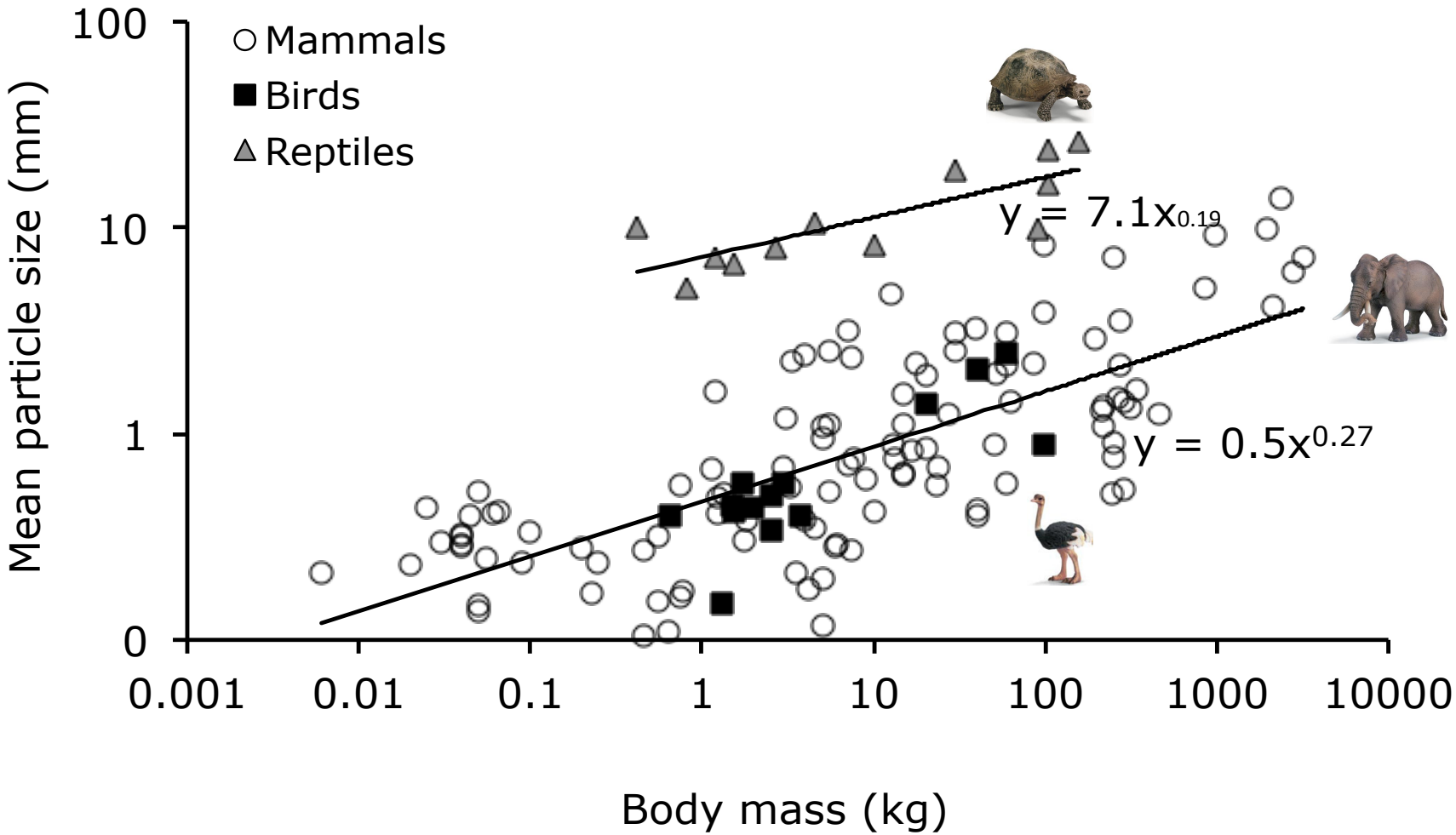

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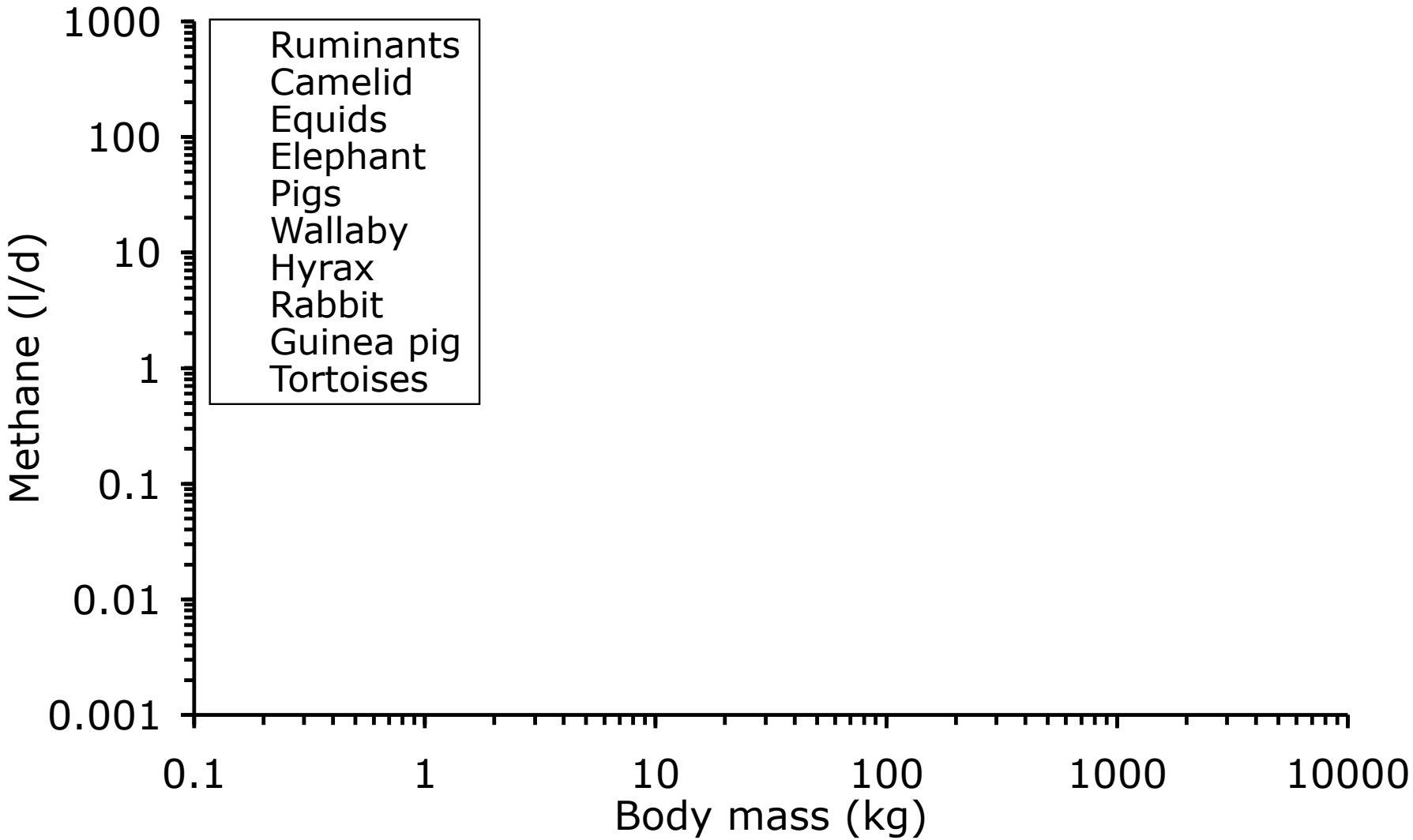
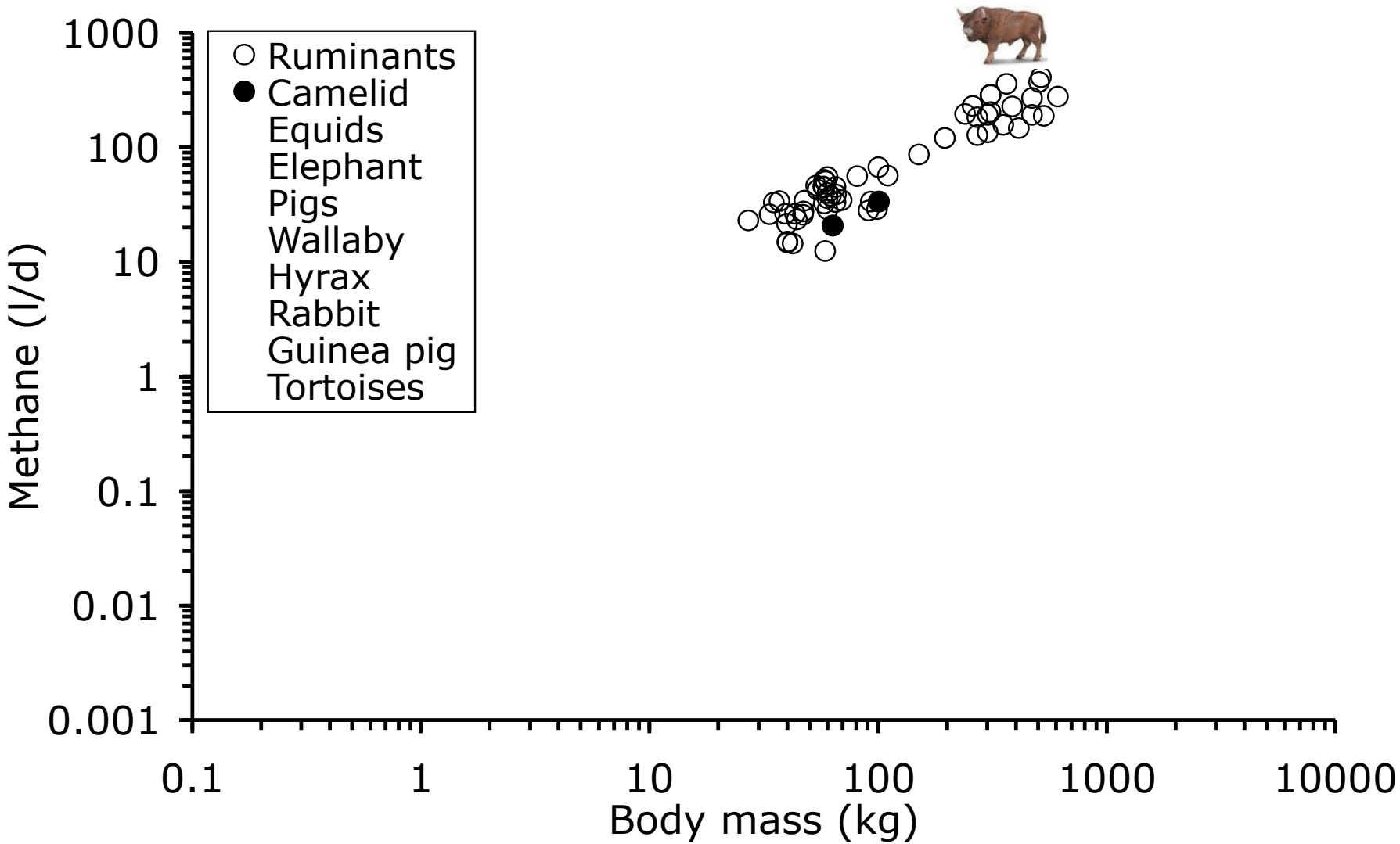
Methane

Methane allometry in herbivores



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

Methane allometry in herbivores



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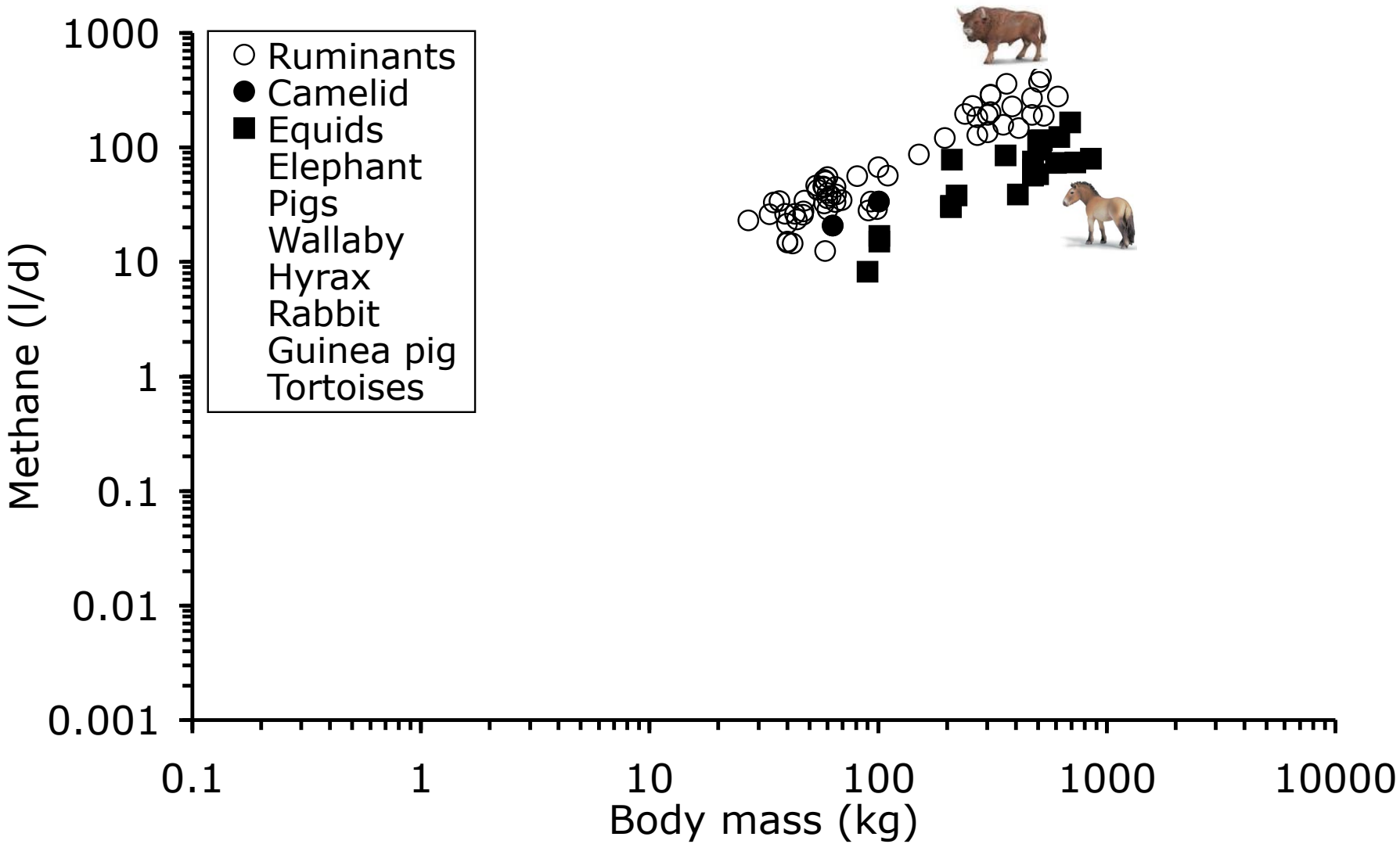

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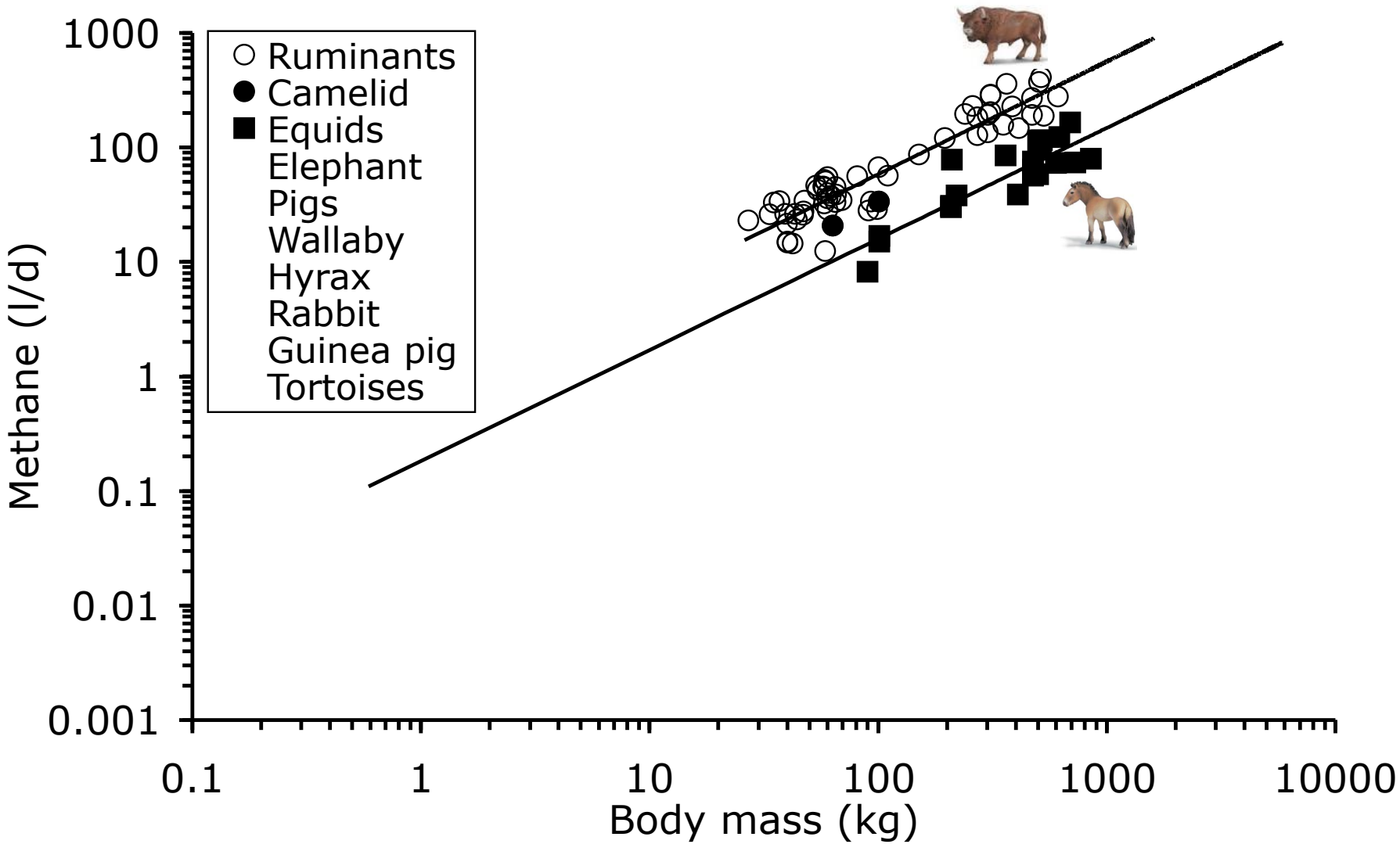

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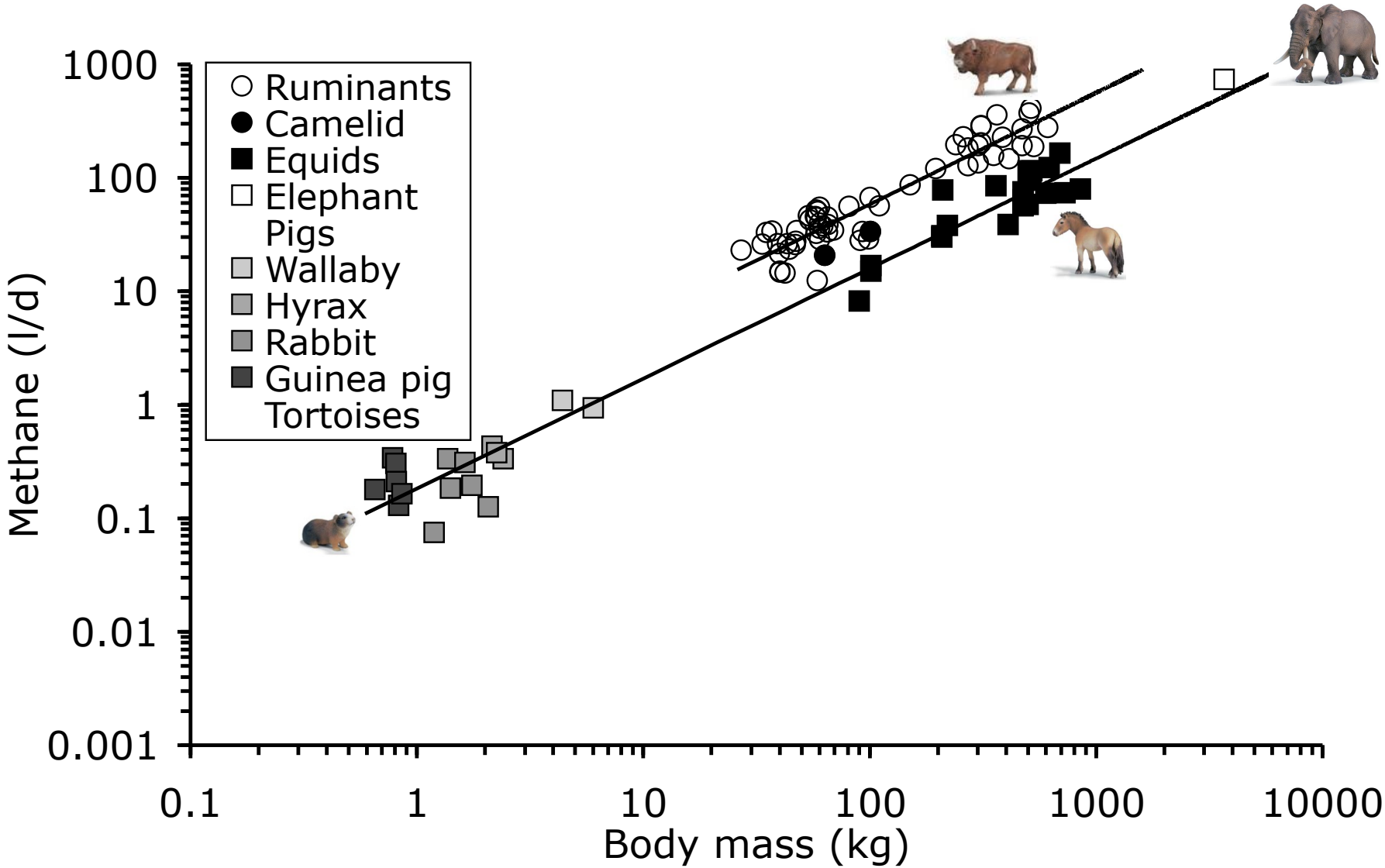

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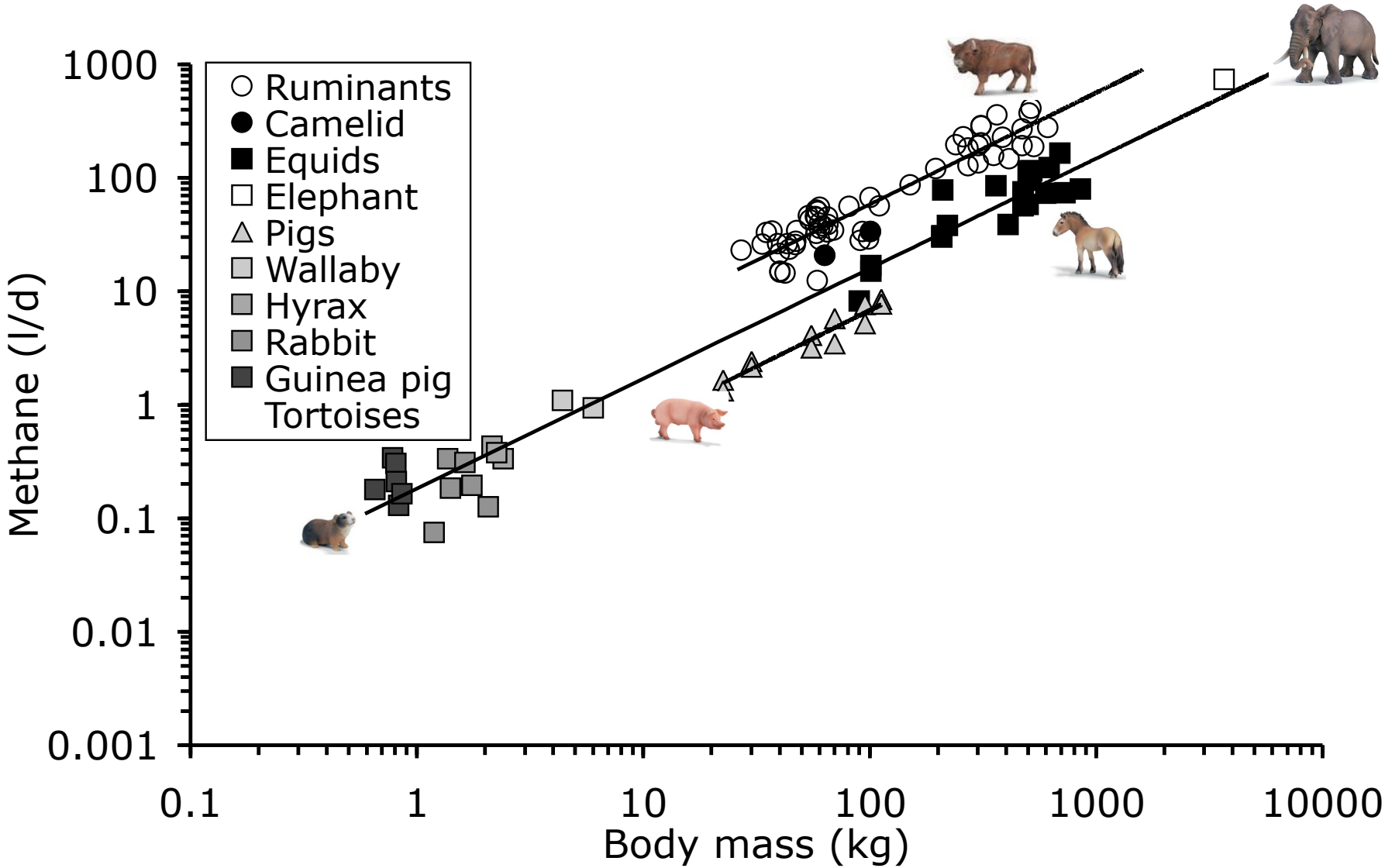
Methane allometry in herbivores



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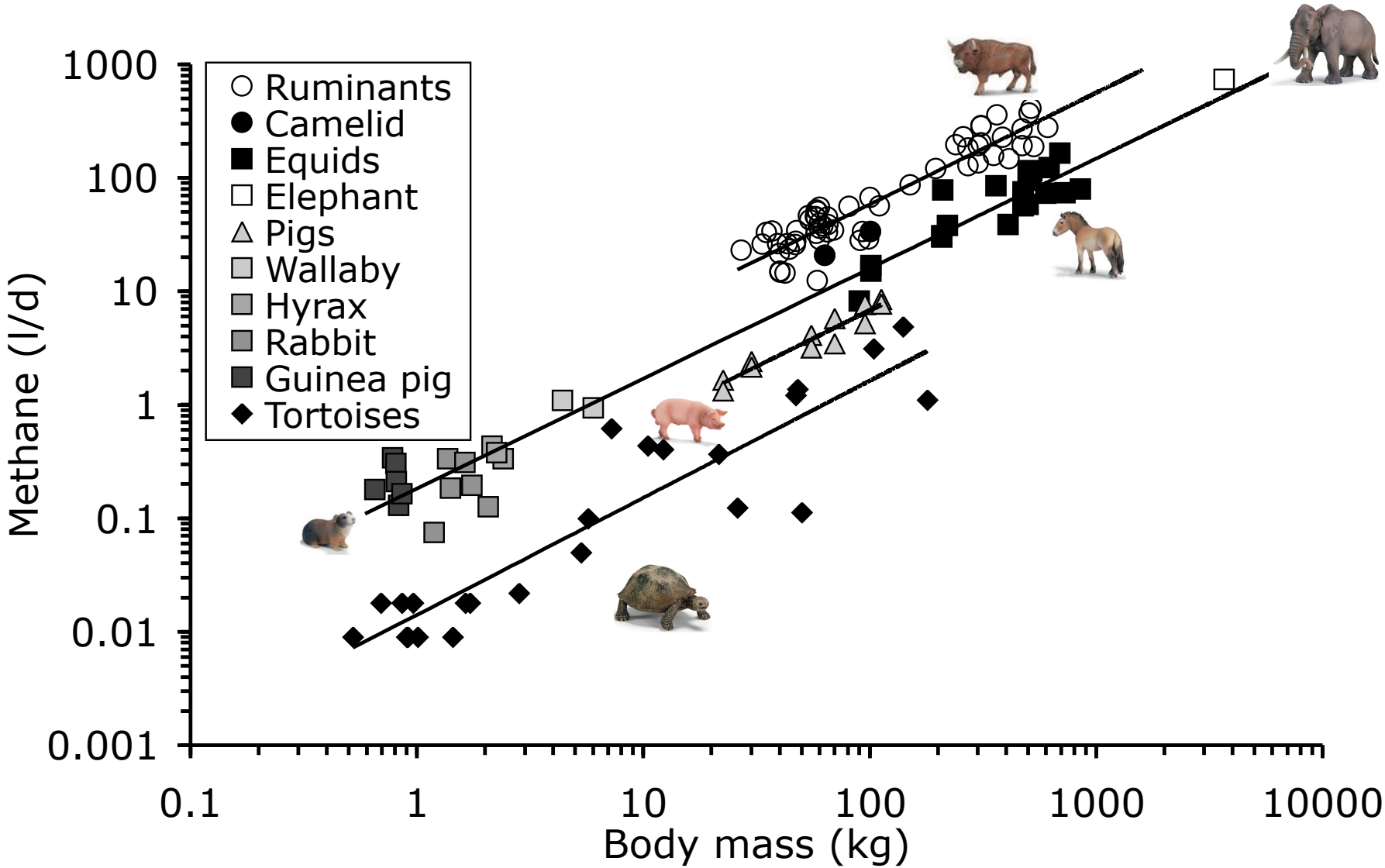
Methane allometry in herbivores



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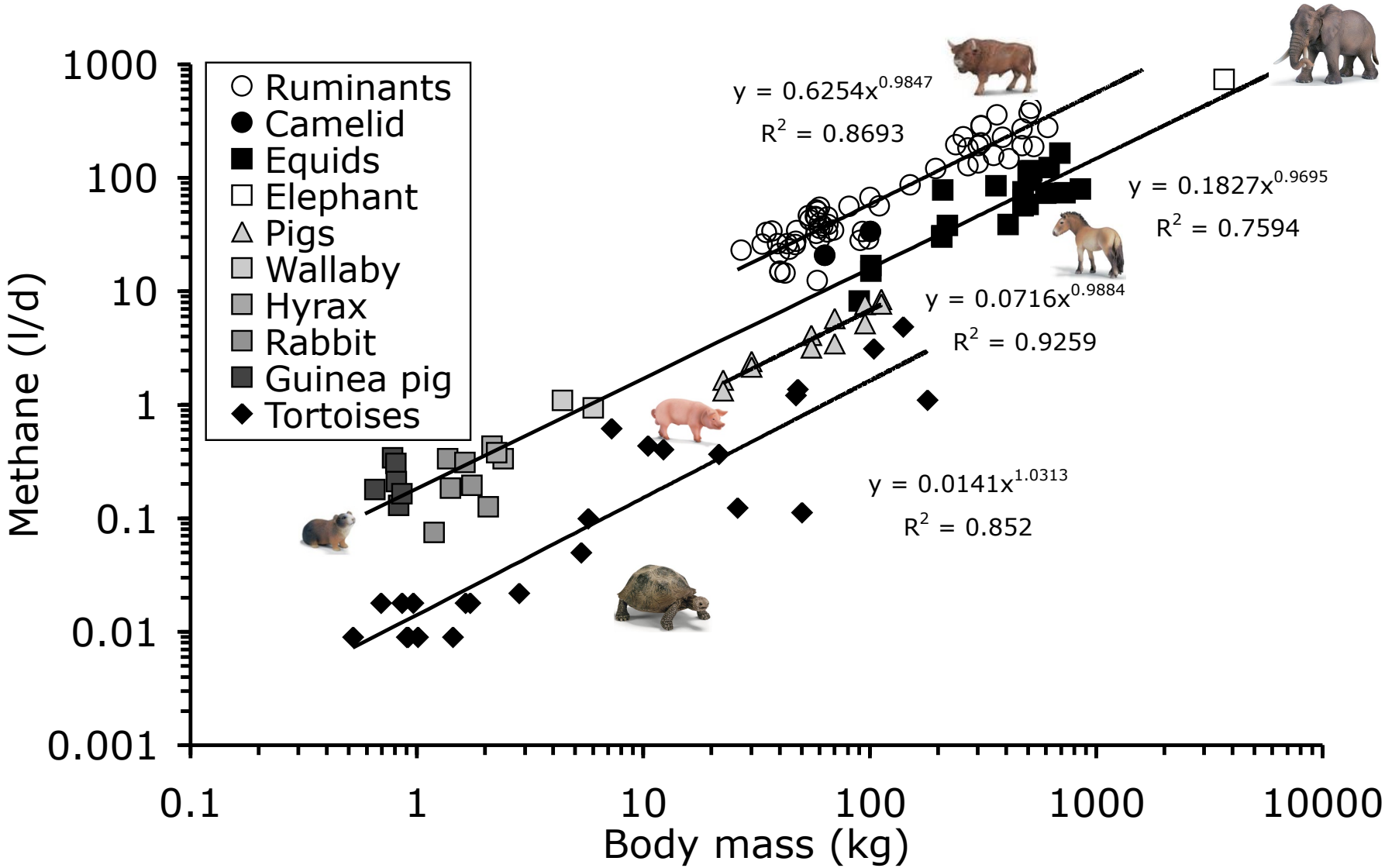

Literature collection and own data (Franz et al. 2010, 2011ab)

Conceptual problems

2. What about other, potential digestive disadvantages linked to larger body size – such as

   - digesta particle size **– less with higher BM**

   - methane losses **– more with higher BM**

Jarman-Bell: solution

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

Jarman-Bell: solution

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

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

Jarman-Bell: solution

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

   a) if intake scales as requirements, then digestive efficiency must increase ***– not in accord with other concepts and empirical data!***

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

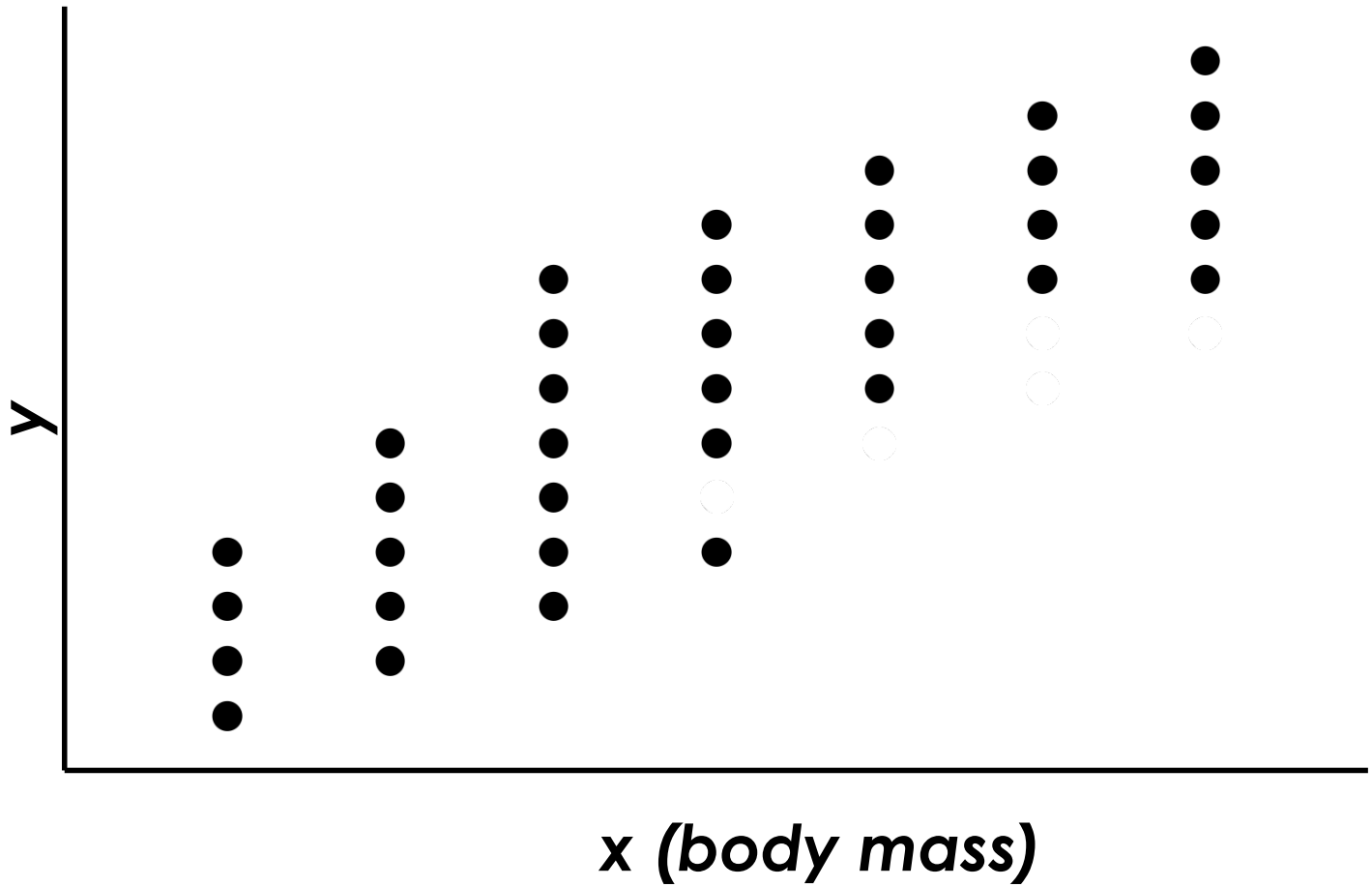
      dry matter intake $BM^{0.89}$

      requirements $BM^{0.75}$

Phylogenetic statistics

Comparative statistics

Conventional regression analysis assumes independence of data points.



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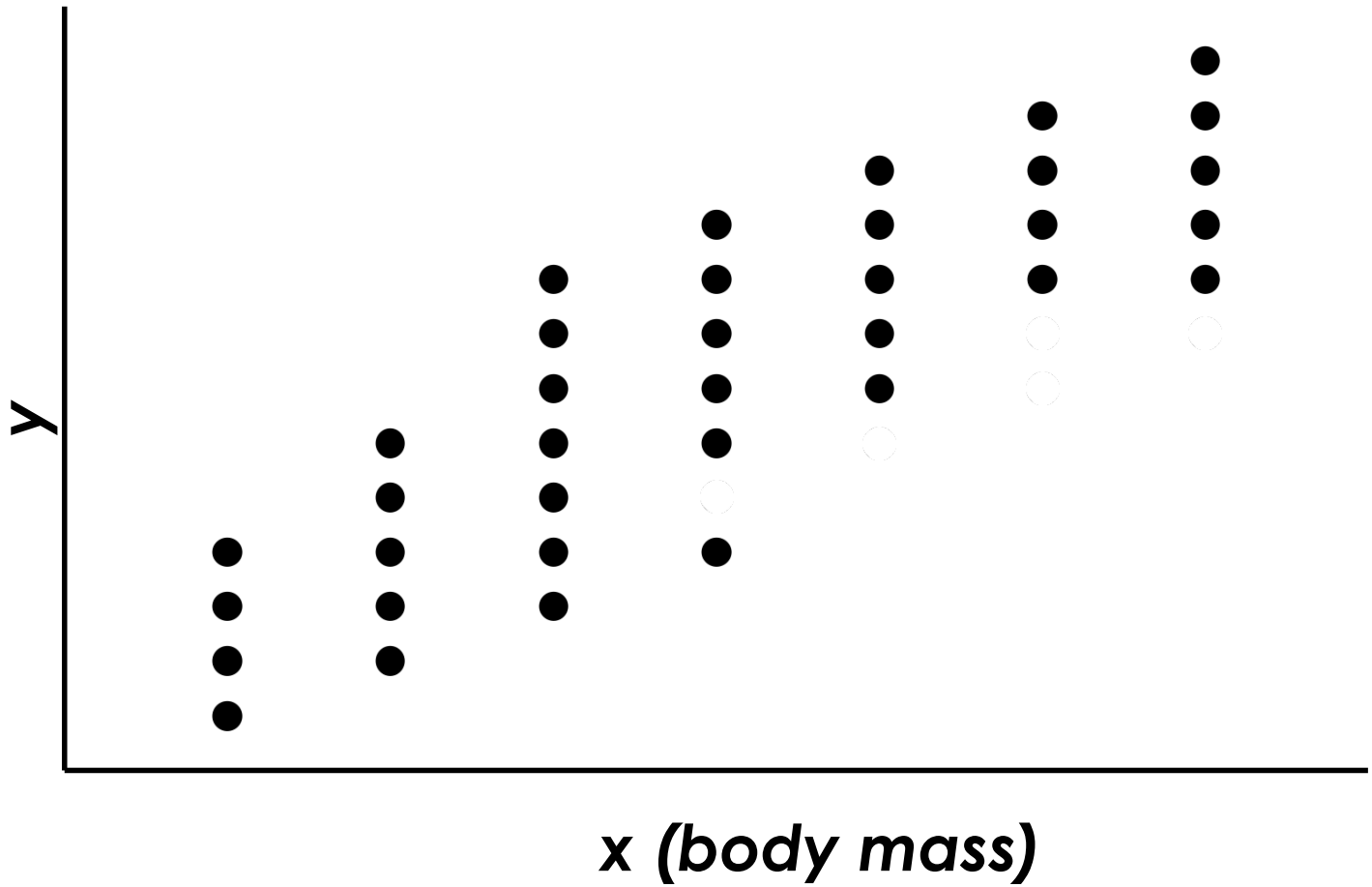
But this is violated by phylogenetic relationships.



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Therefore, we perform allometric analyses also with accounting for phylogeny, using PGLS (Phylogenetic Generalized Least Squares).

Comparative statistics

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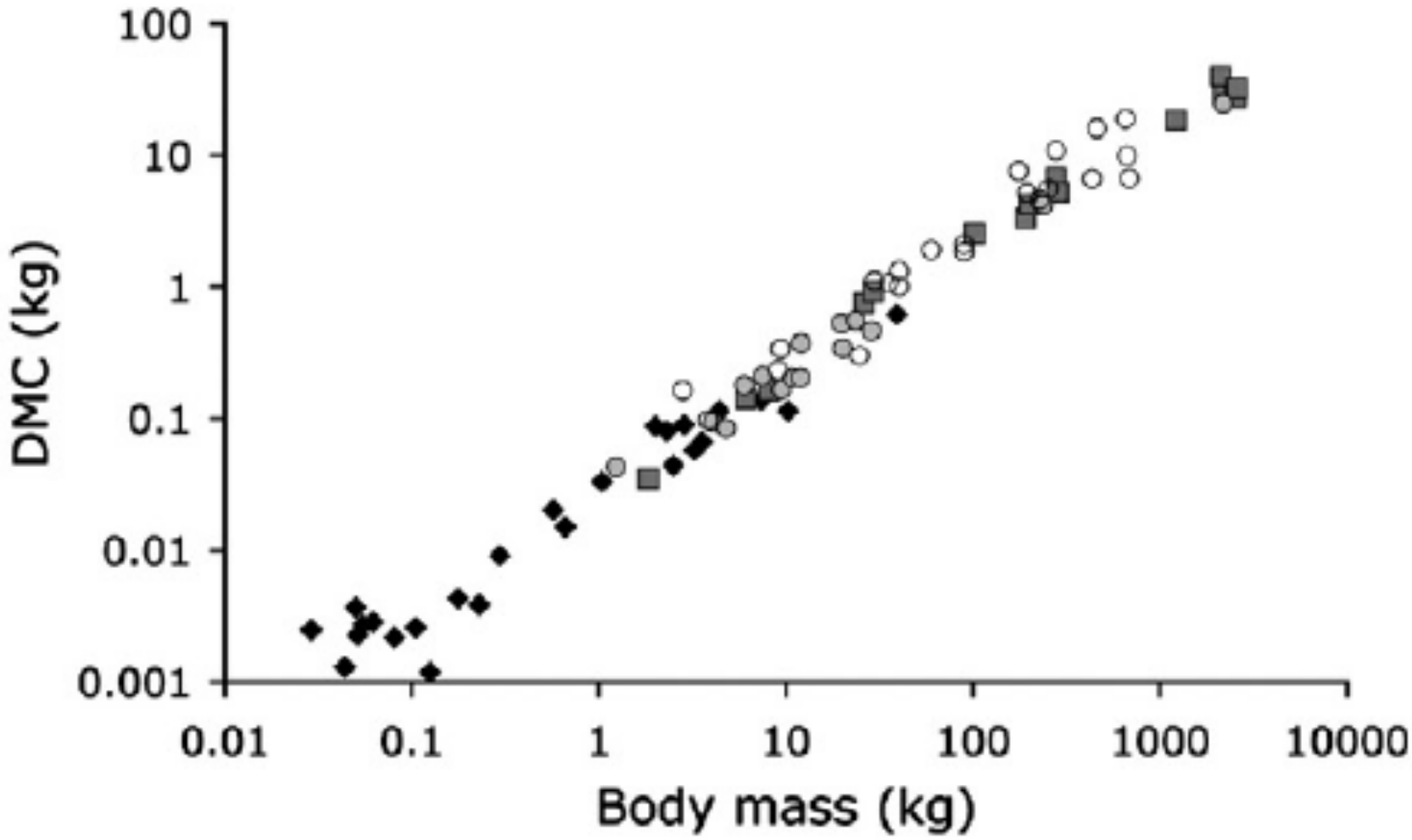
But this is violated by phylogenetic relationships.

Therefore, we perform allometric analyses also with accounting for phylogeny, using PGLS (Phylogenetic Generalized Least Squares).

Results mostly did not differ from conventional statistics in a relevant way, but the intensive use of comparative statistics (also with additional examples) led to formulation of some concepts new to ourselves.

Example I: gut contents



from Müller et al. (2013) CBP A

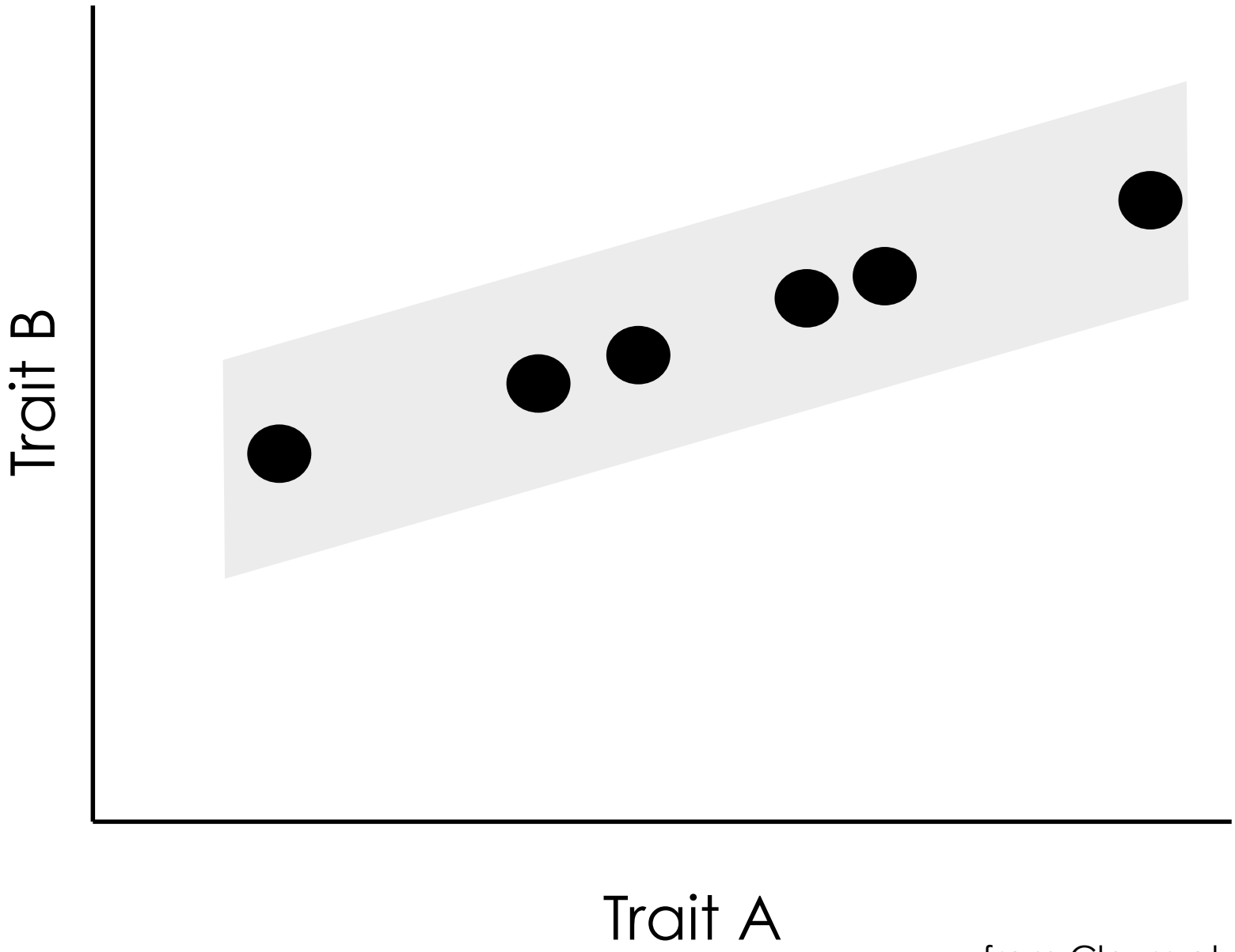
Accounting for phylogeny

from Clauss et al. (2013)

Accounting for phylogeny

from Clauss et al. (2013)

Accounting for phylogeny



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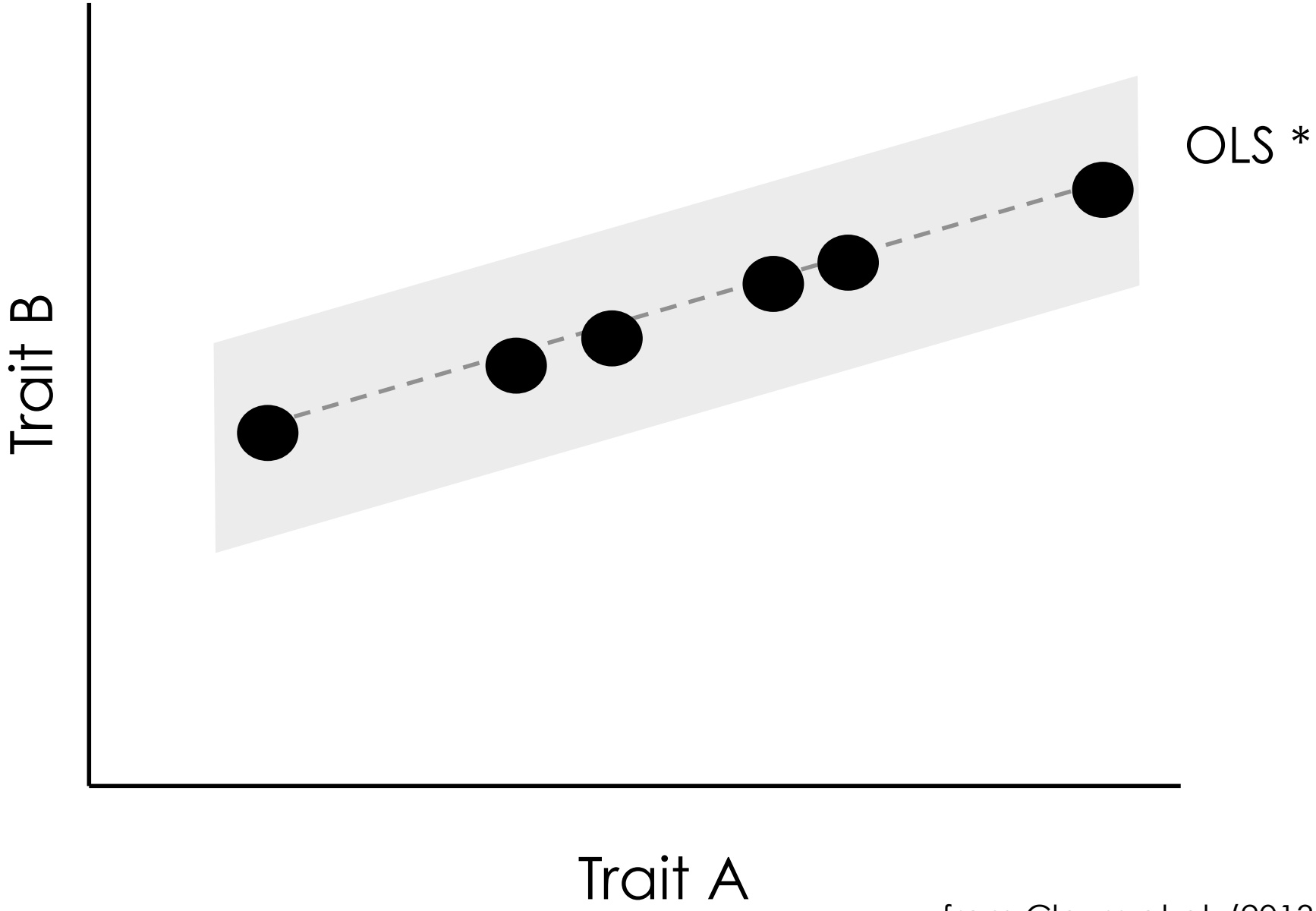
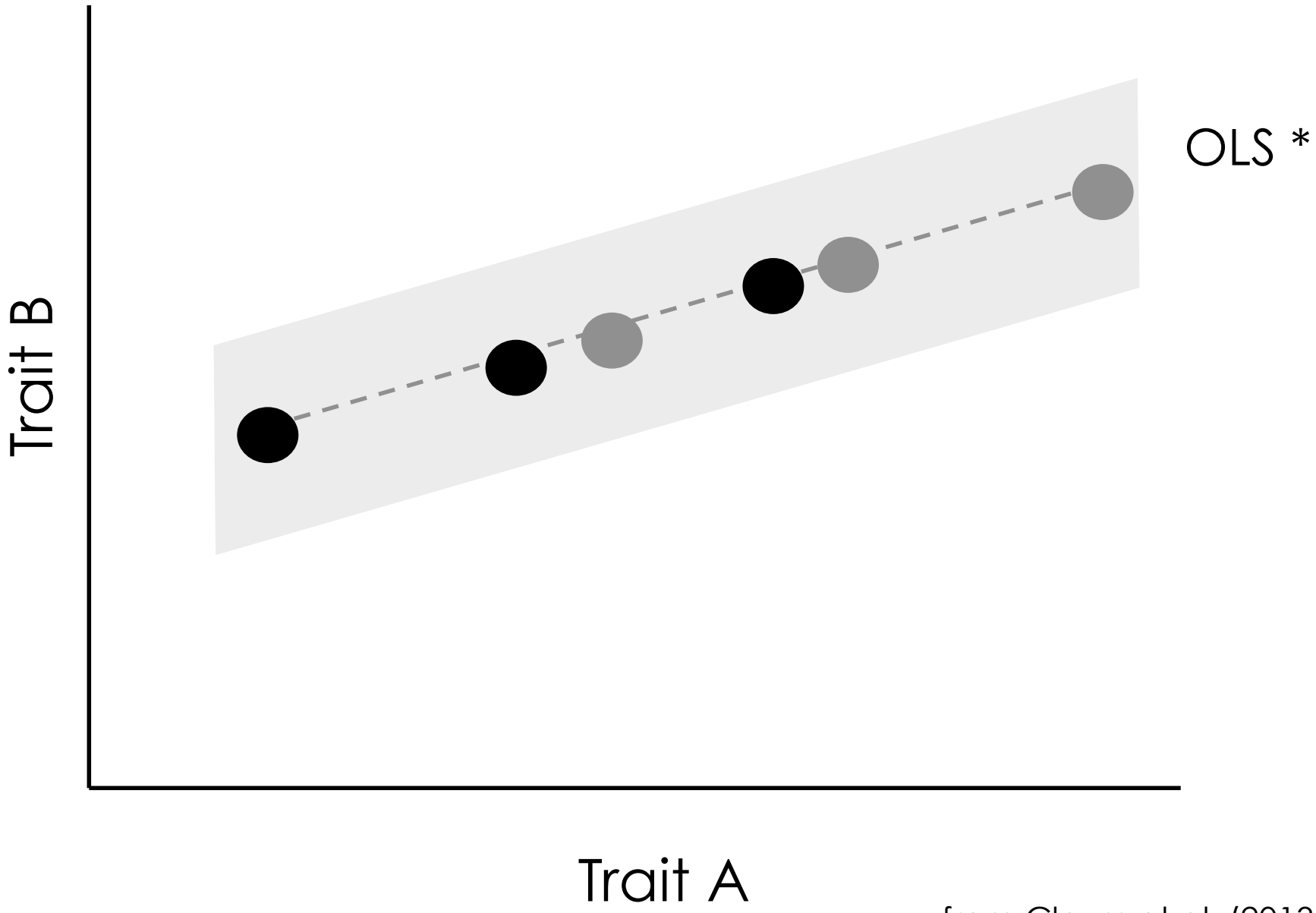
Accounting for phylogeny



from Clauss et al. (2013)

Accounting for phylogeny



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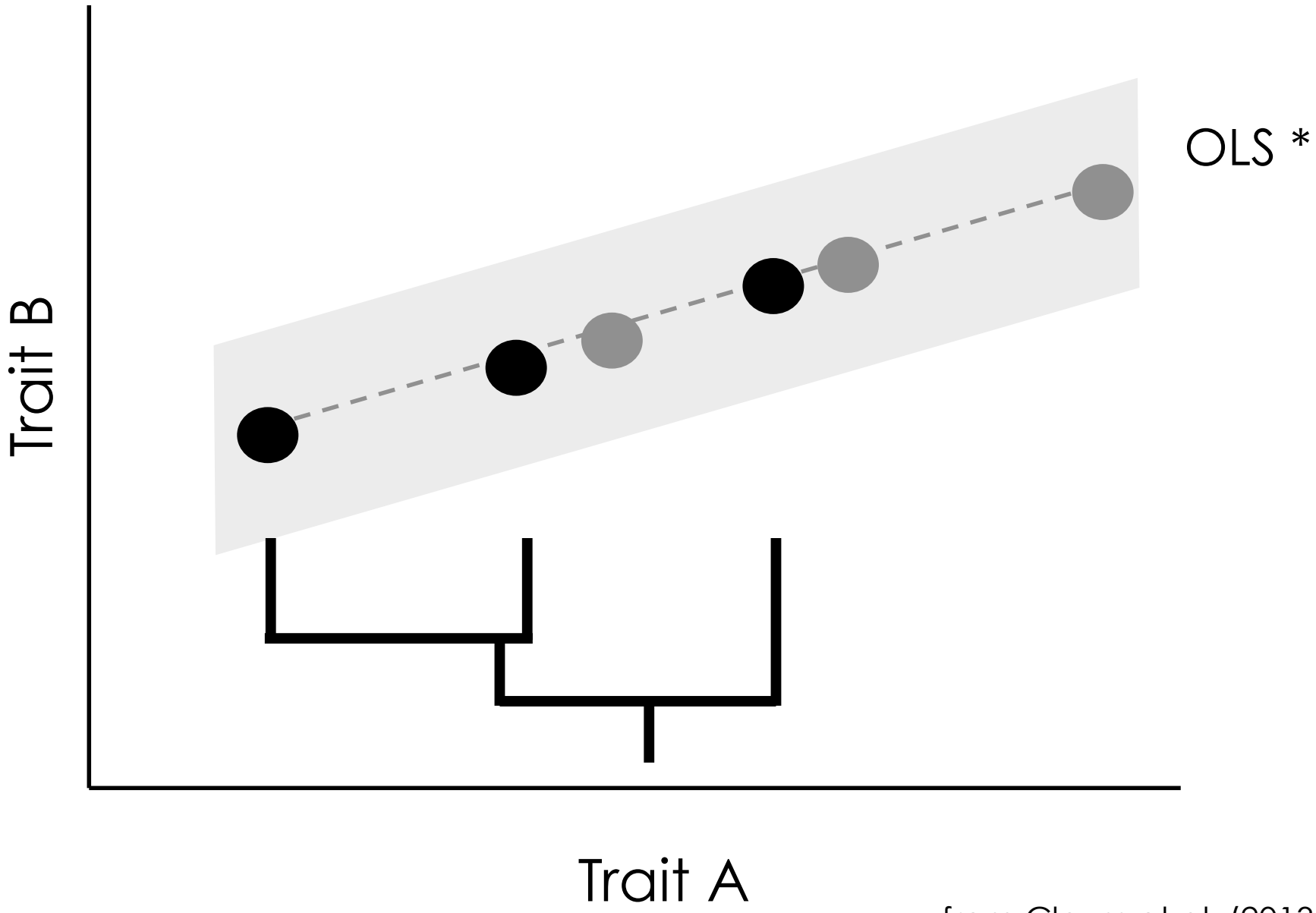
Accounting for phylogeny



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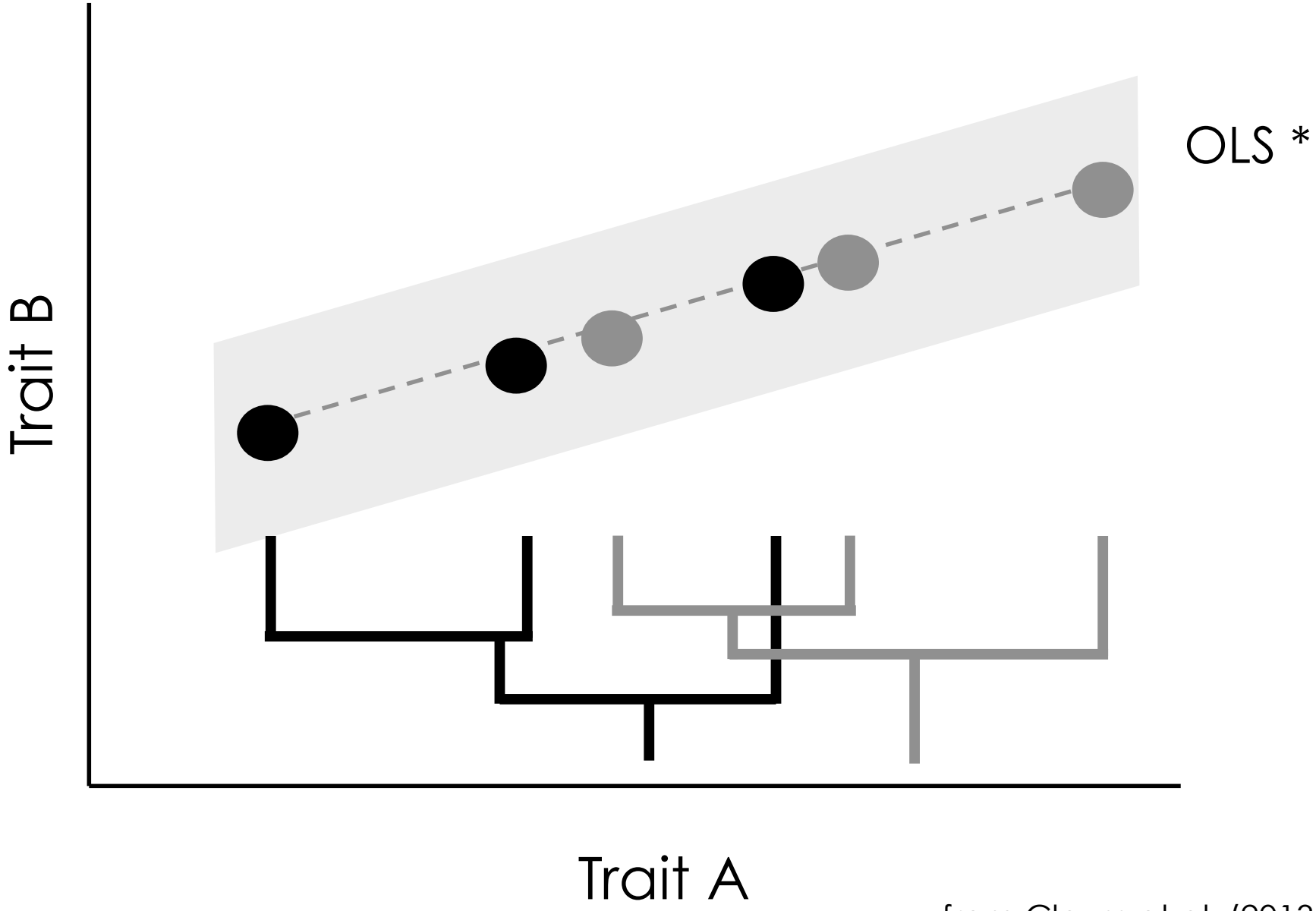

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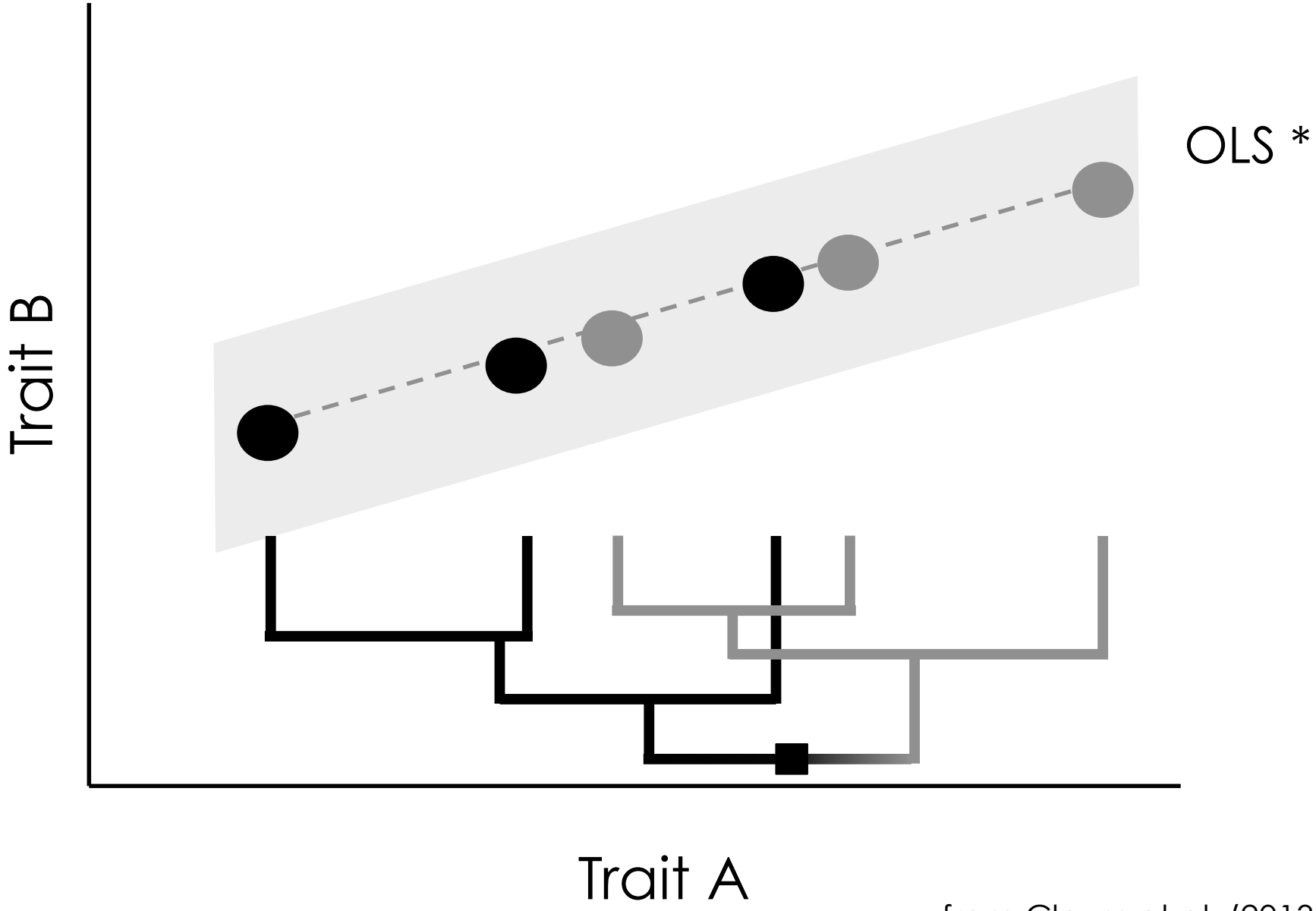
Accounting for phylogeny



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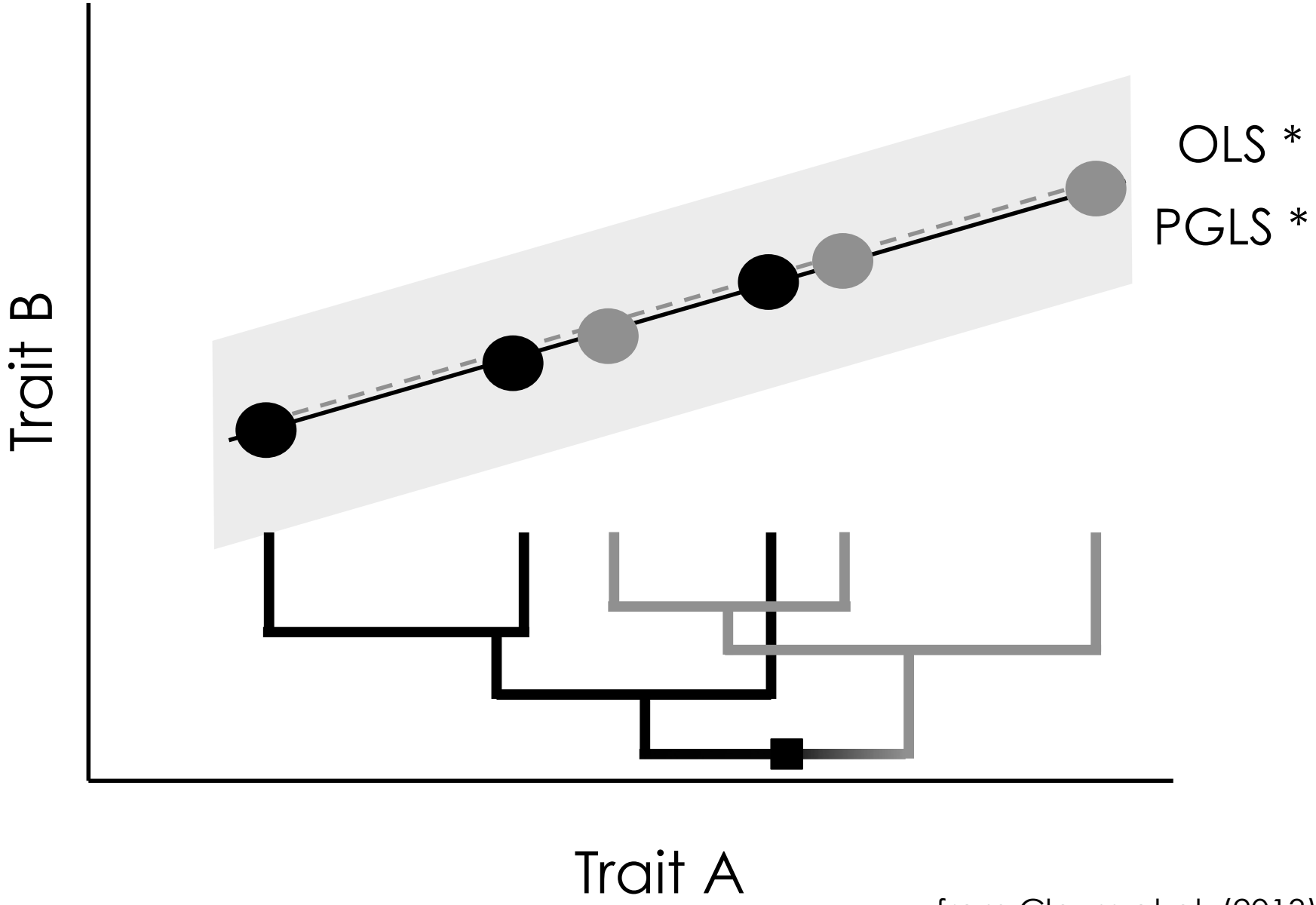

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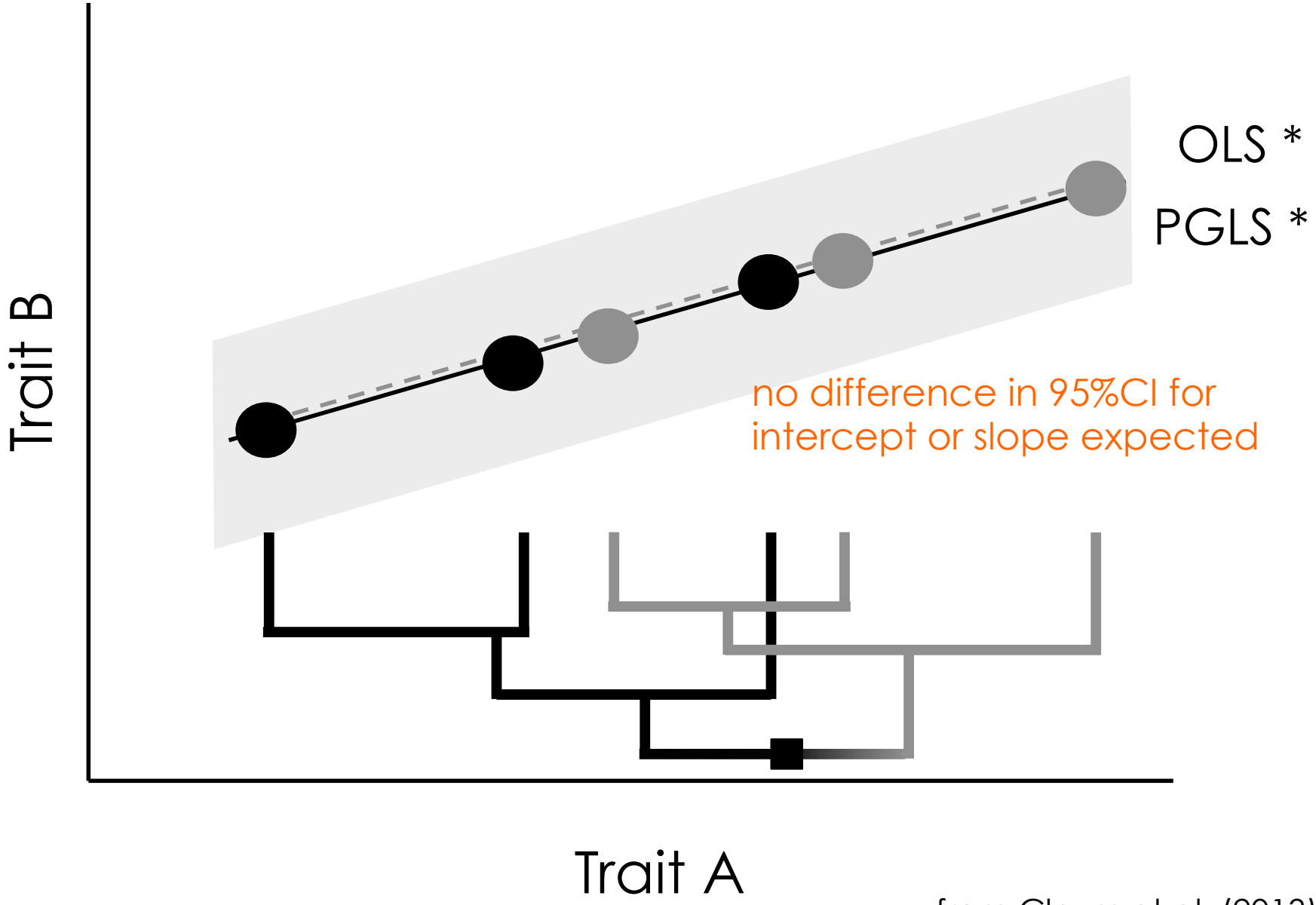

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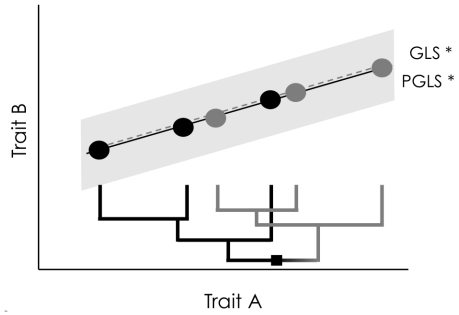
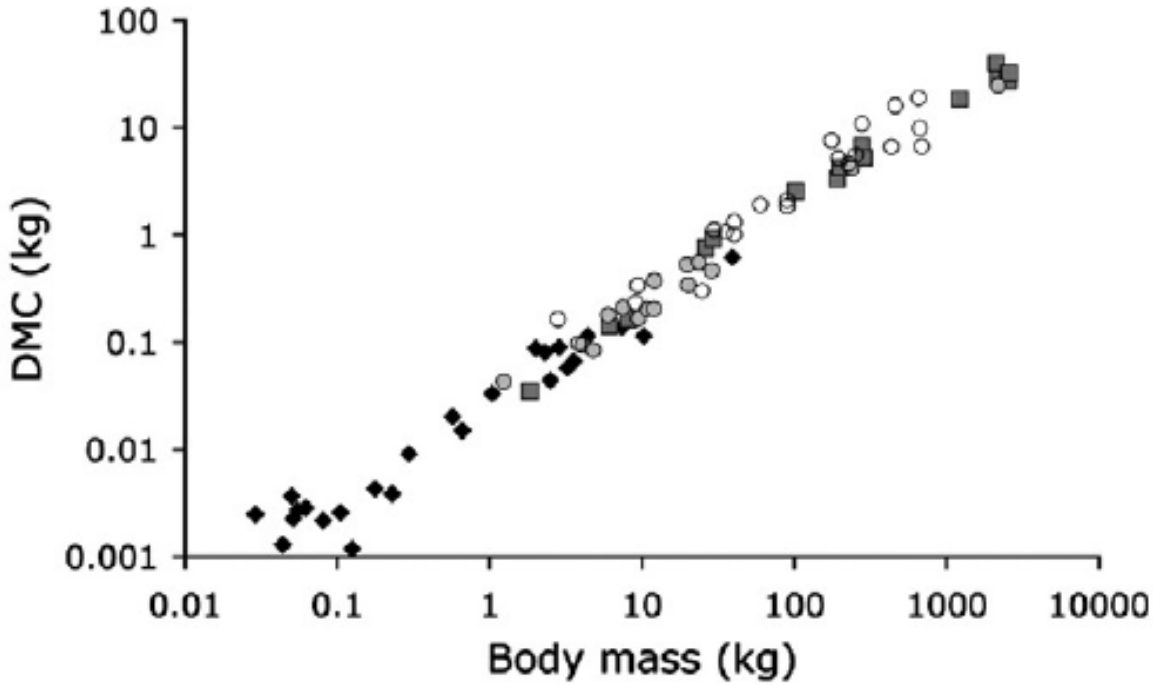


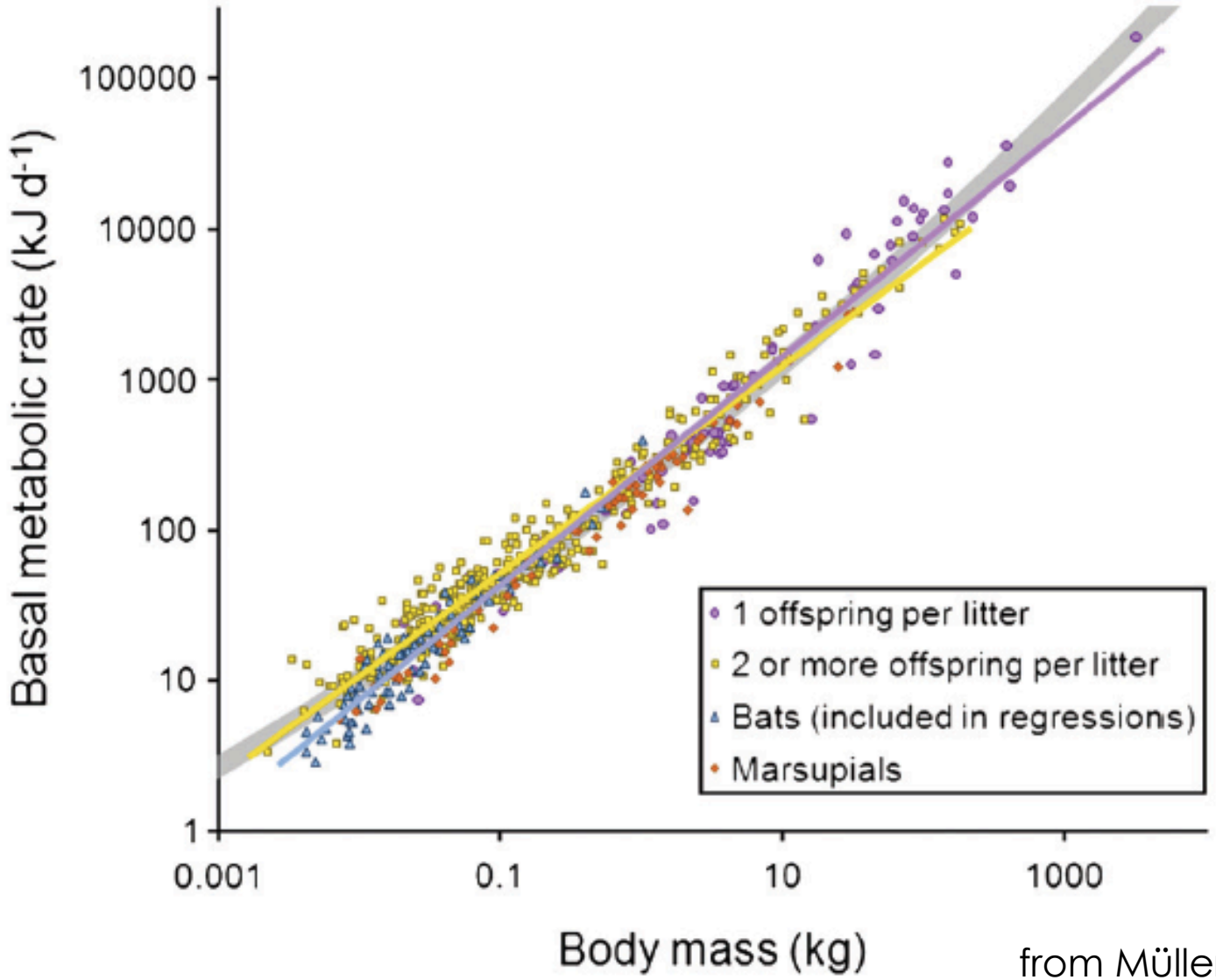
OLS: 0.03 (0.025-0.032) $BM^{0.93\ (0.90\text{-}0.96)}$

PGLS: 0.03 (0.010-0.075) $BM^{0.92\ (0.85\text{-}0.98)}$



from Müller et al. (2013)

Example II: basal metabolic rate



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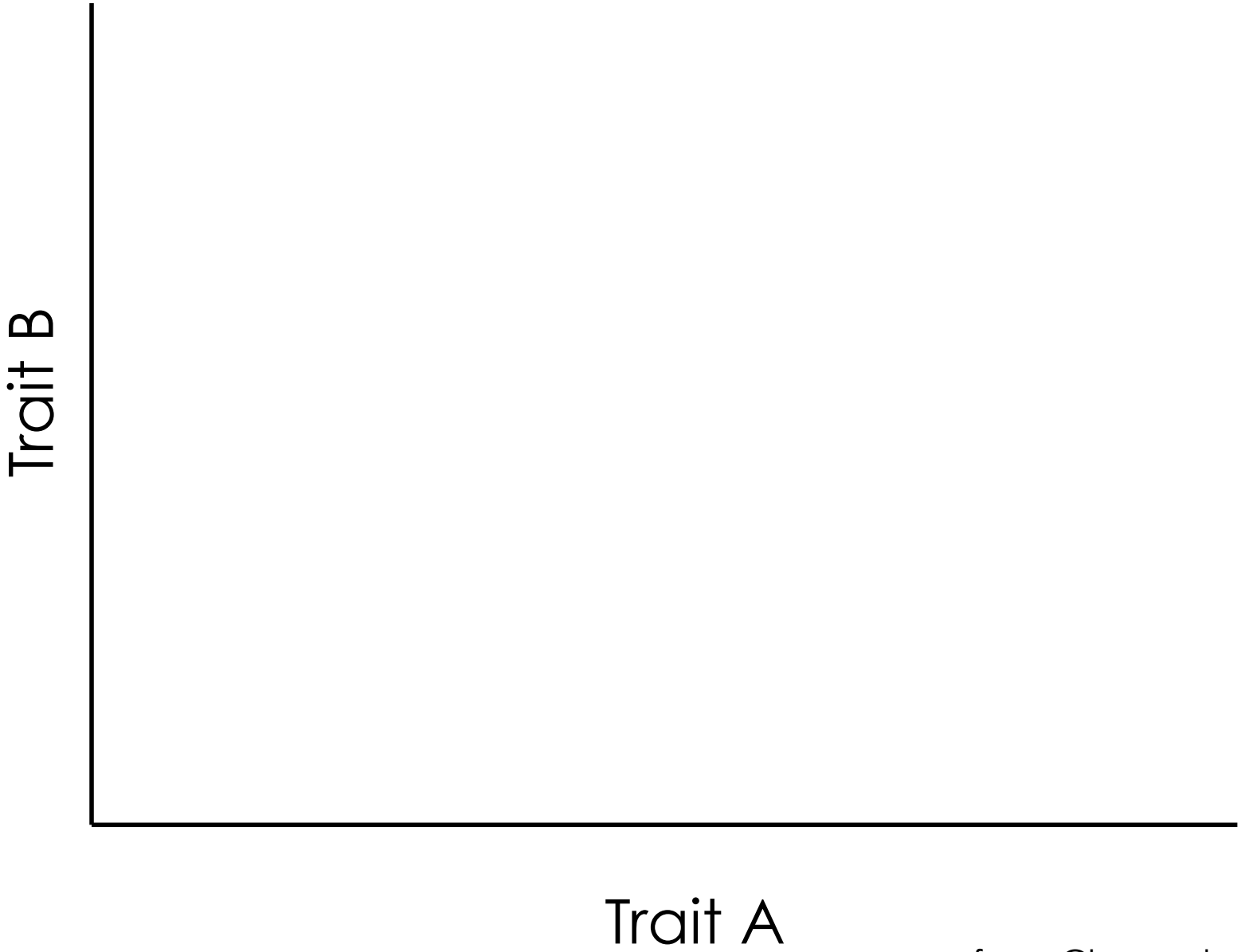

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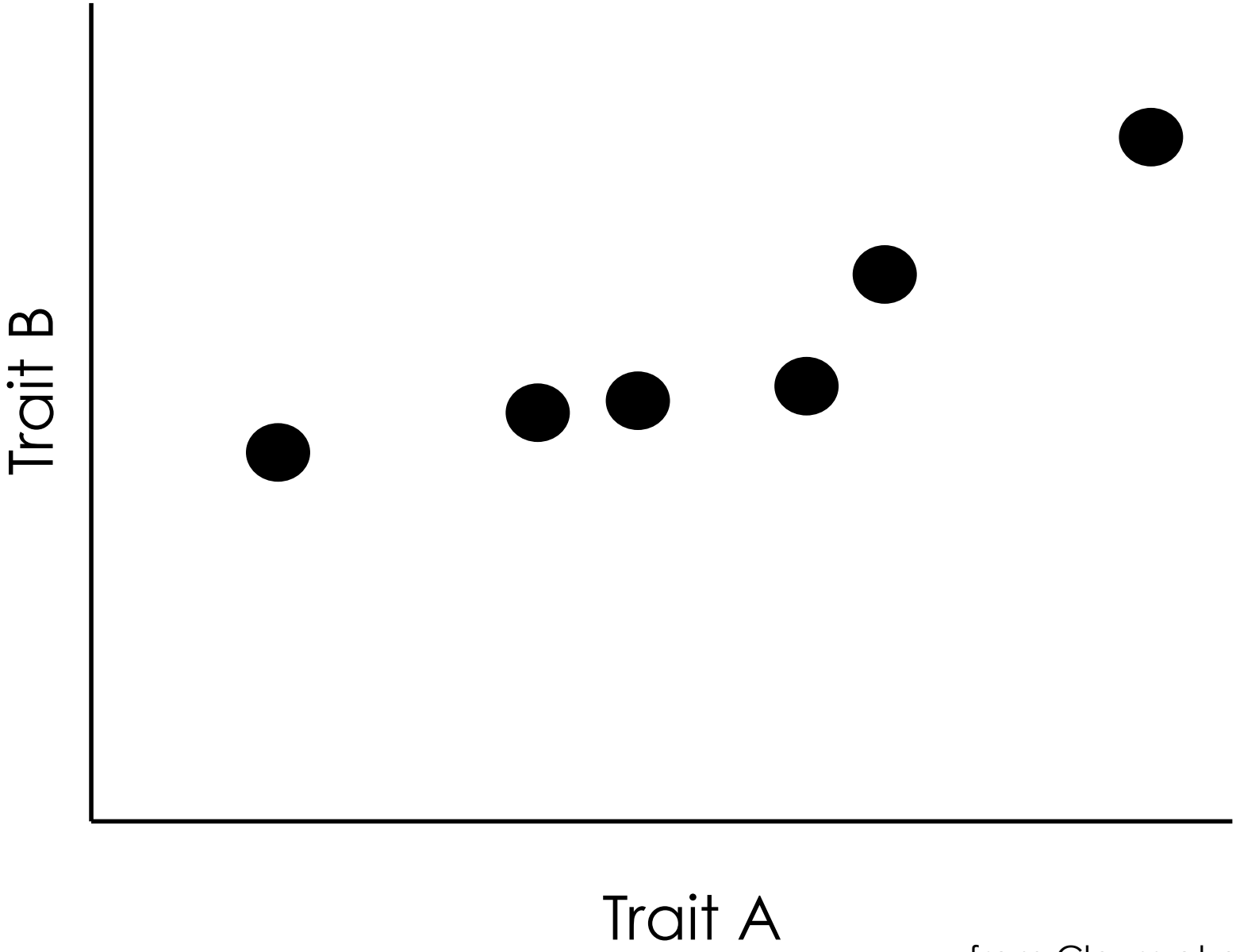

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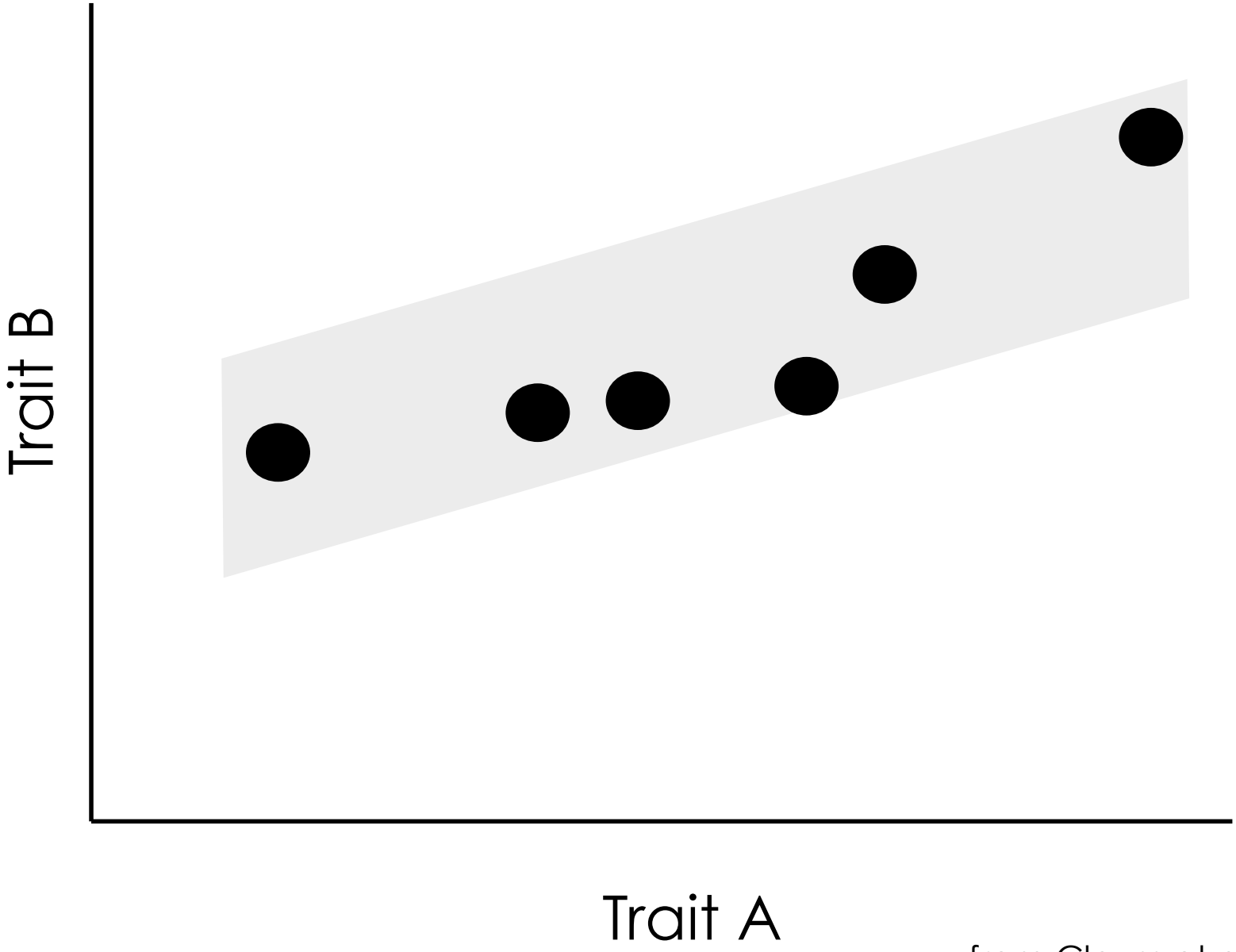

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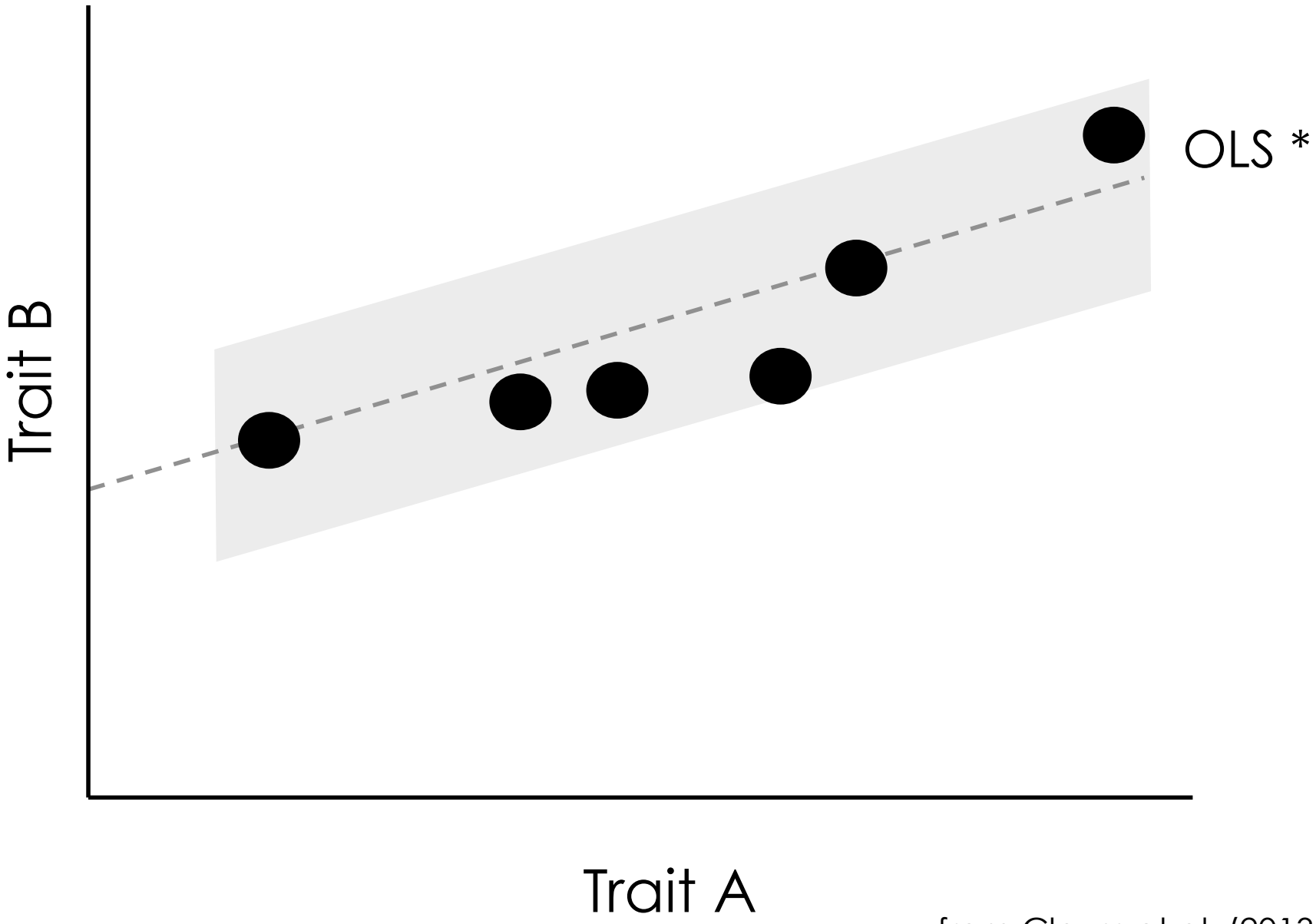

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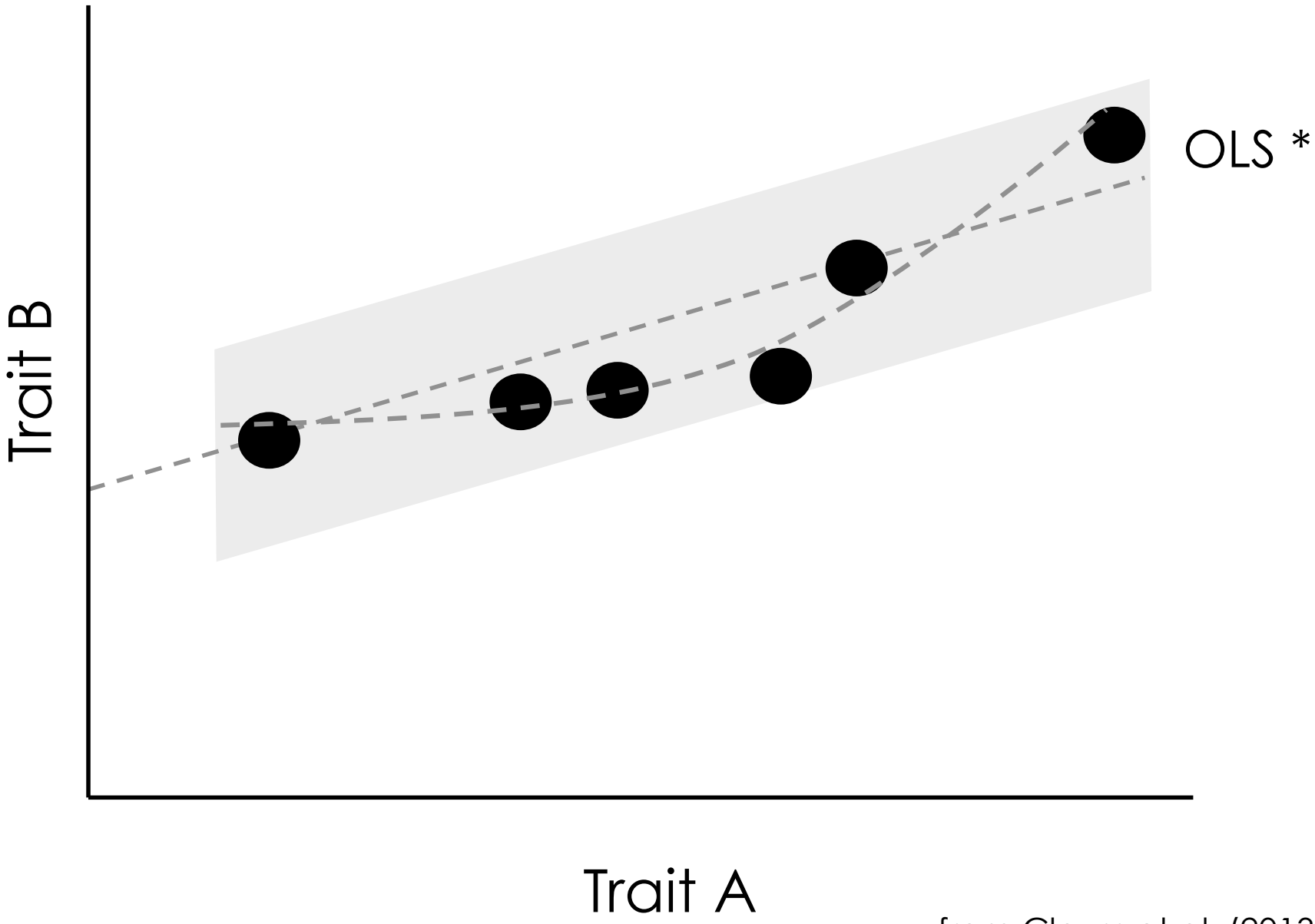

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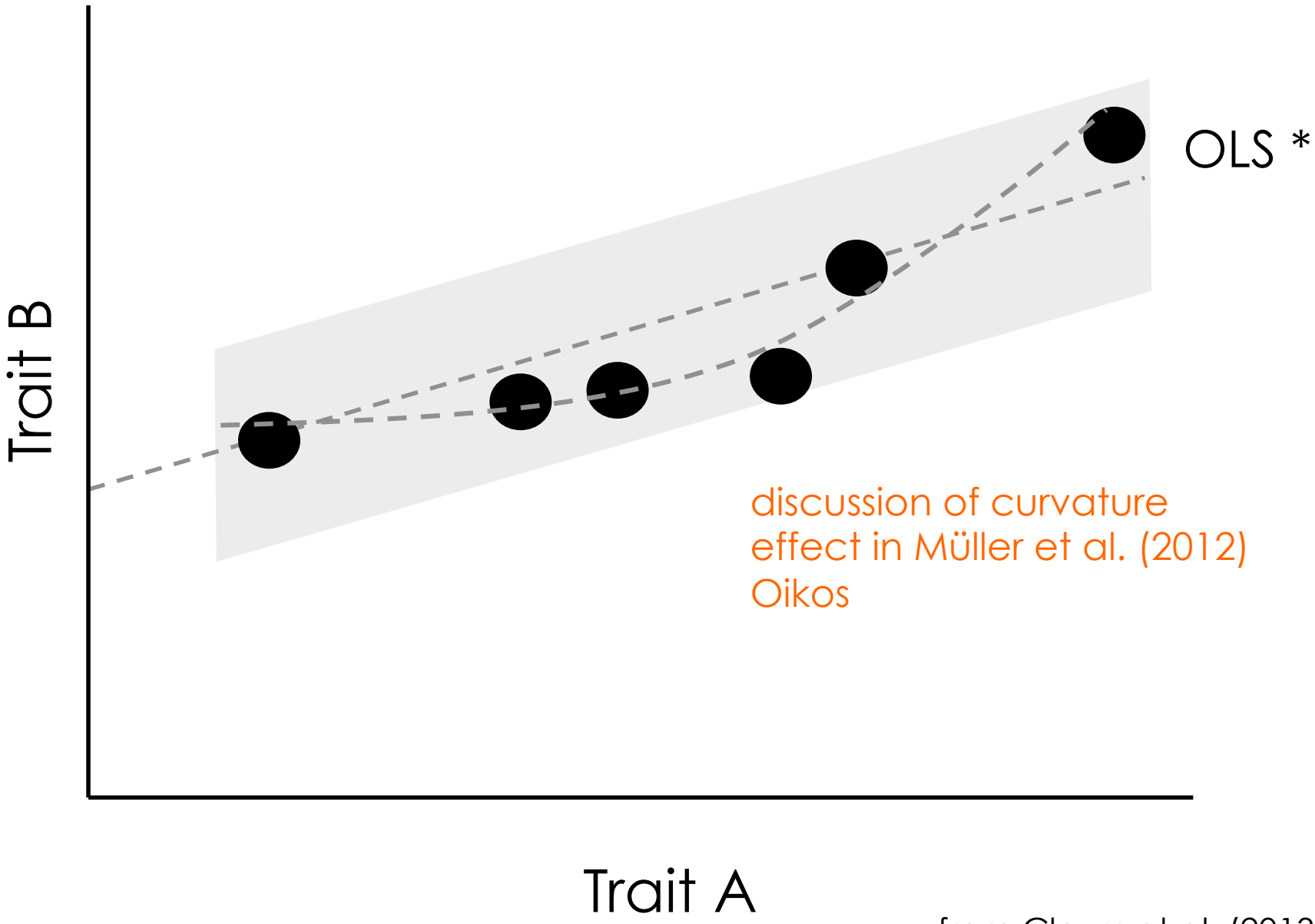
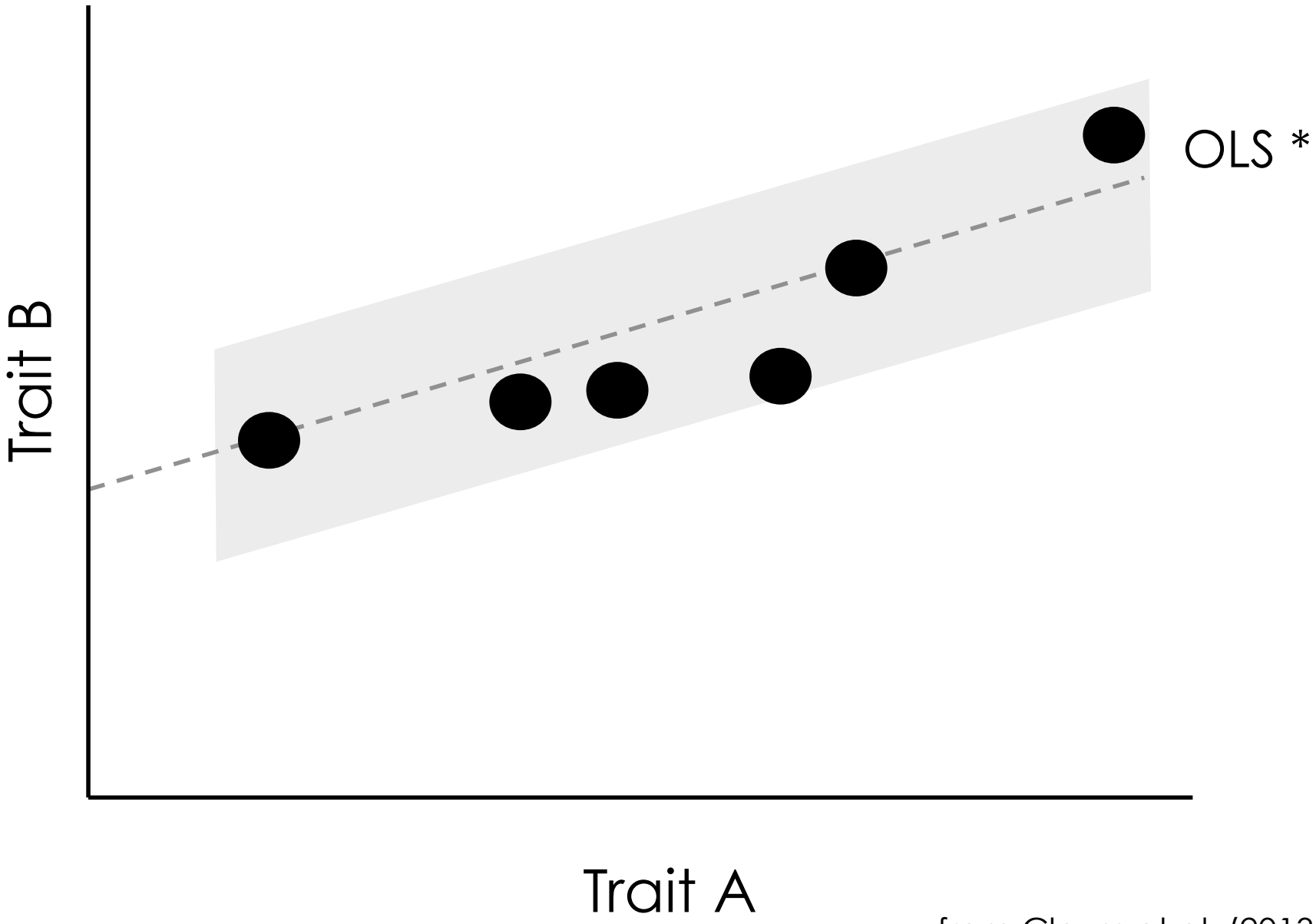


discussion of curvature effect in Müller et al. (2012) Oikos

from Clauss et al. (2013)

Accounting for phylogeny



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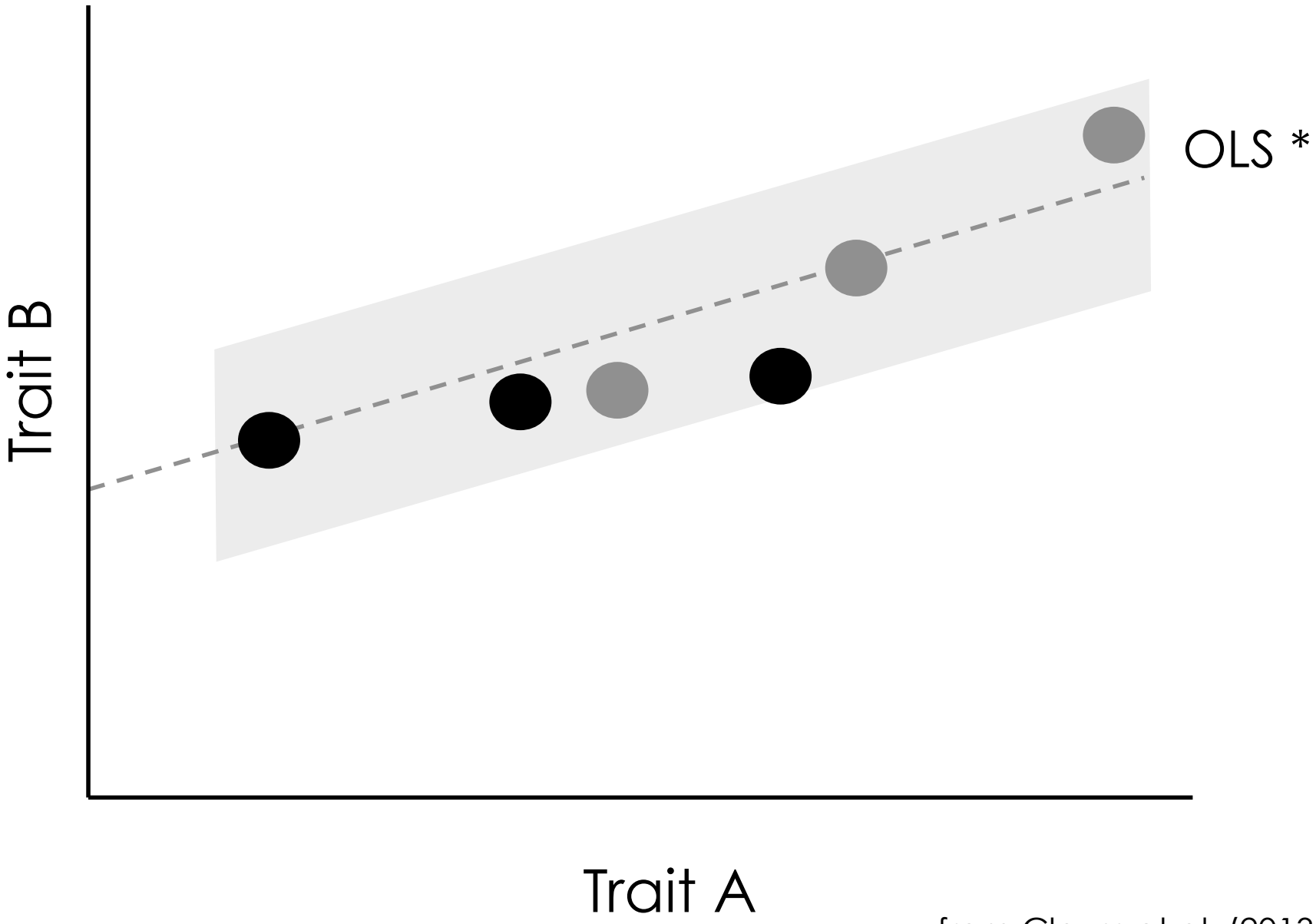

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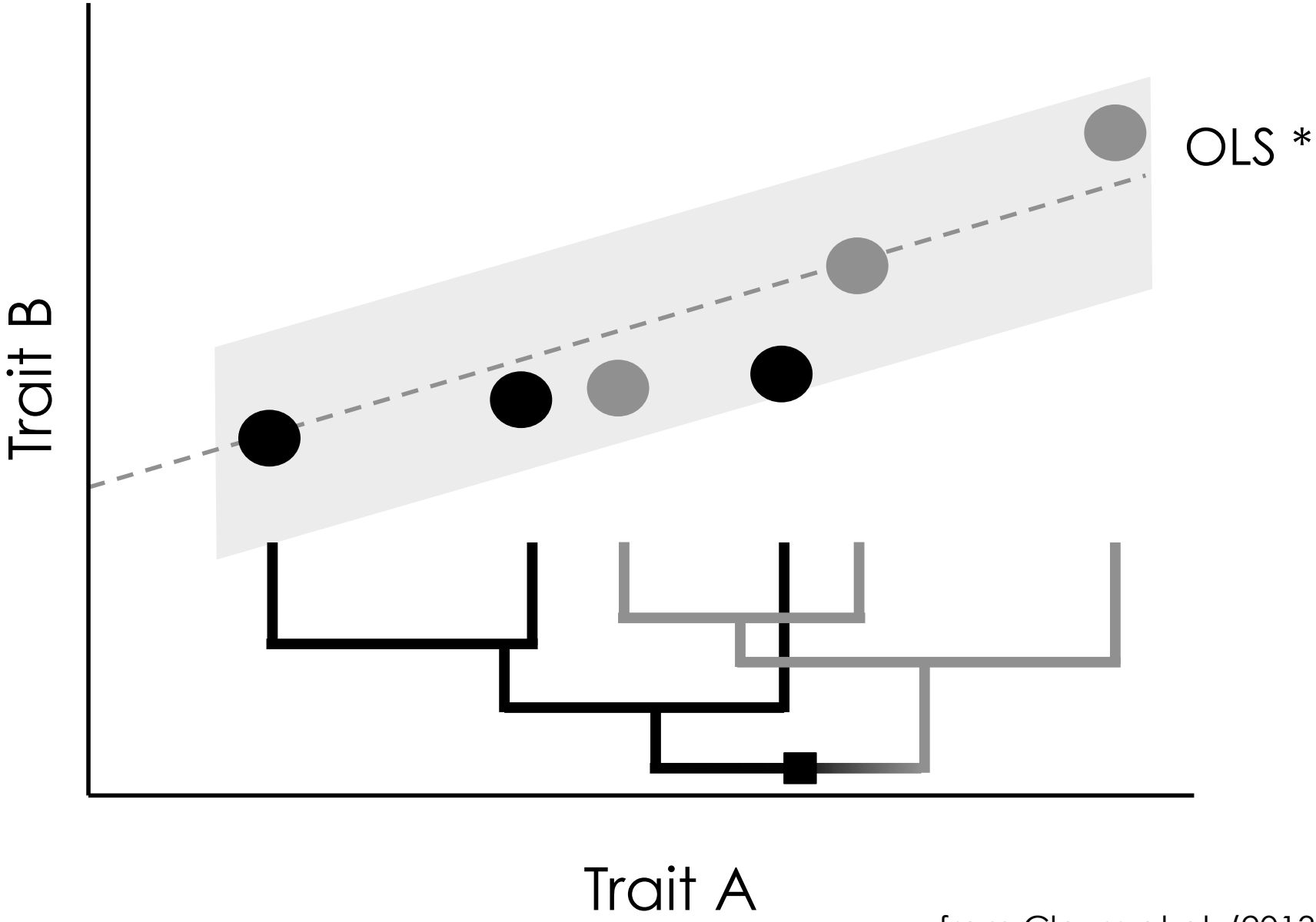

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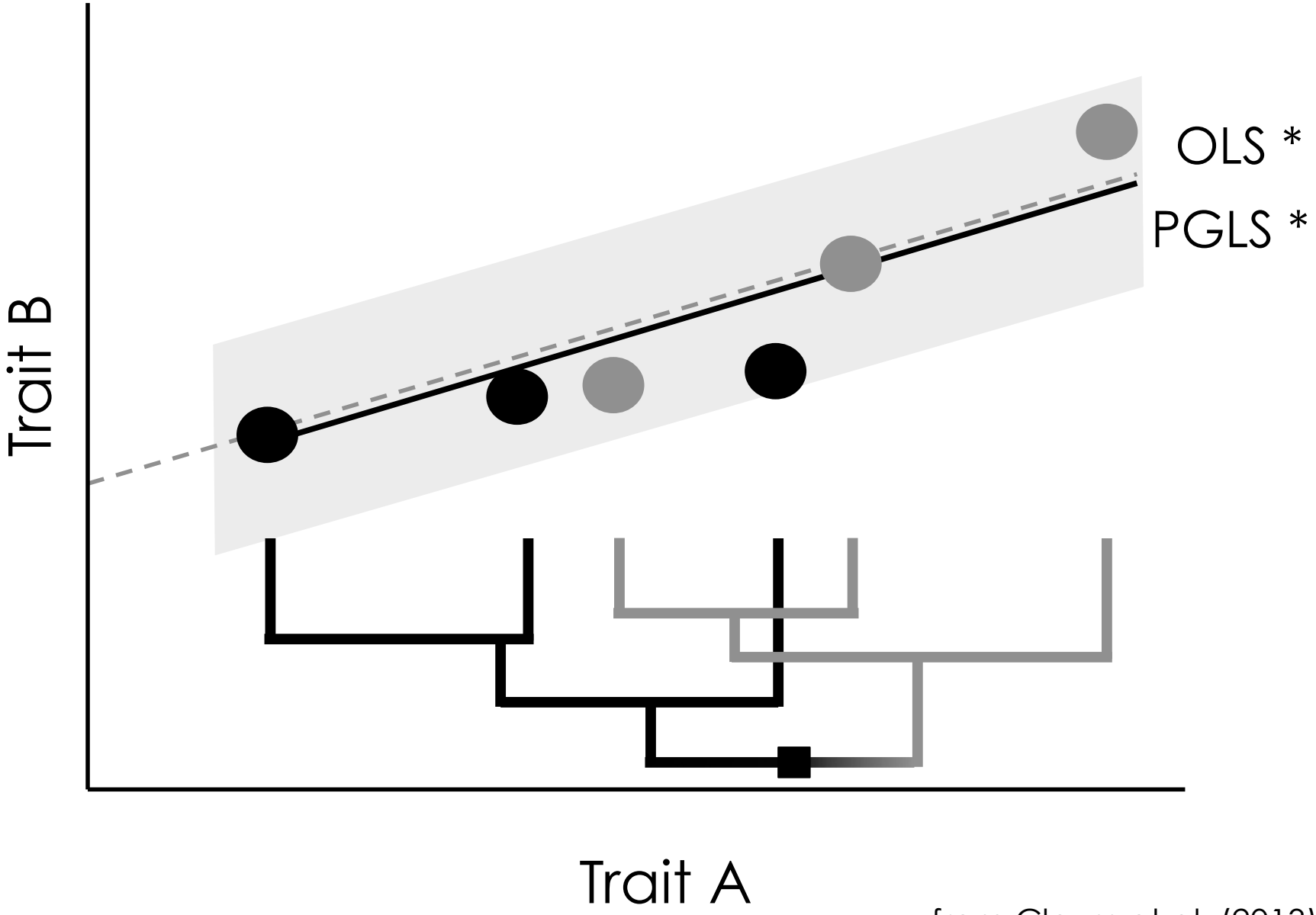

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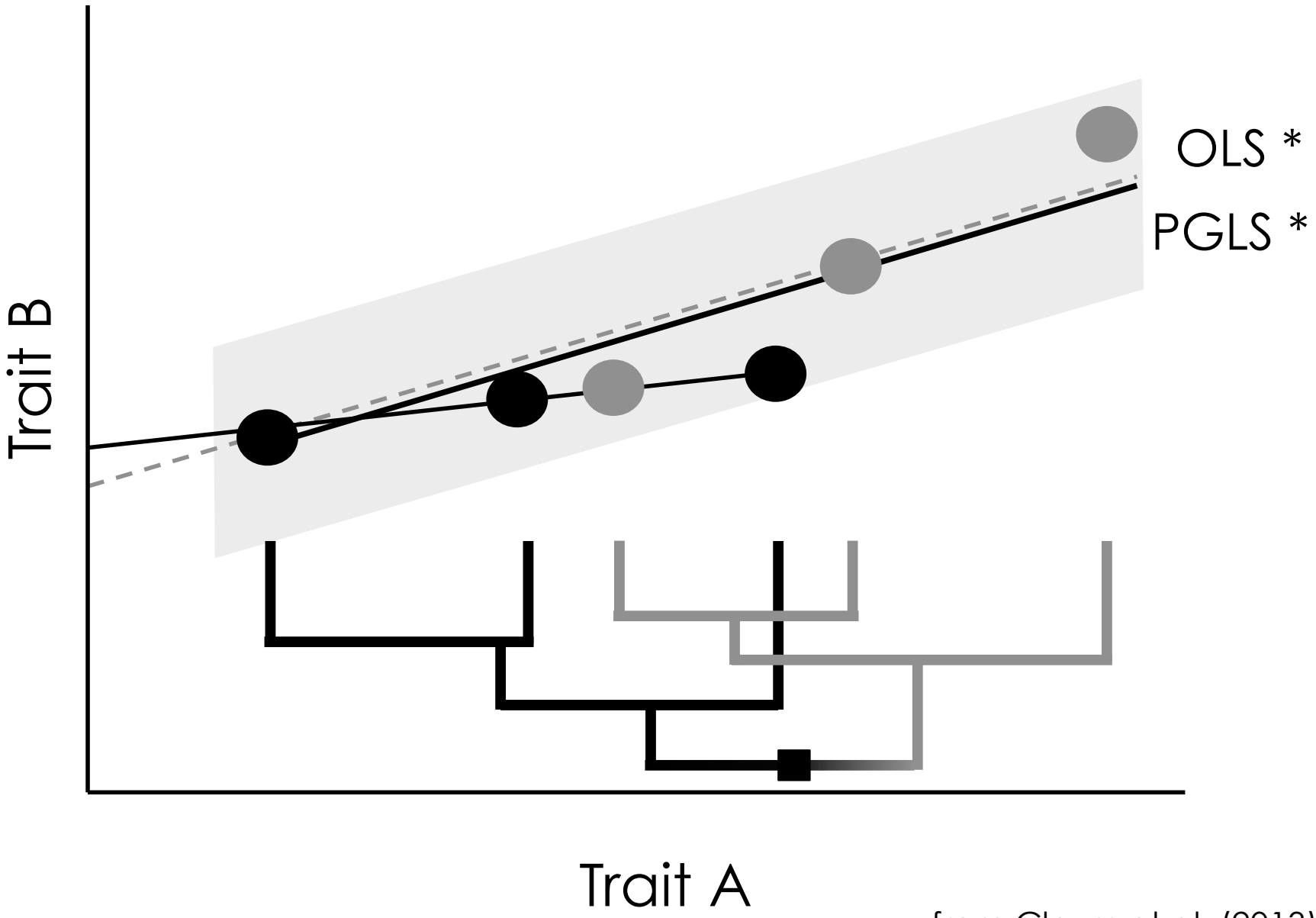

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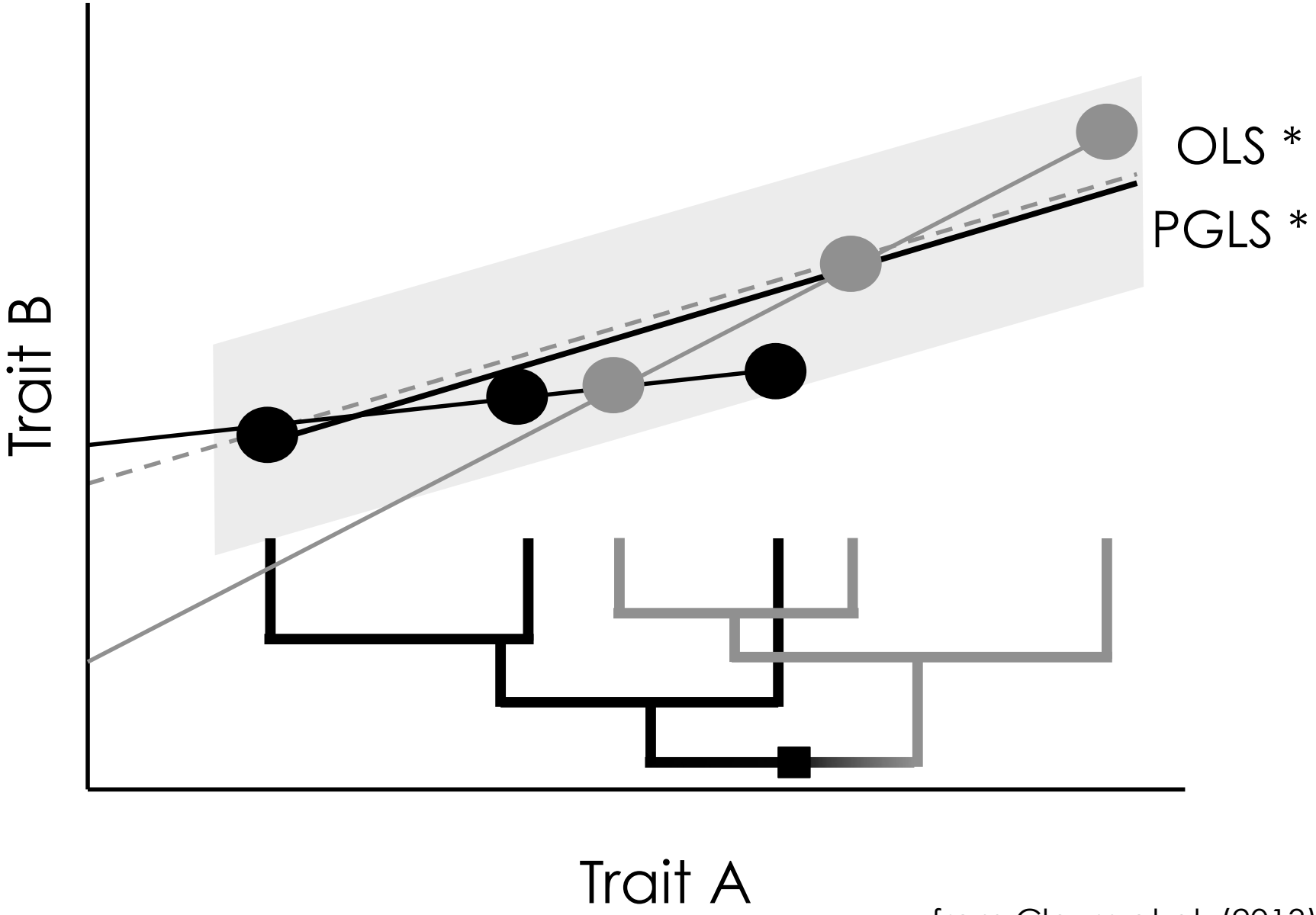

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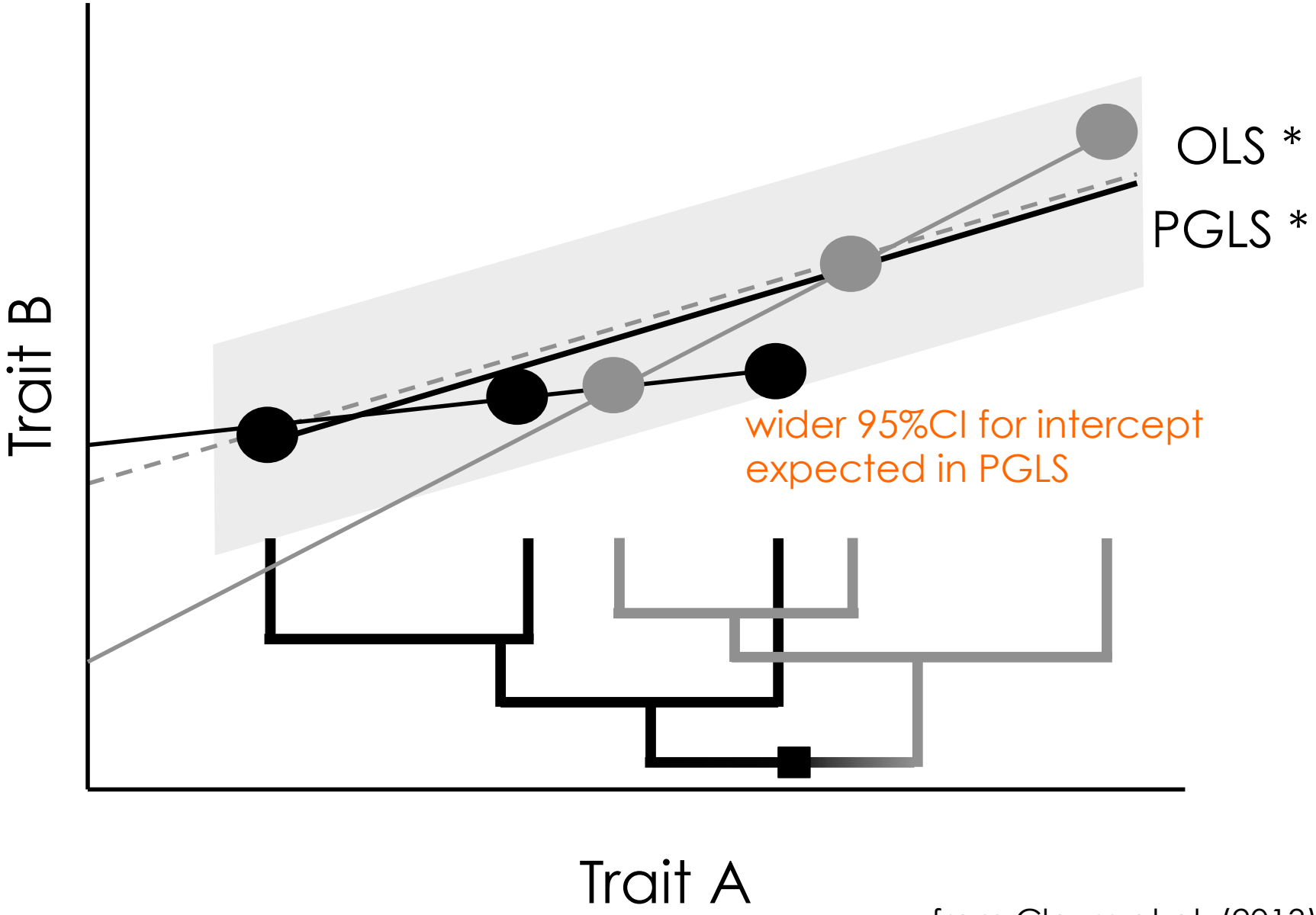

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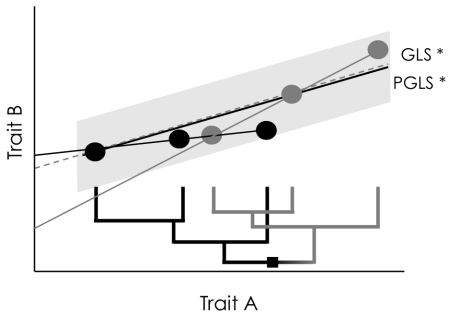
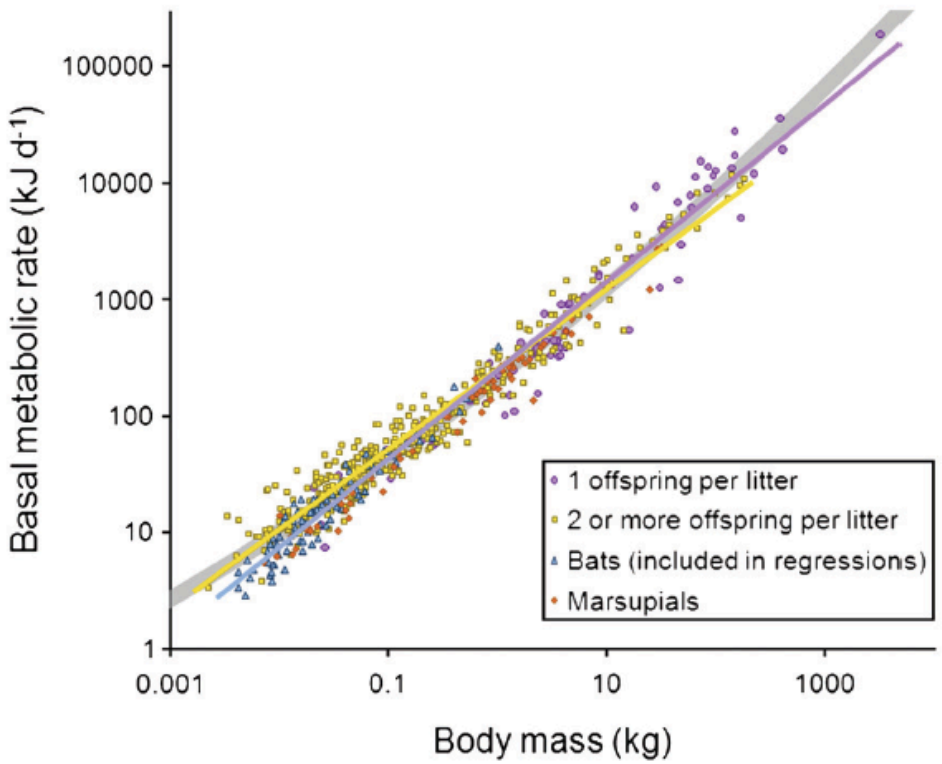
Example II: basal metabolic rate



OLS: 2.38 (2.37-2.40) $BM^{0.72\ (0.71\text{-}0.73)}$

PGLS: 2.25 (2.05-2.44) $BM^{0.73\ (0.71\text{-}0.75)}$



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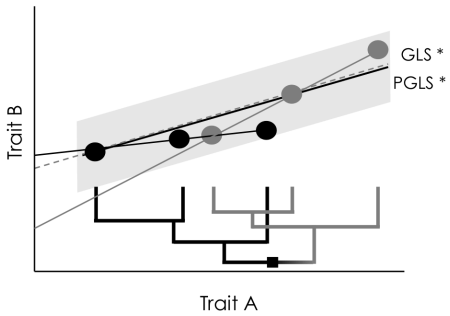

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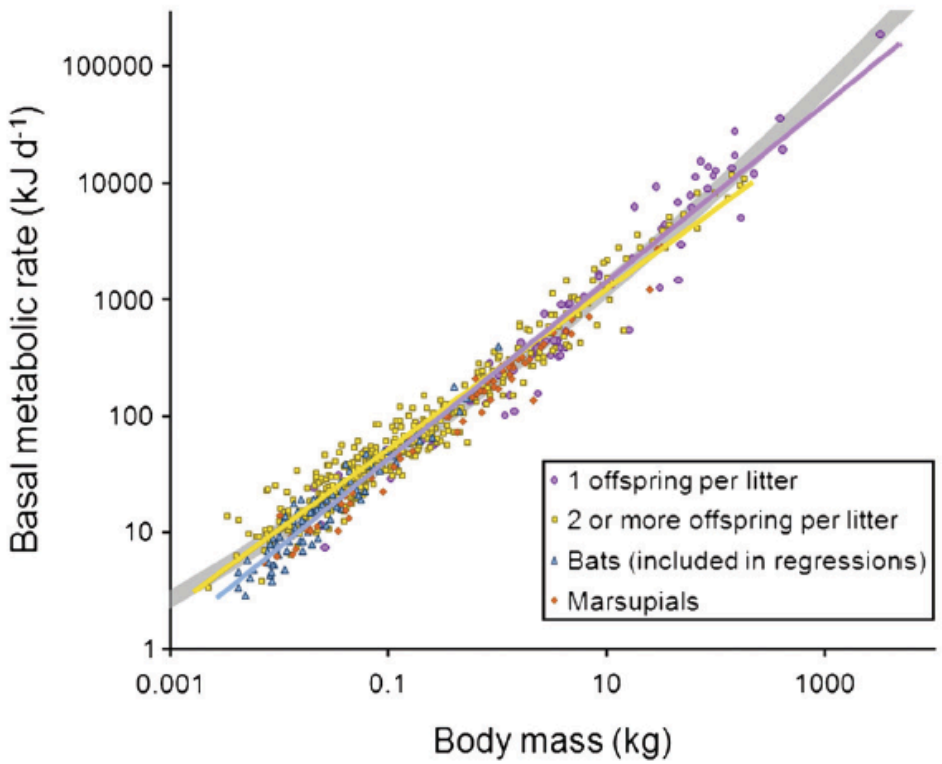

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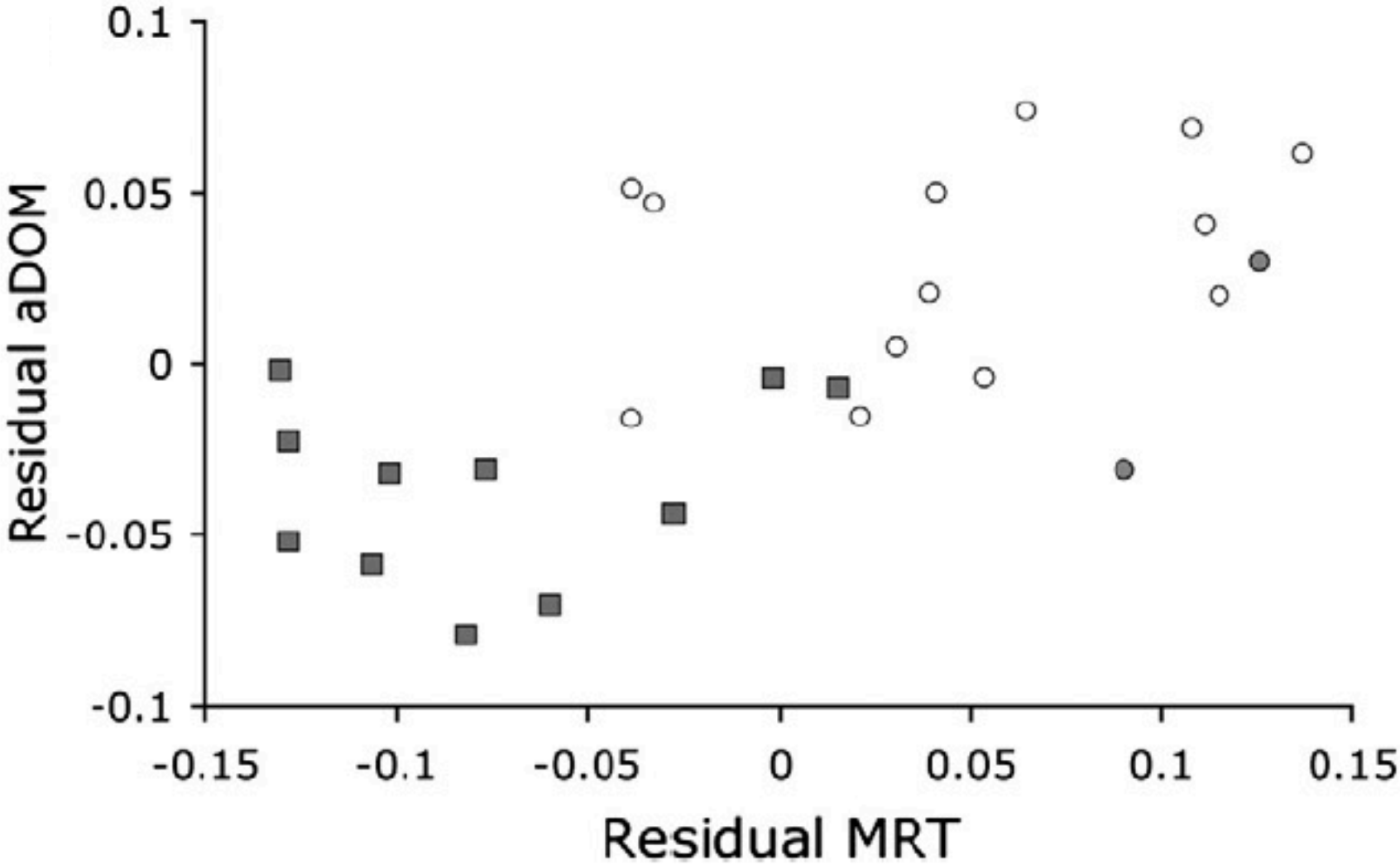
Example III: retention/digestibility



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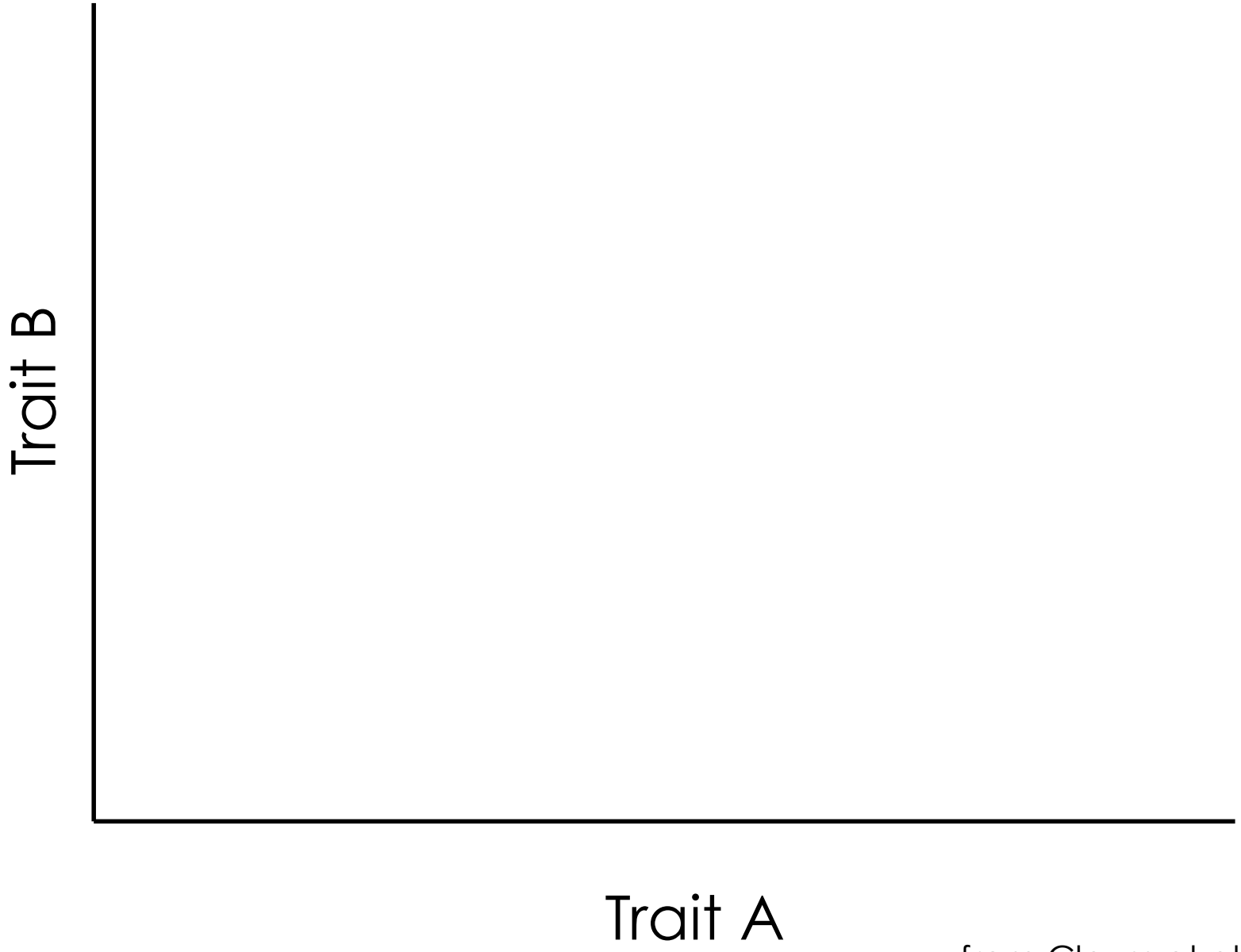
Accounting for phylogeny



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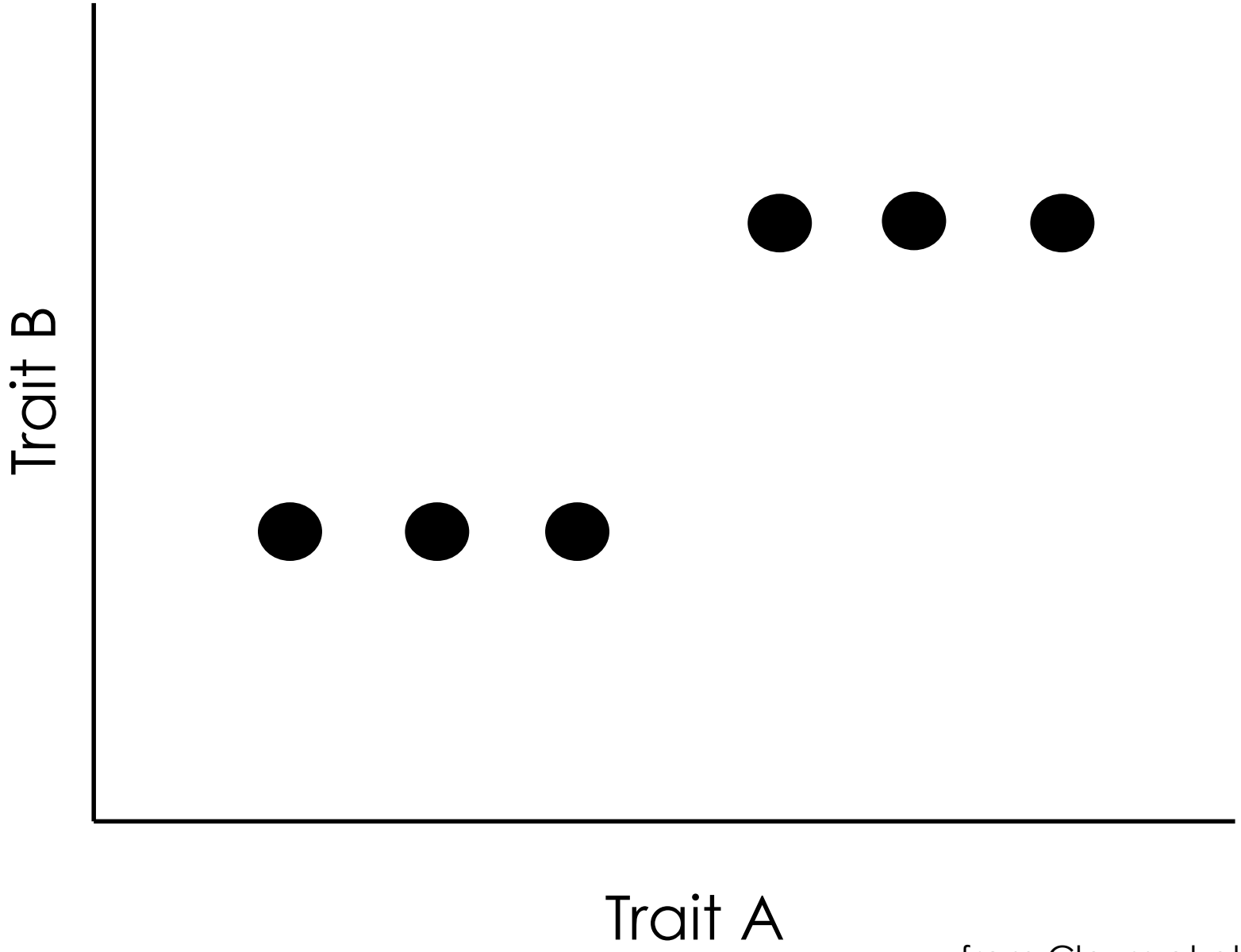

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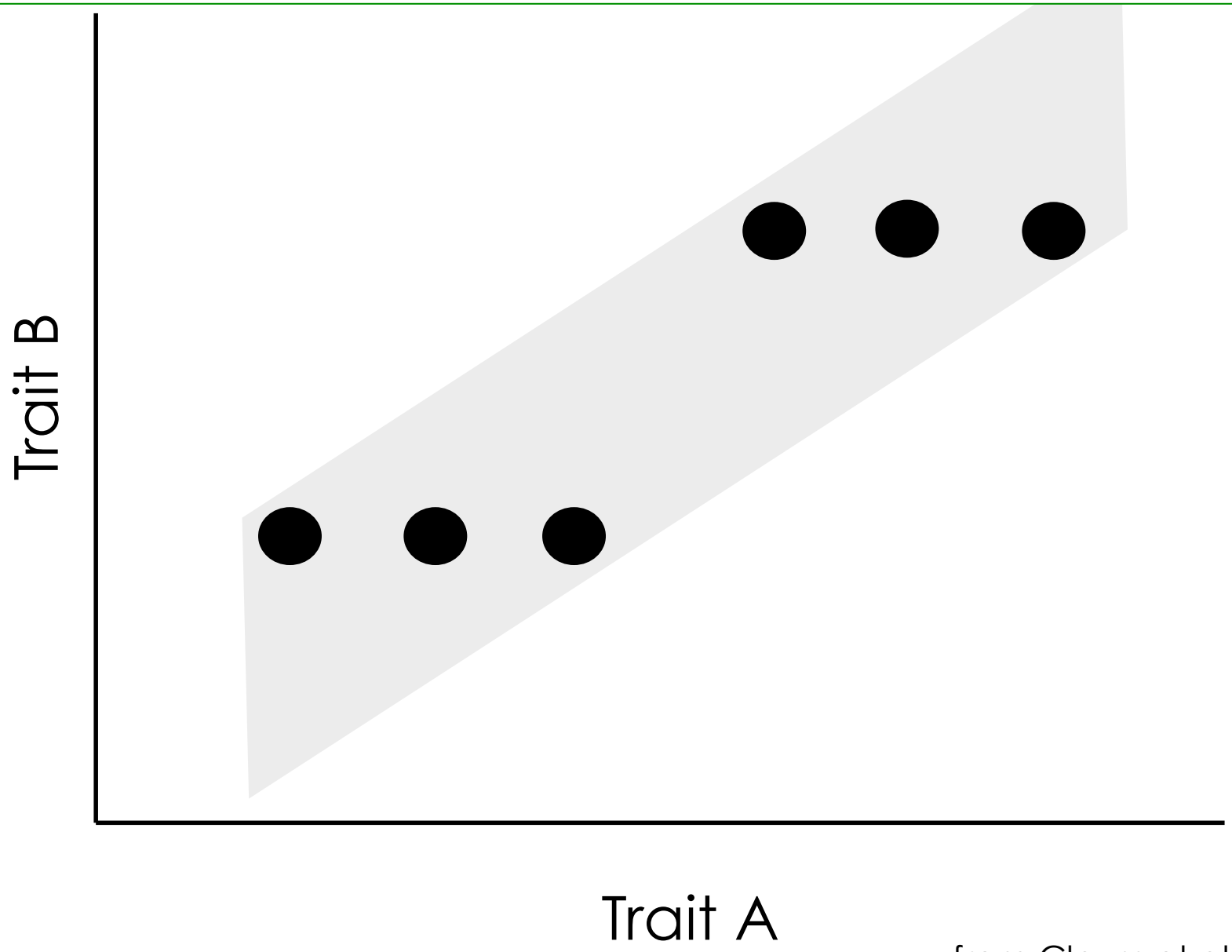

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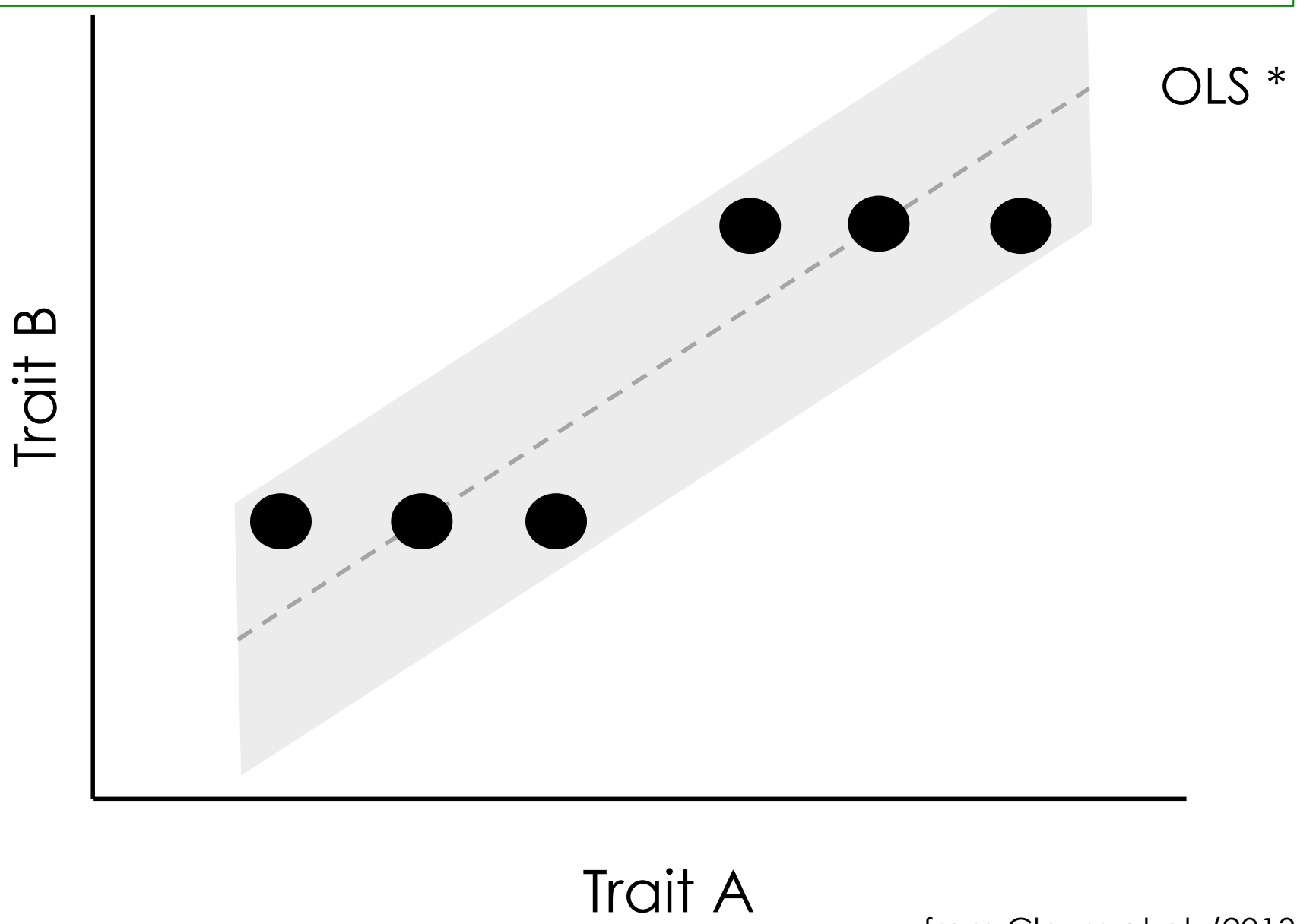

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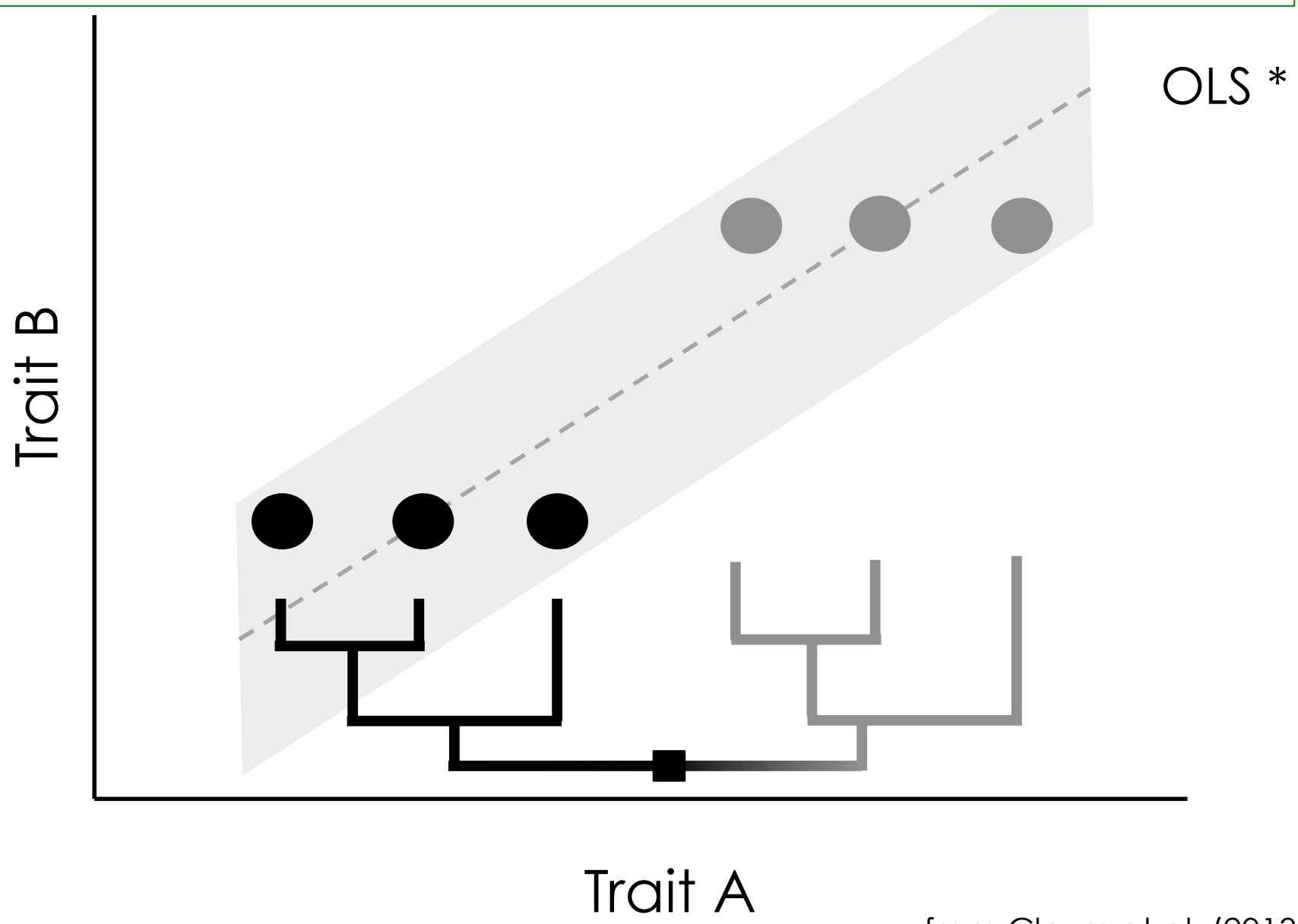

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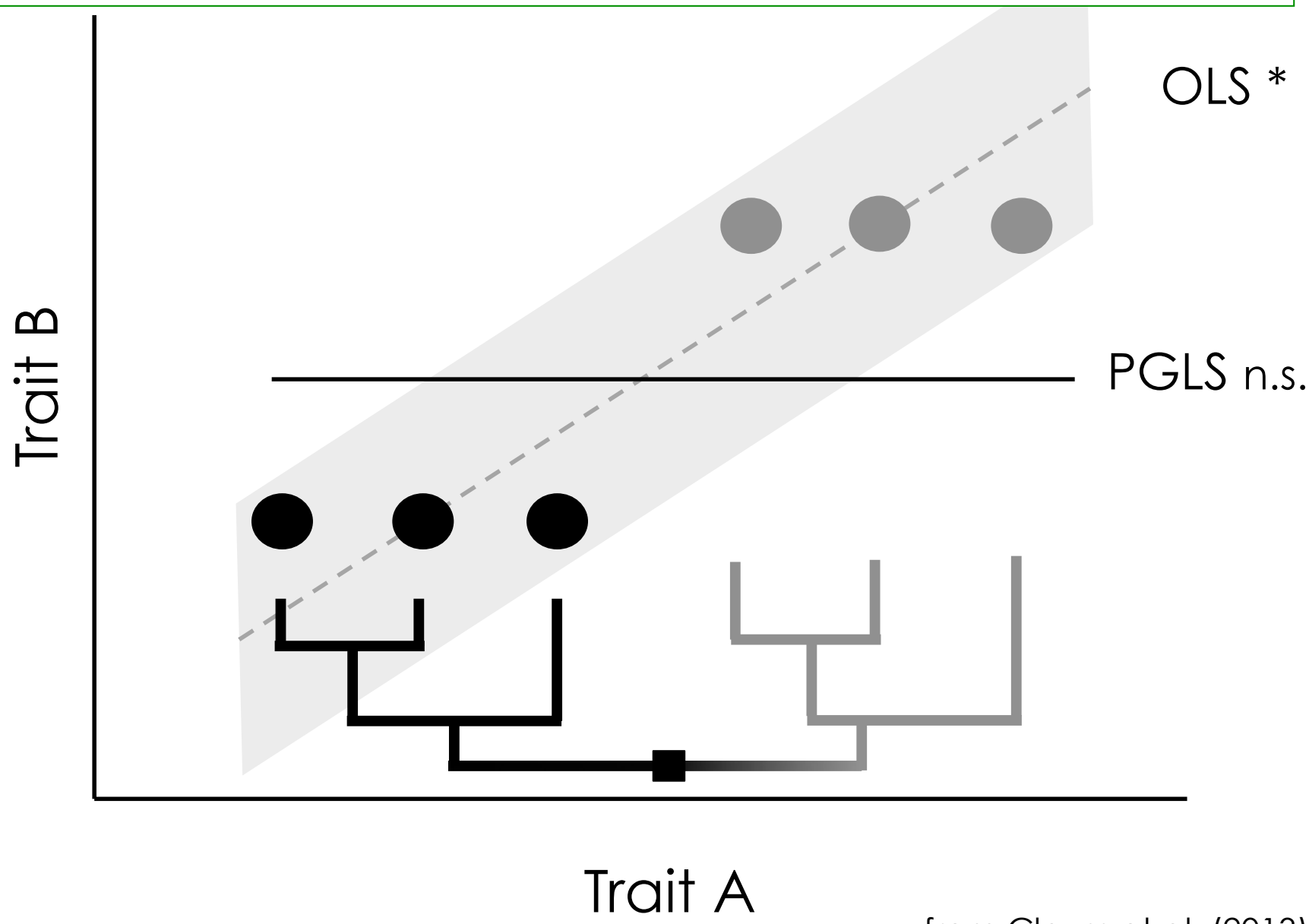
Accounting for phylogeny



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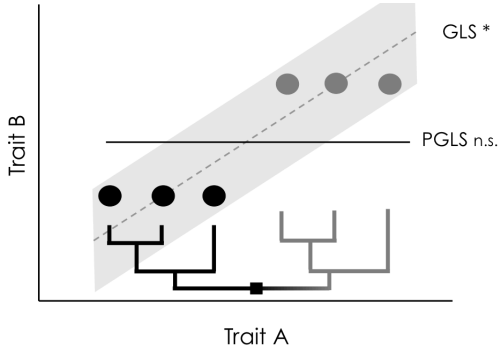
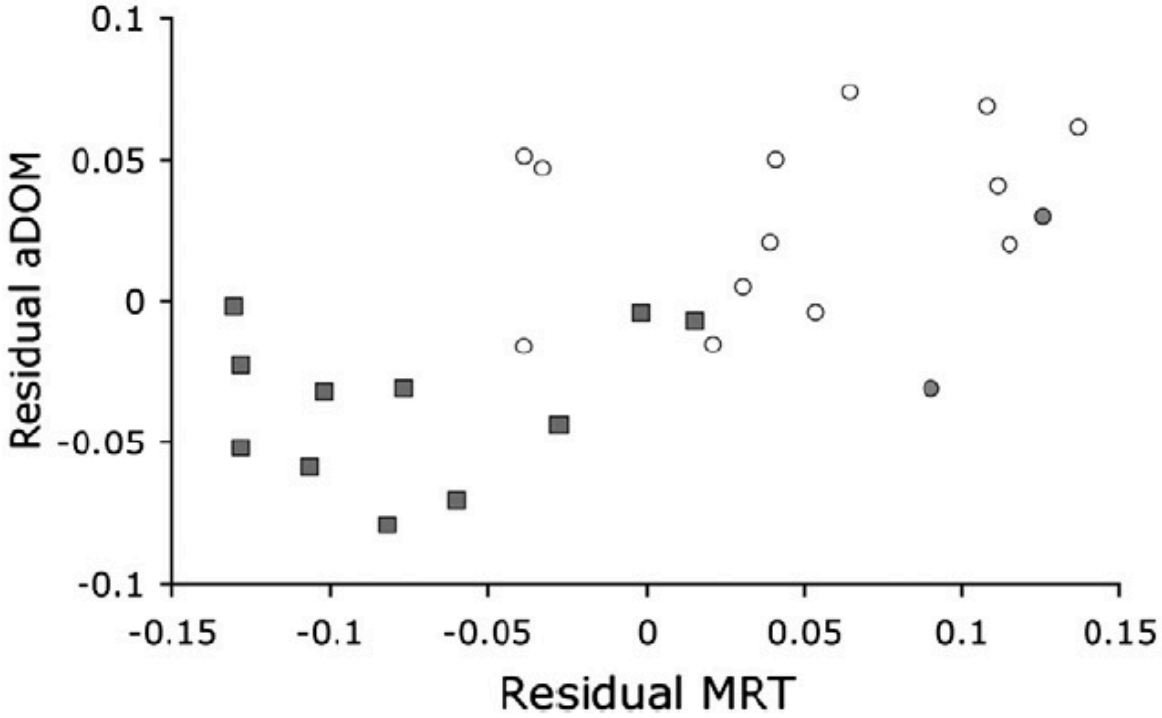


OLS: significant

PGLS: not significant



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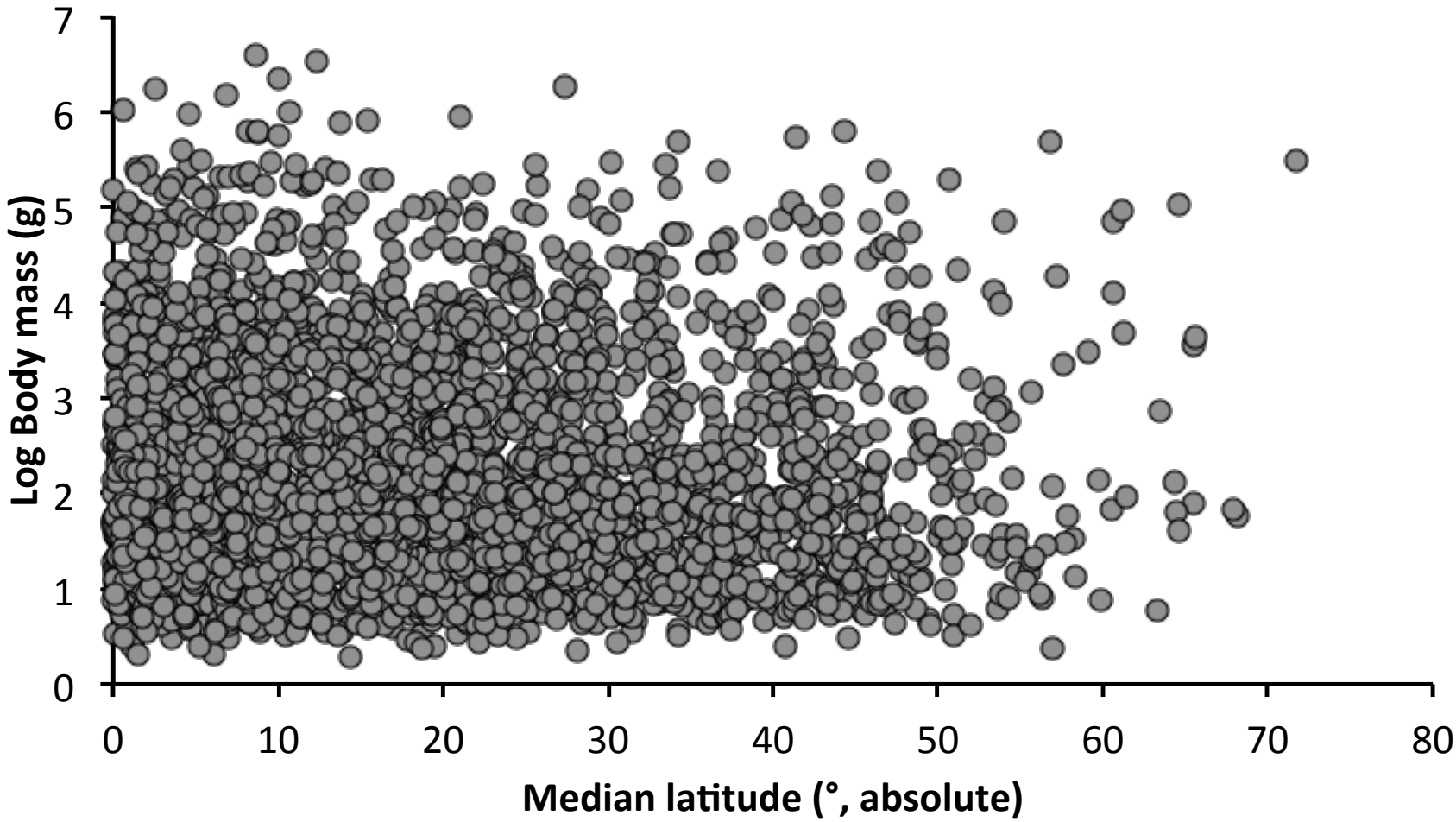
Example IV: Bergmann's rule



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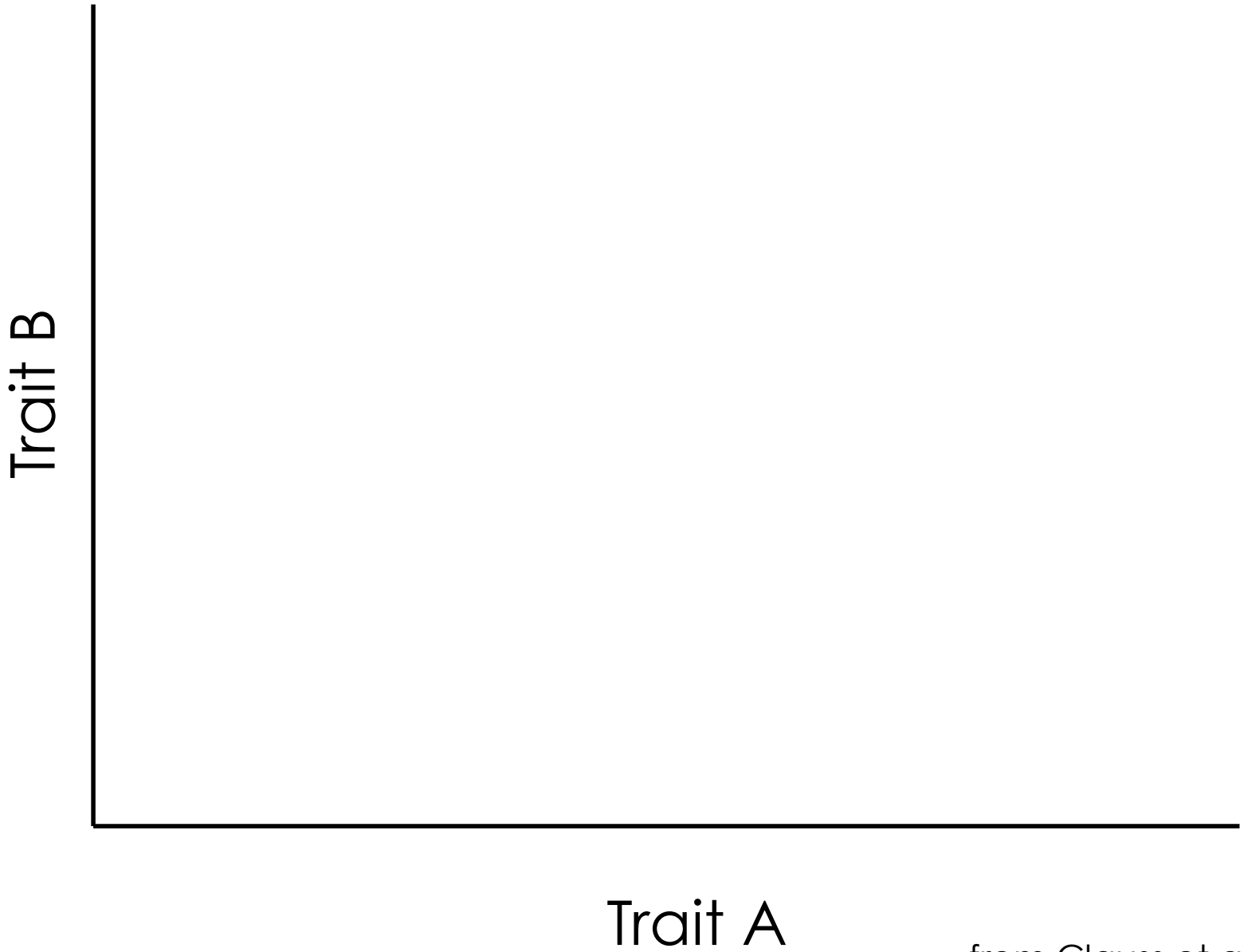
Accounting for phylogeny



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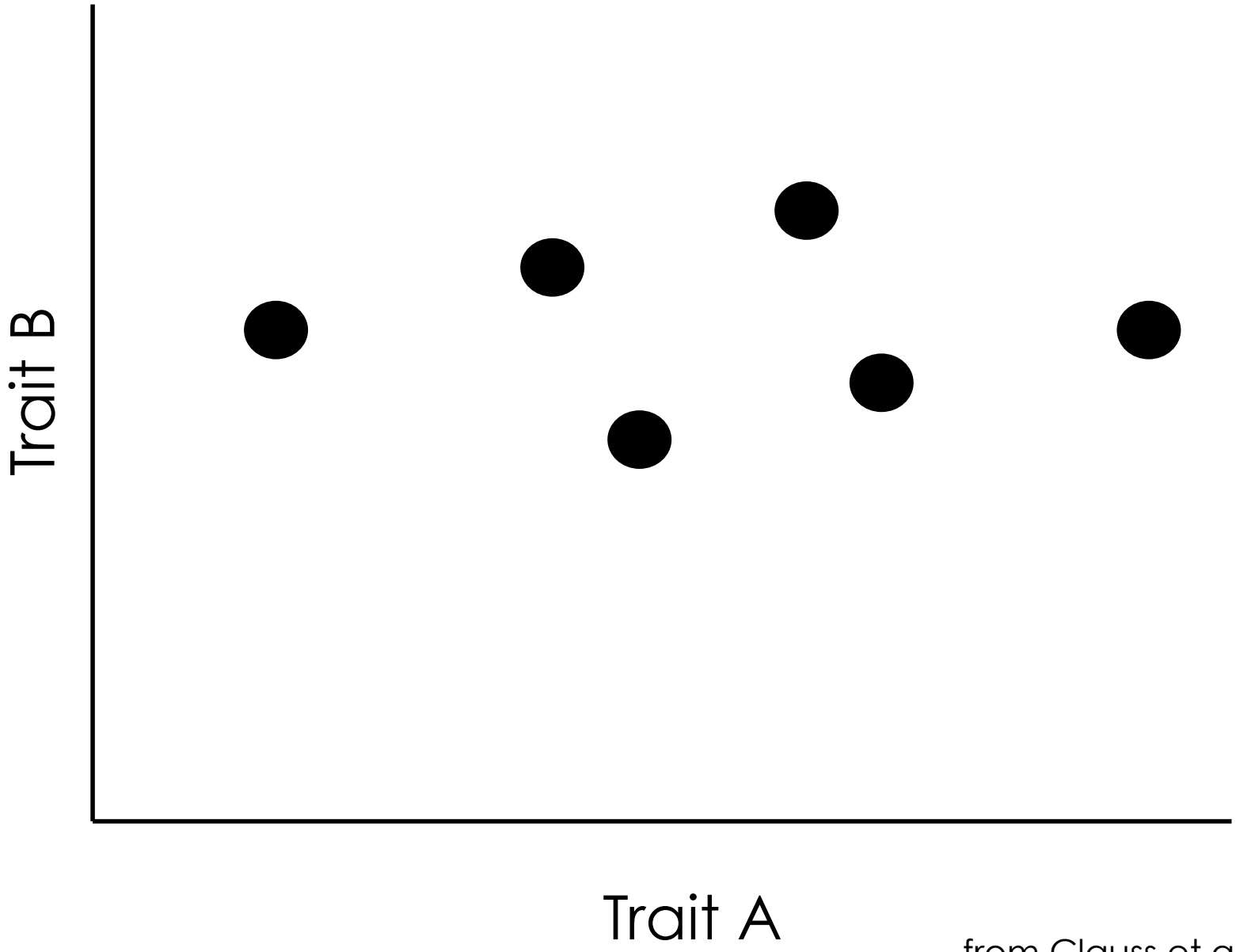
Accounting for phylogeny



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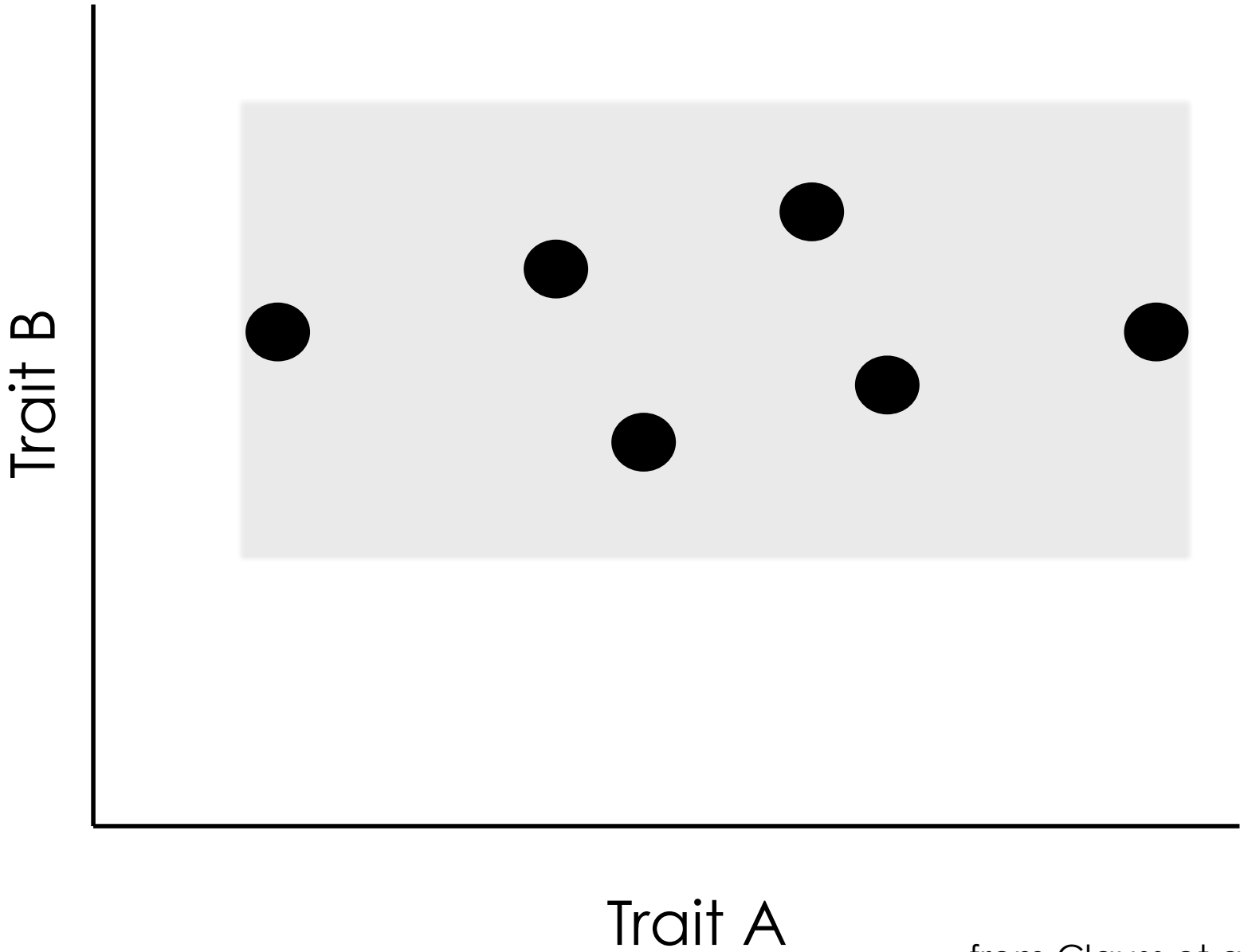

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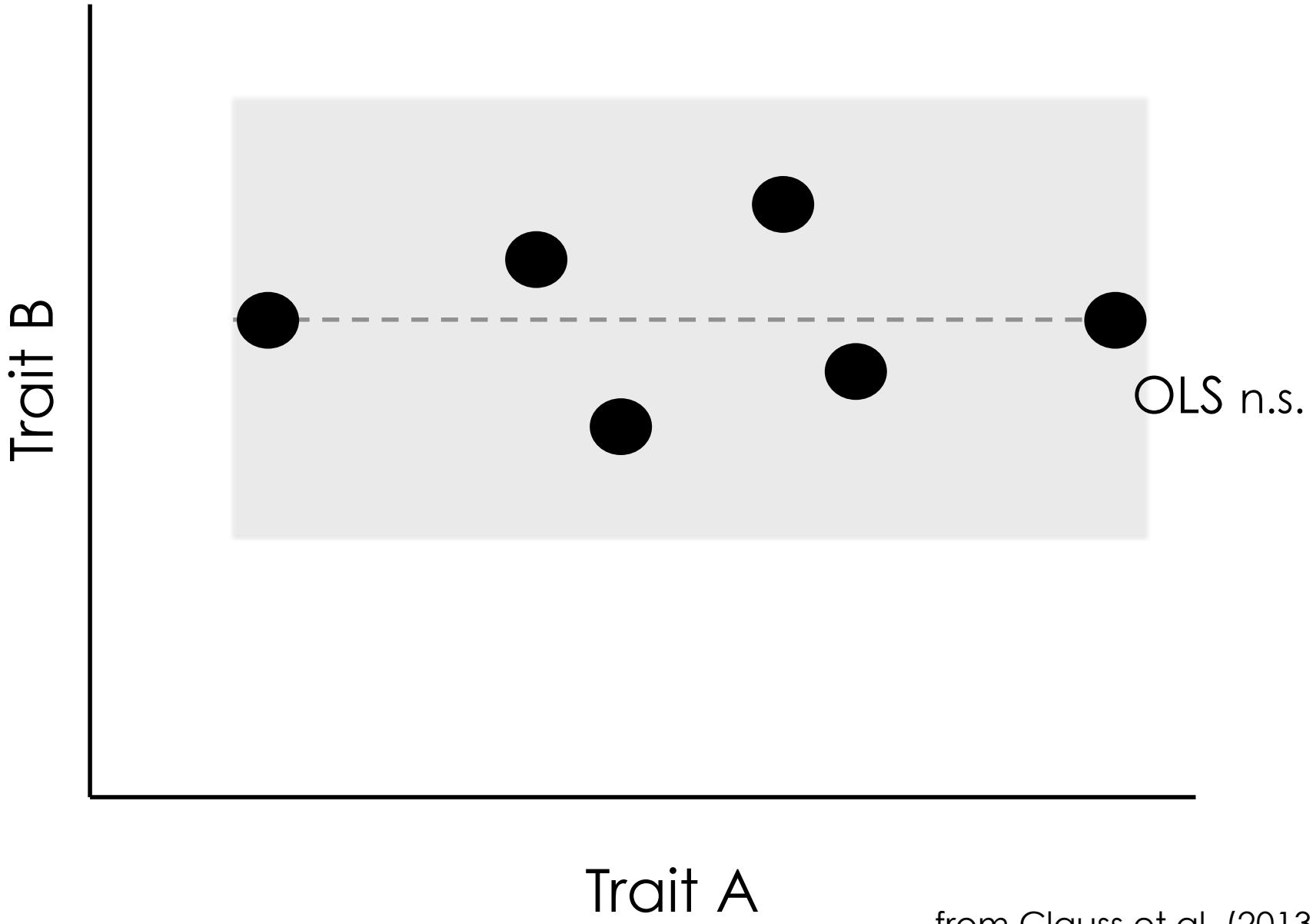

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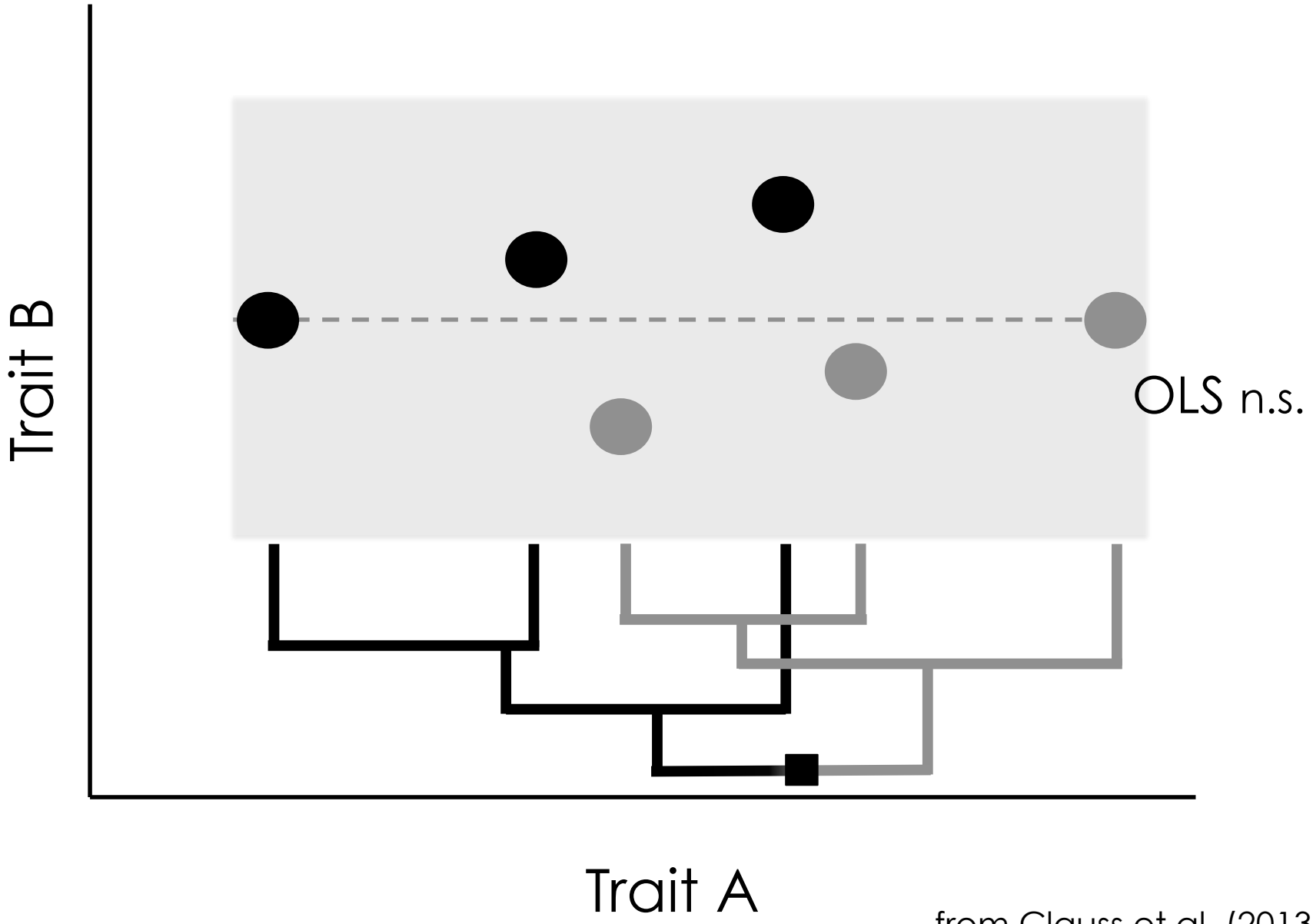

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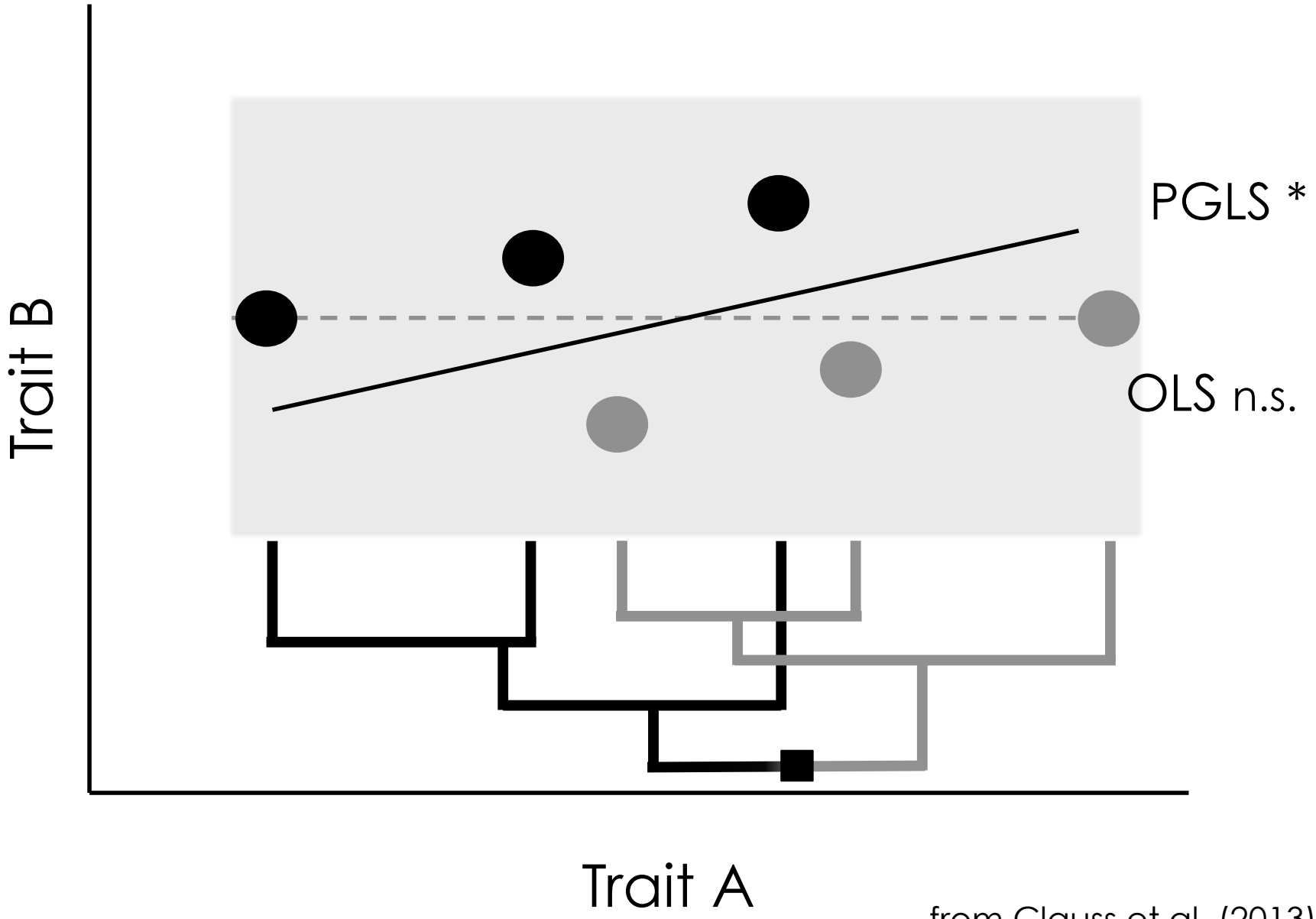

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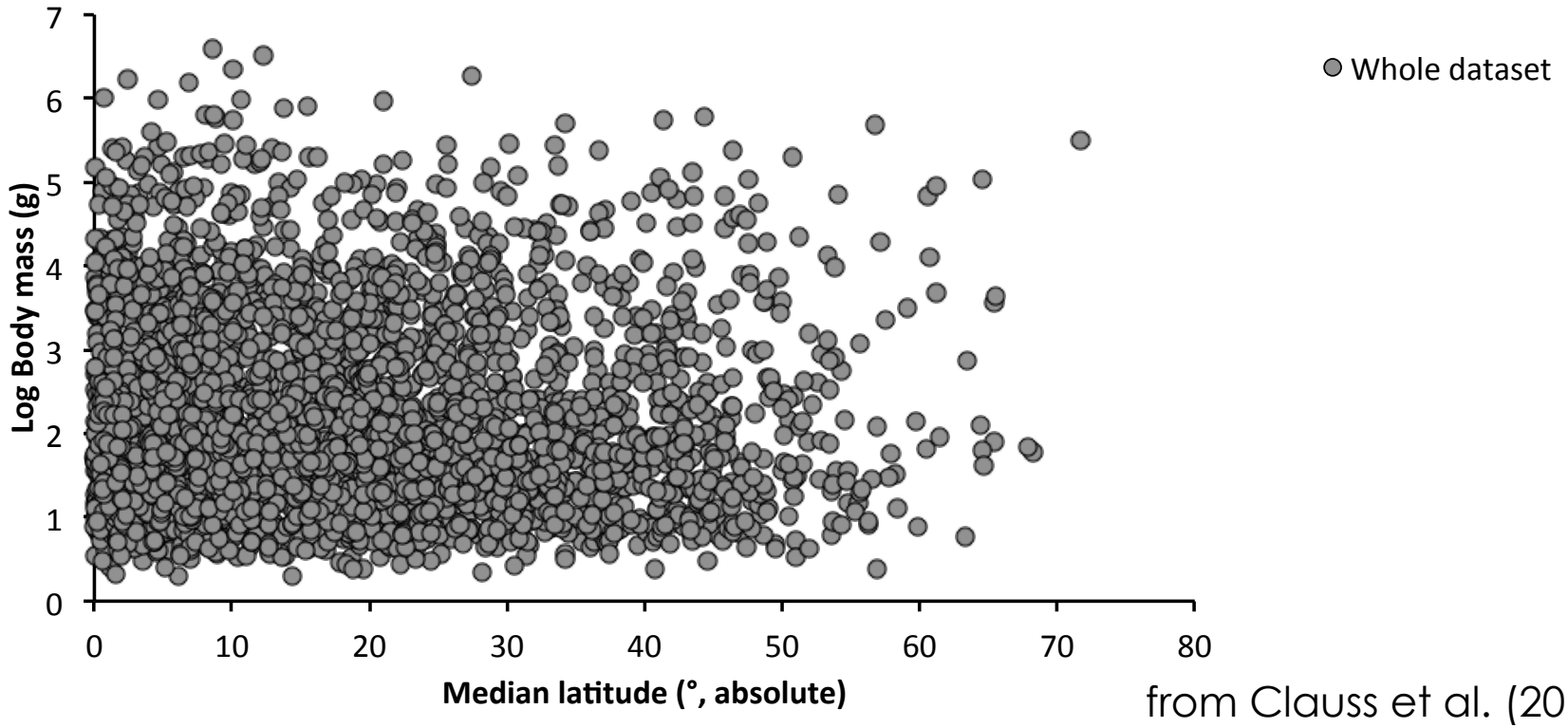
Example IV: Bergmann's rule

OLS: 2.19 (±0.03) - 0.0012 (±0.0013) Lat.

PGLS: 2.79 (±0.47) + 0.0016 (±0.0005) Lat.



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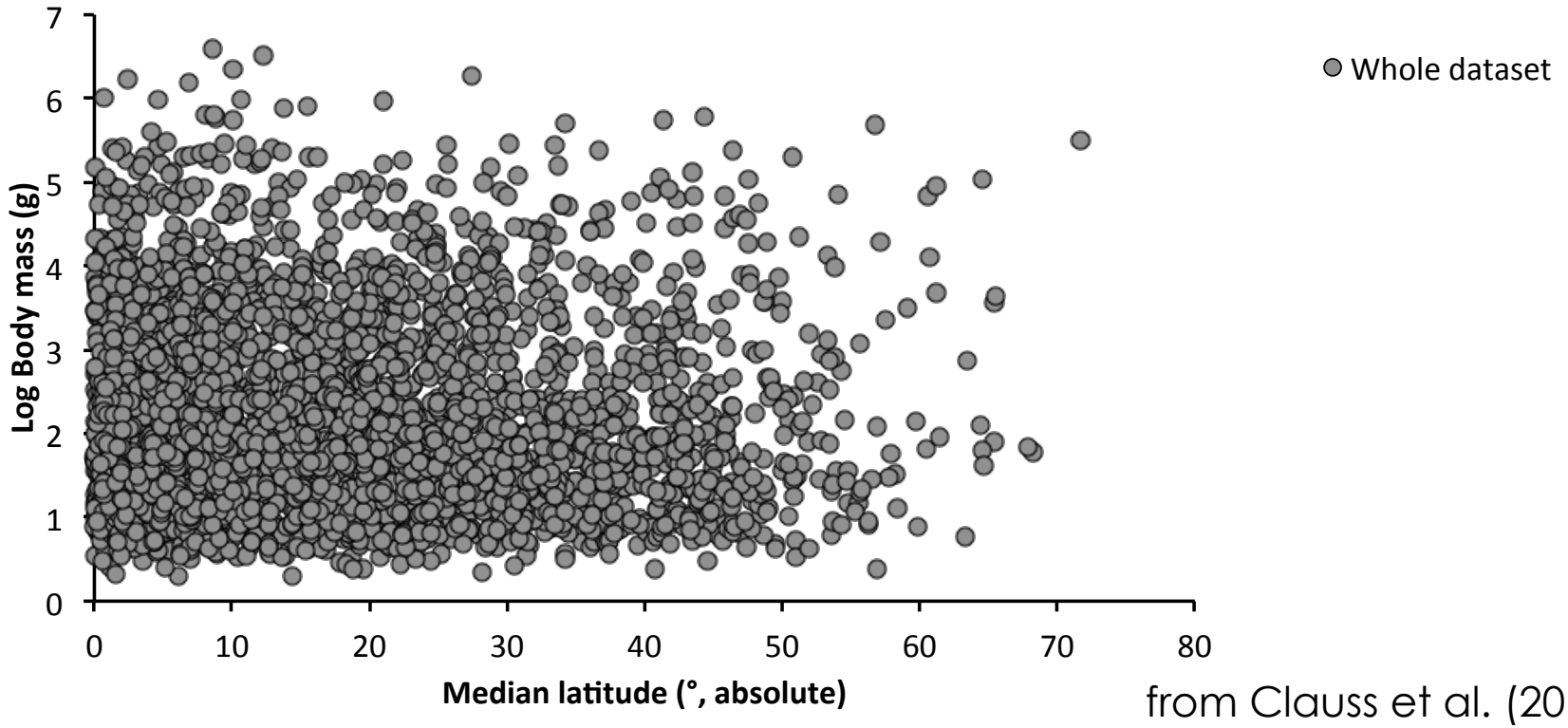

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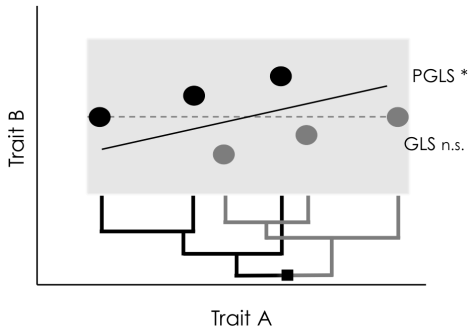

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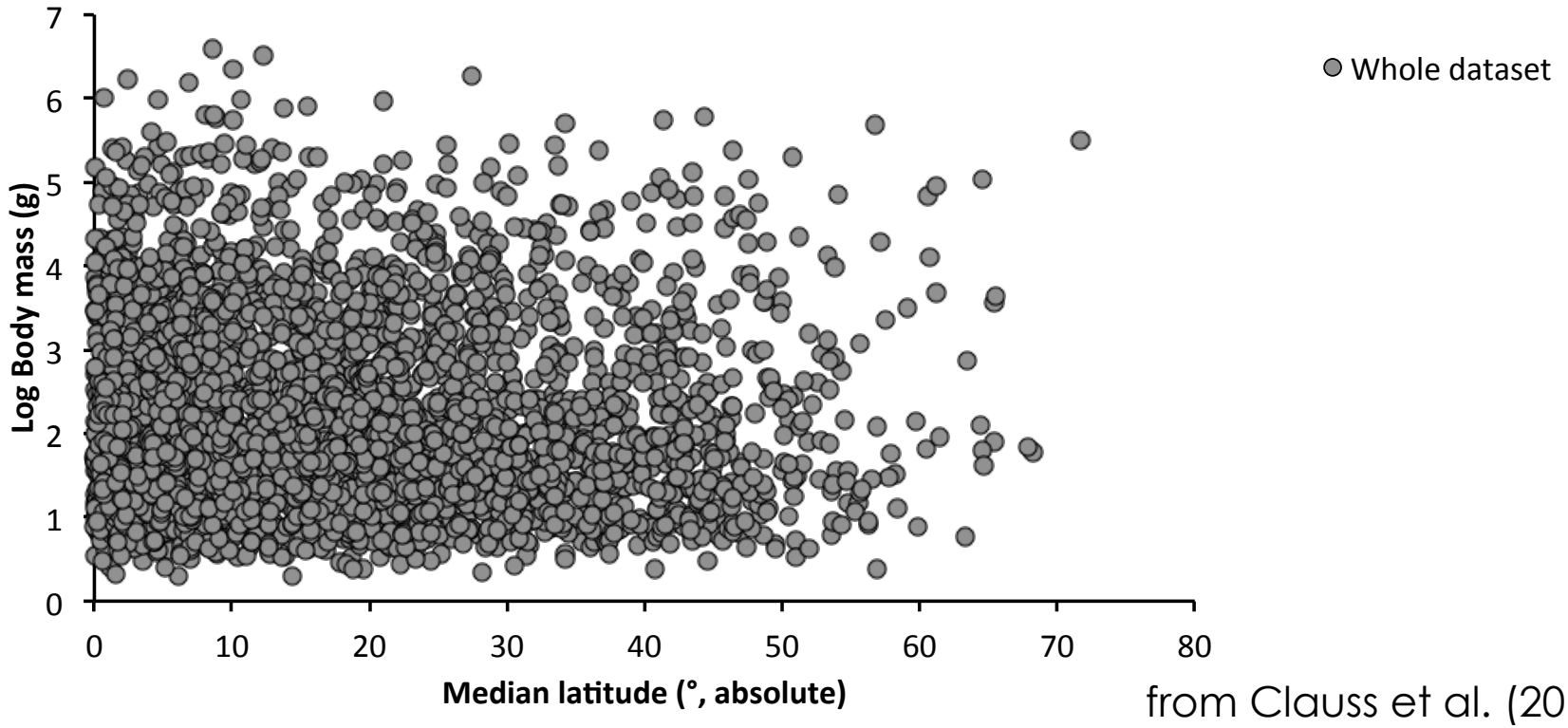

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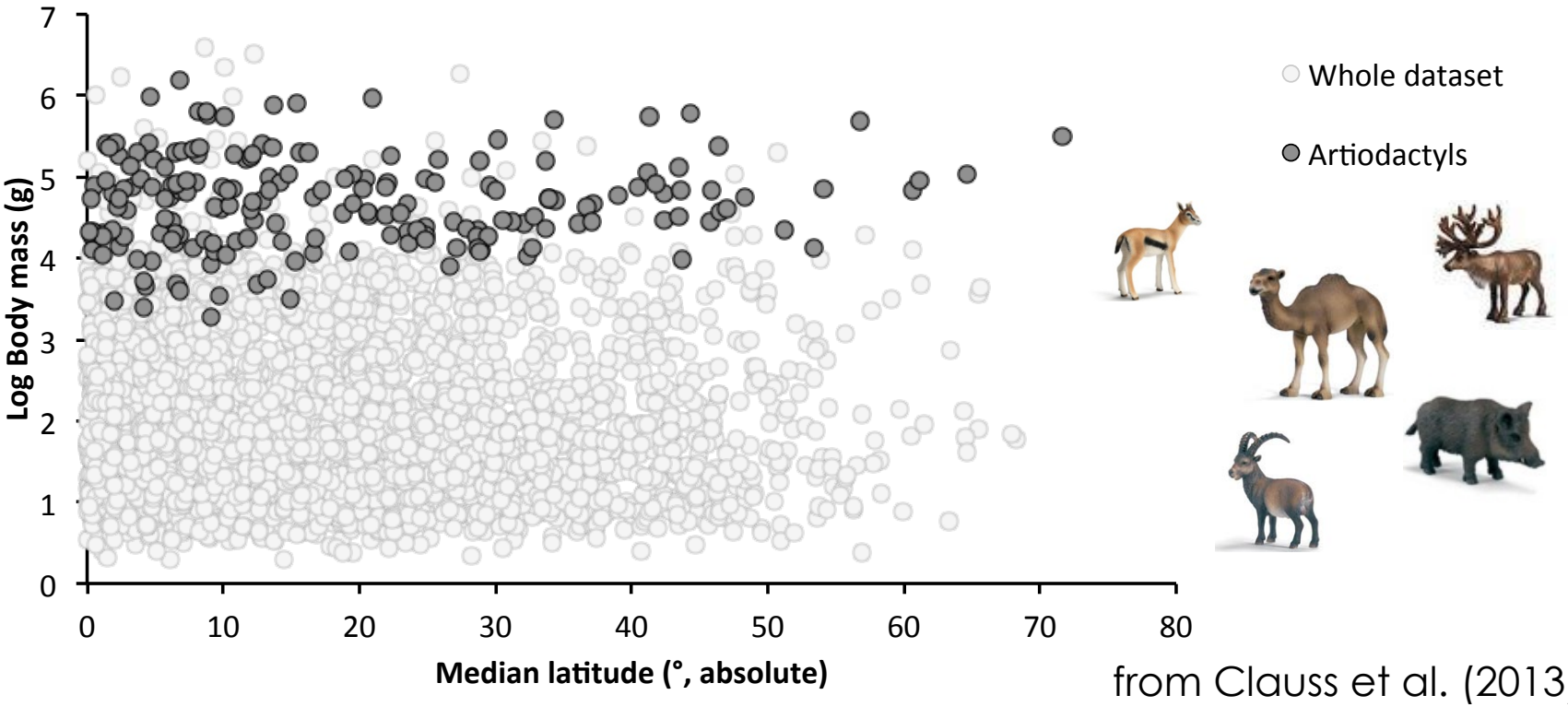

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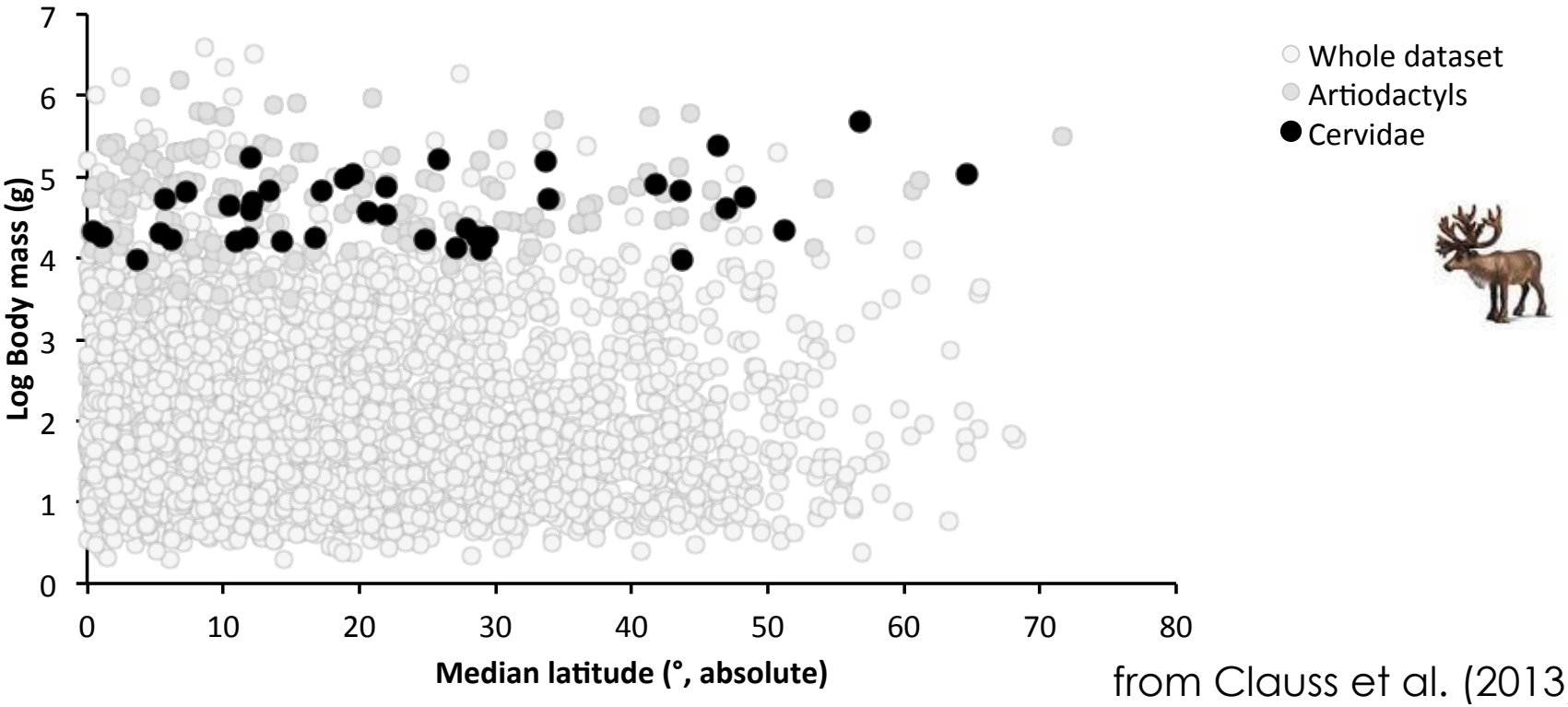

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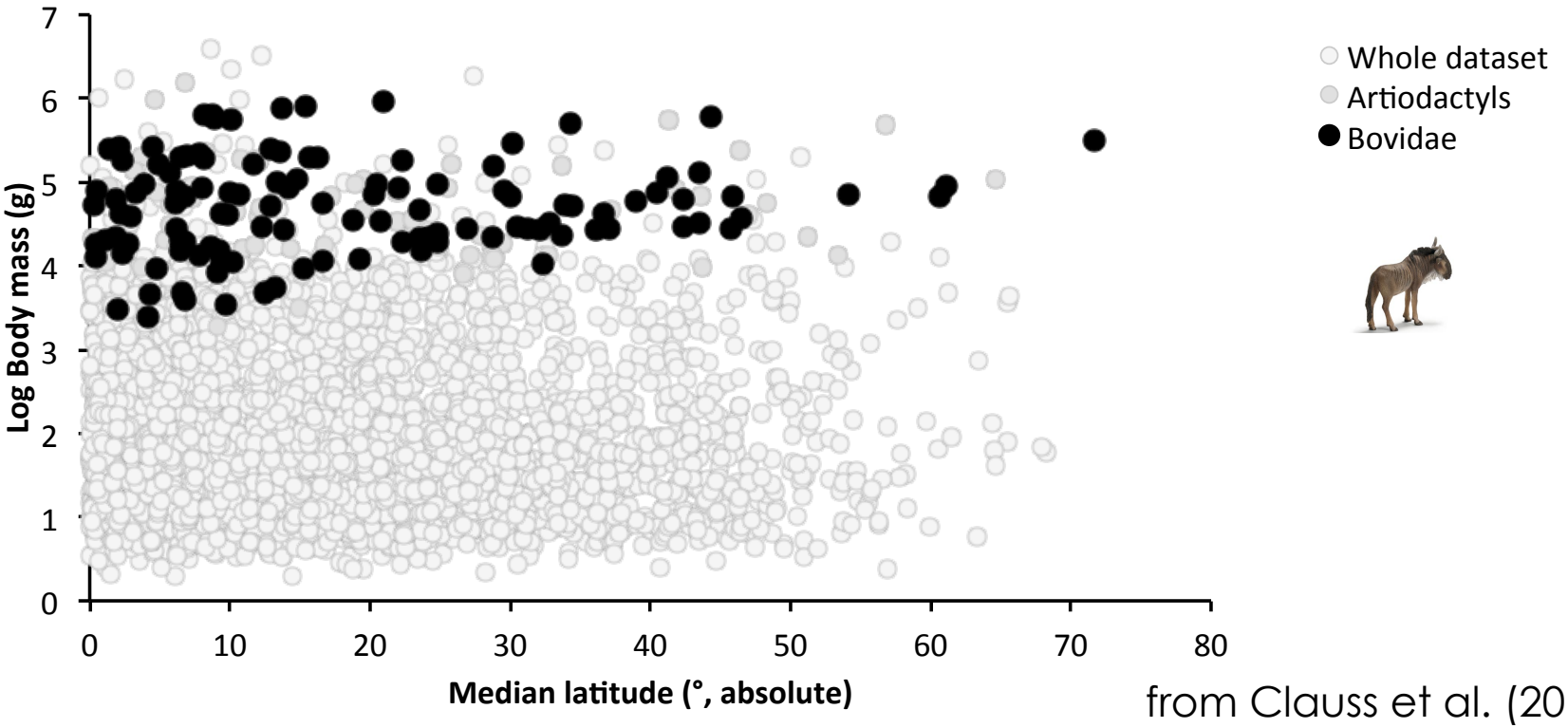

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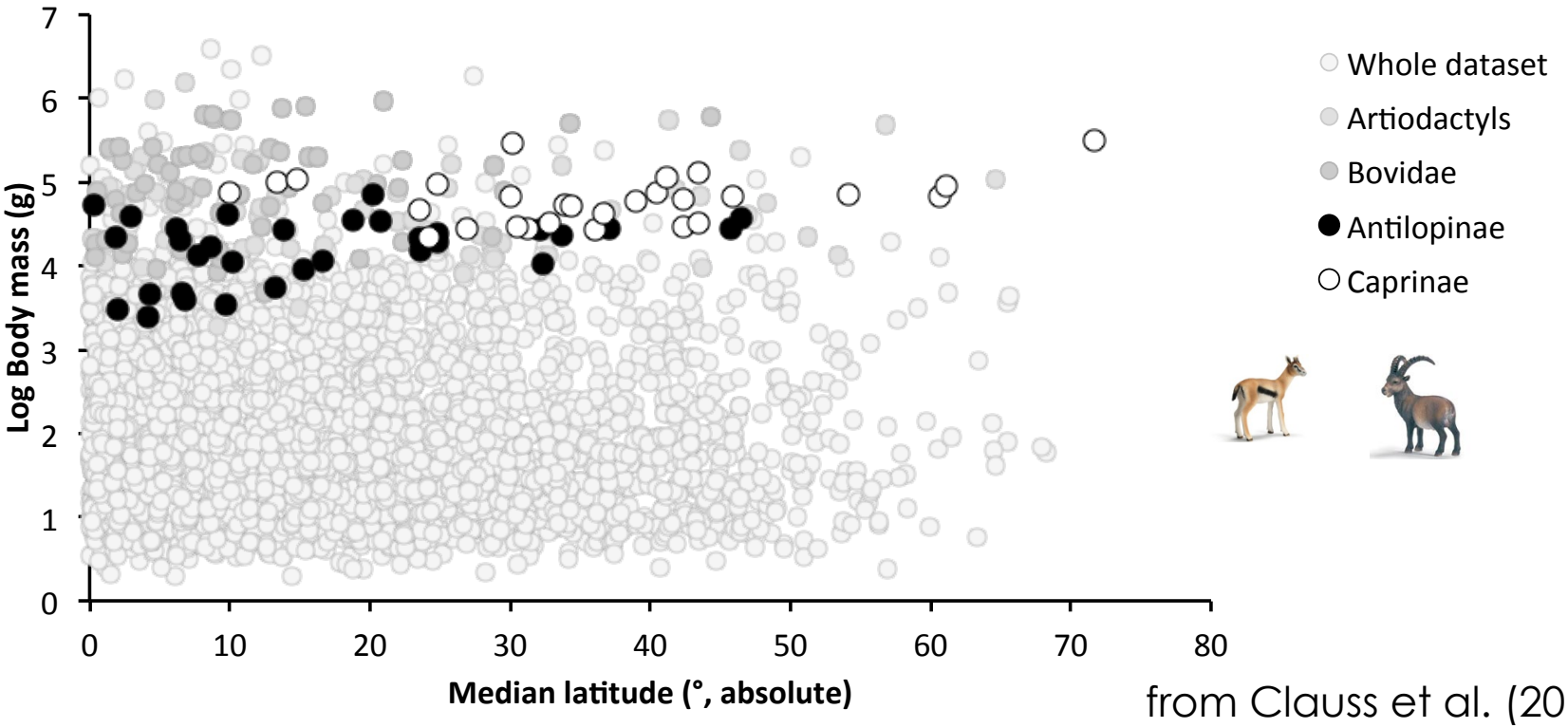

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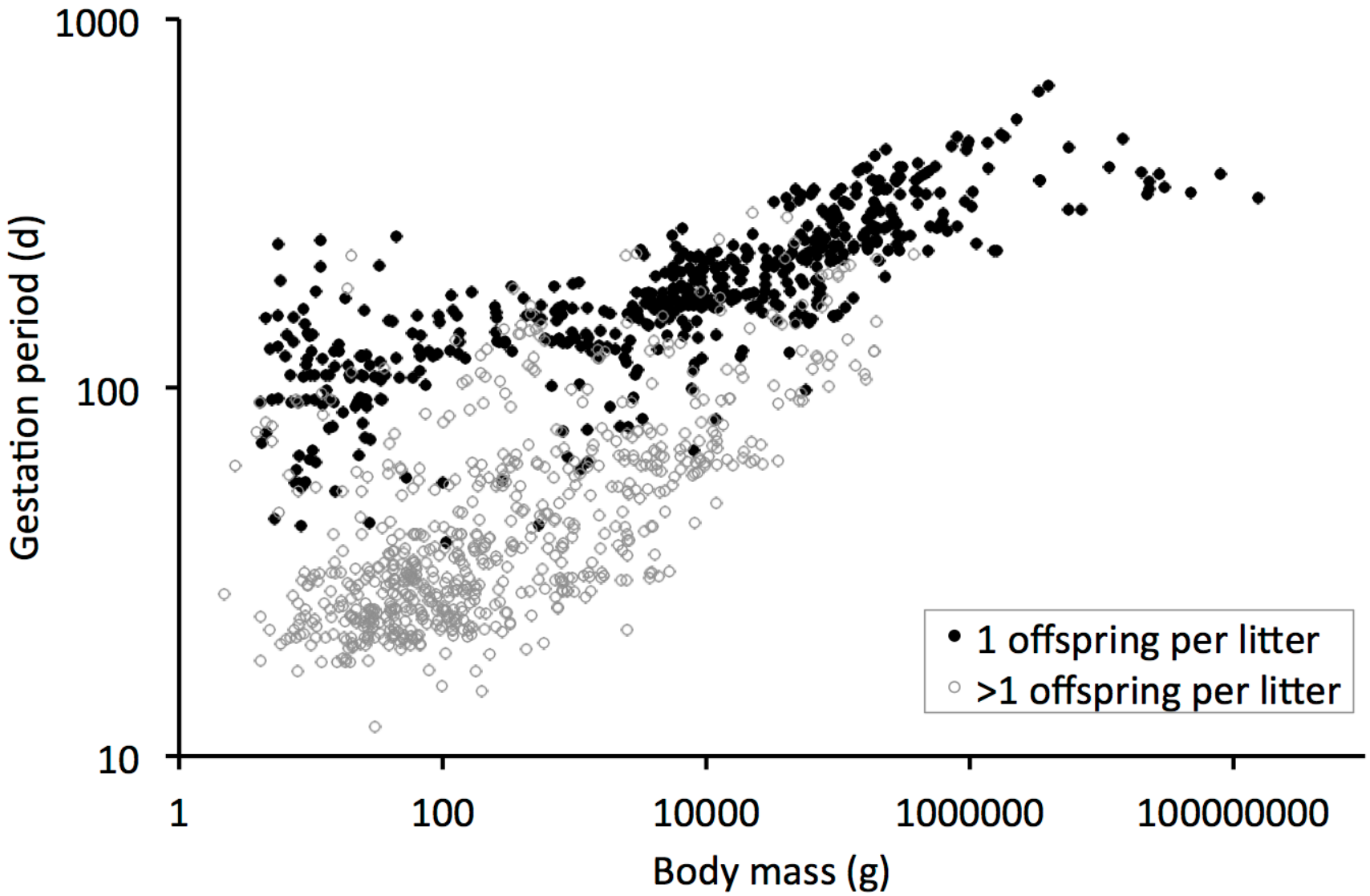
Example V: Gestation time



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Accounting for phylogeny

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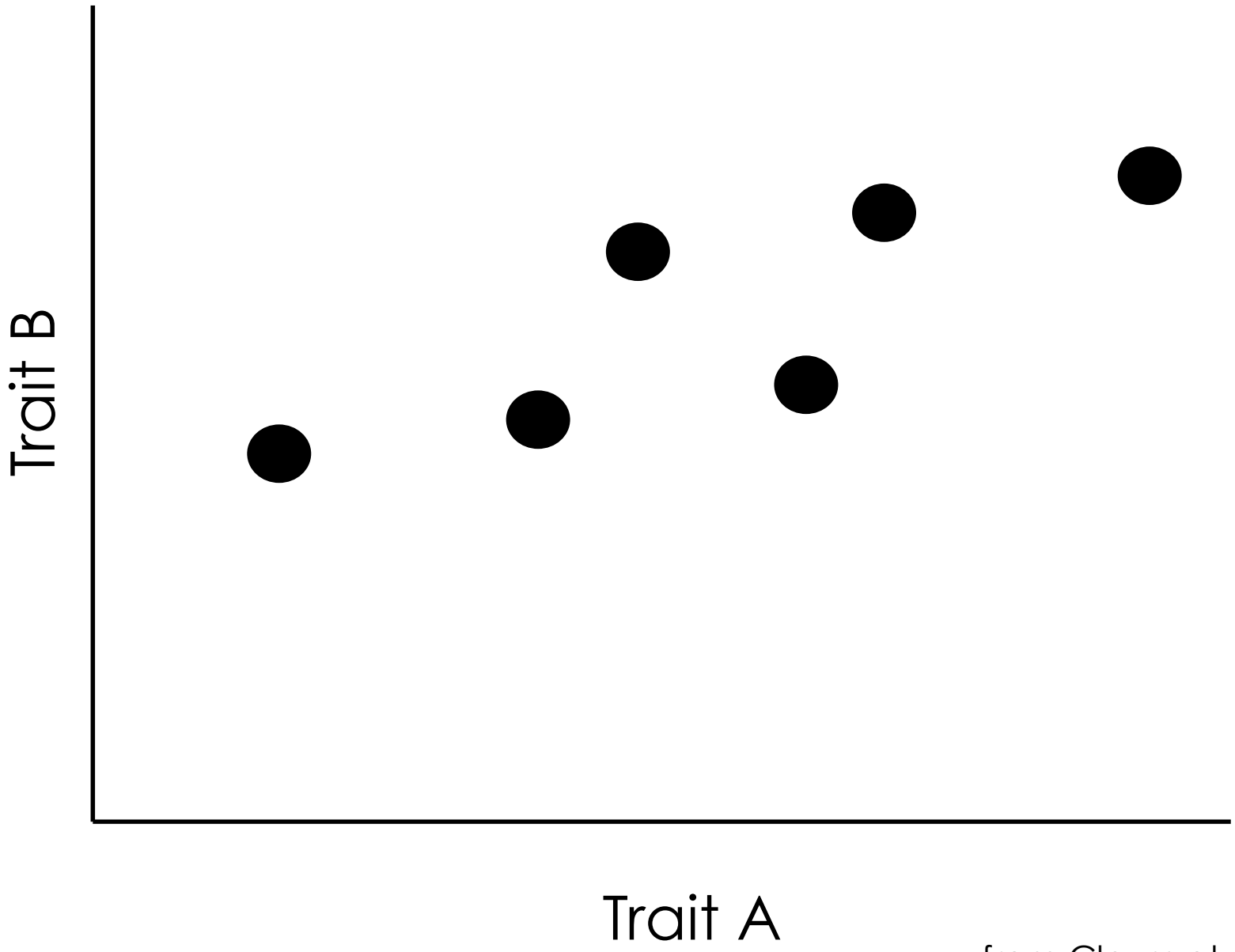

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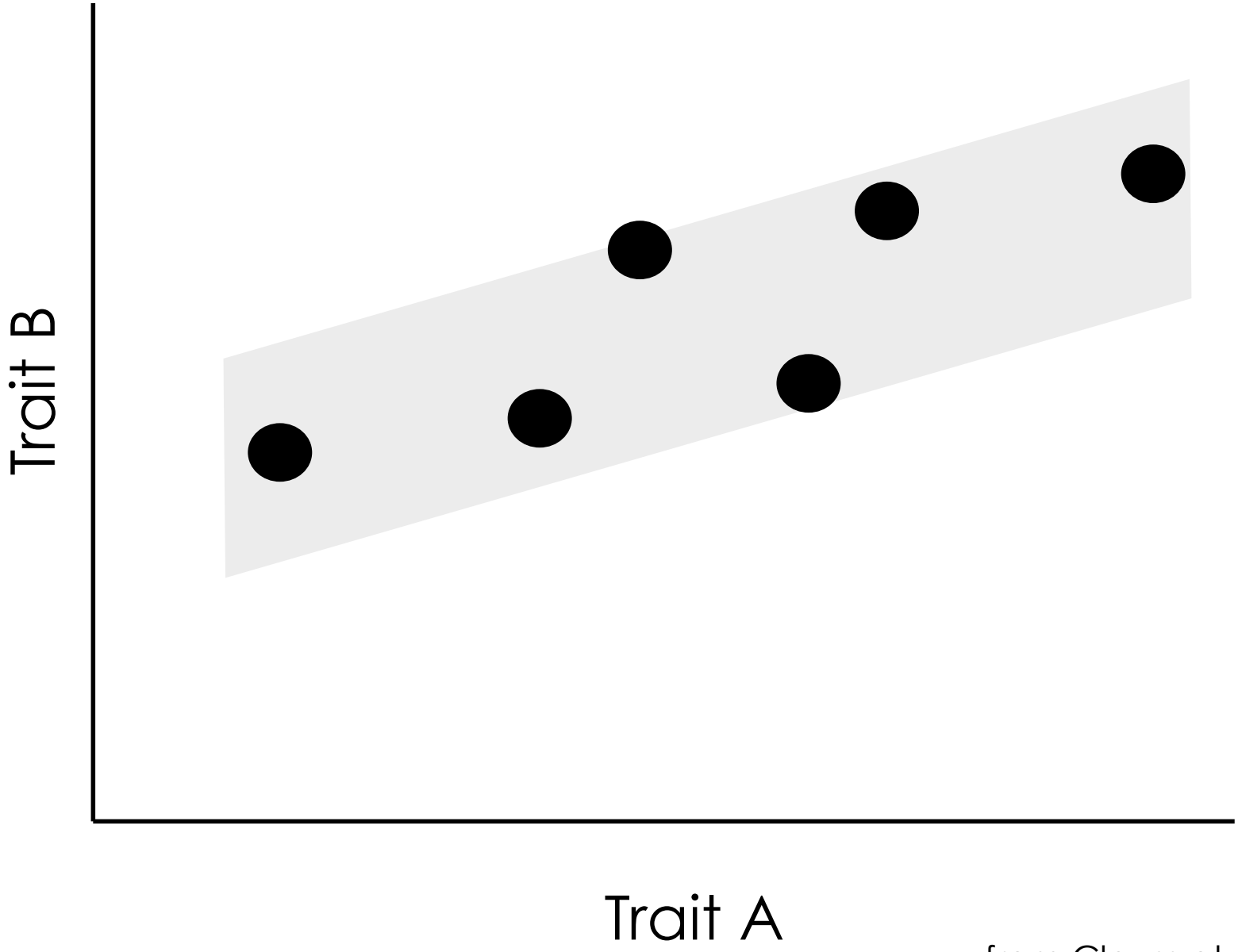

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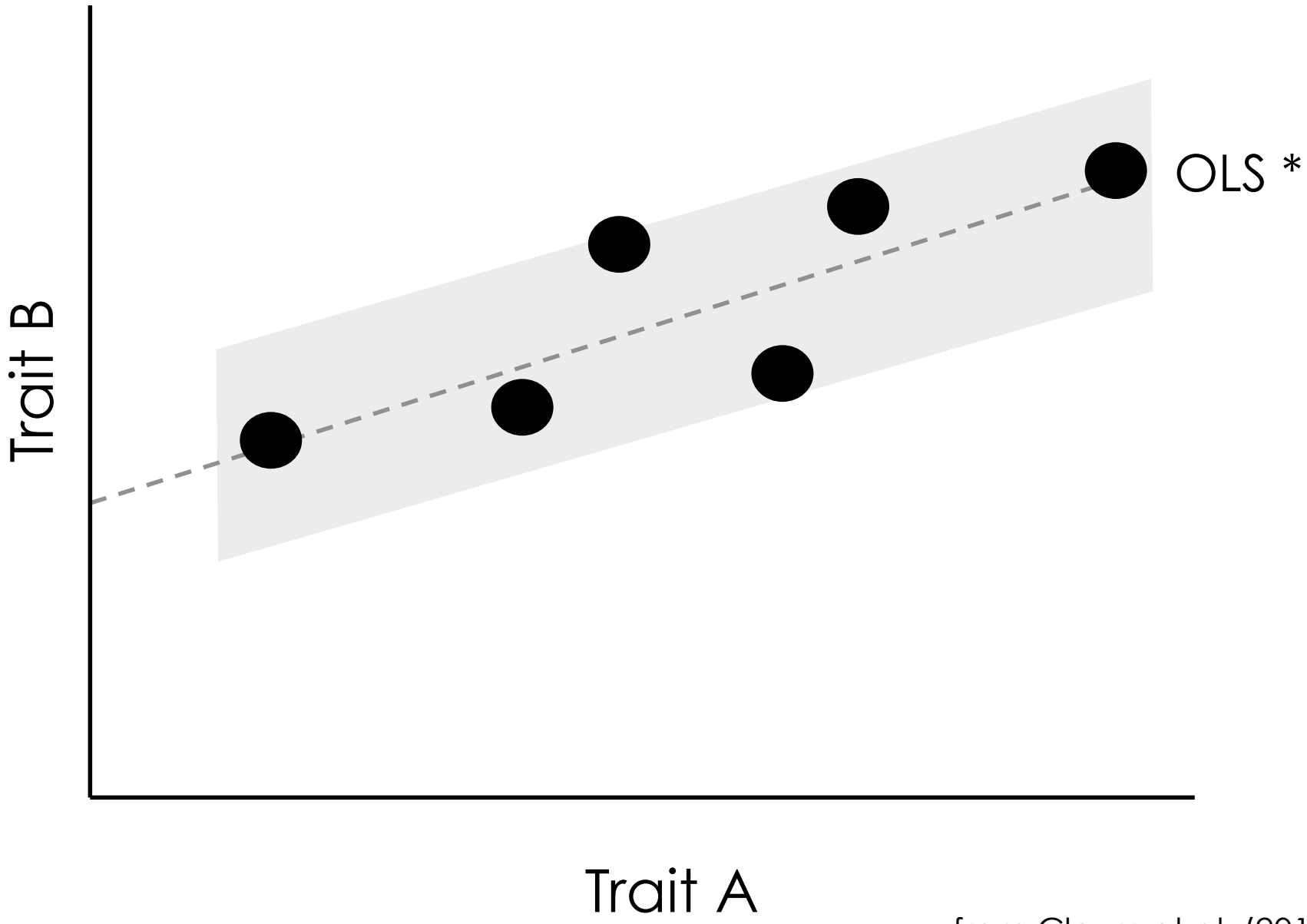

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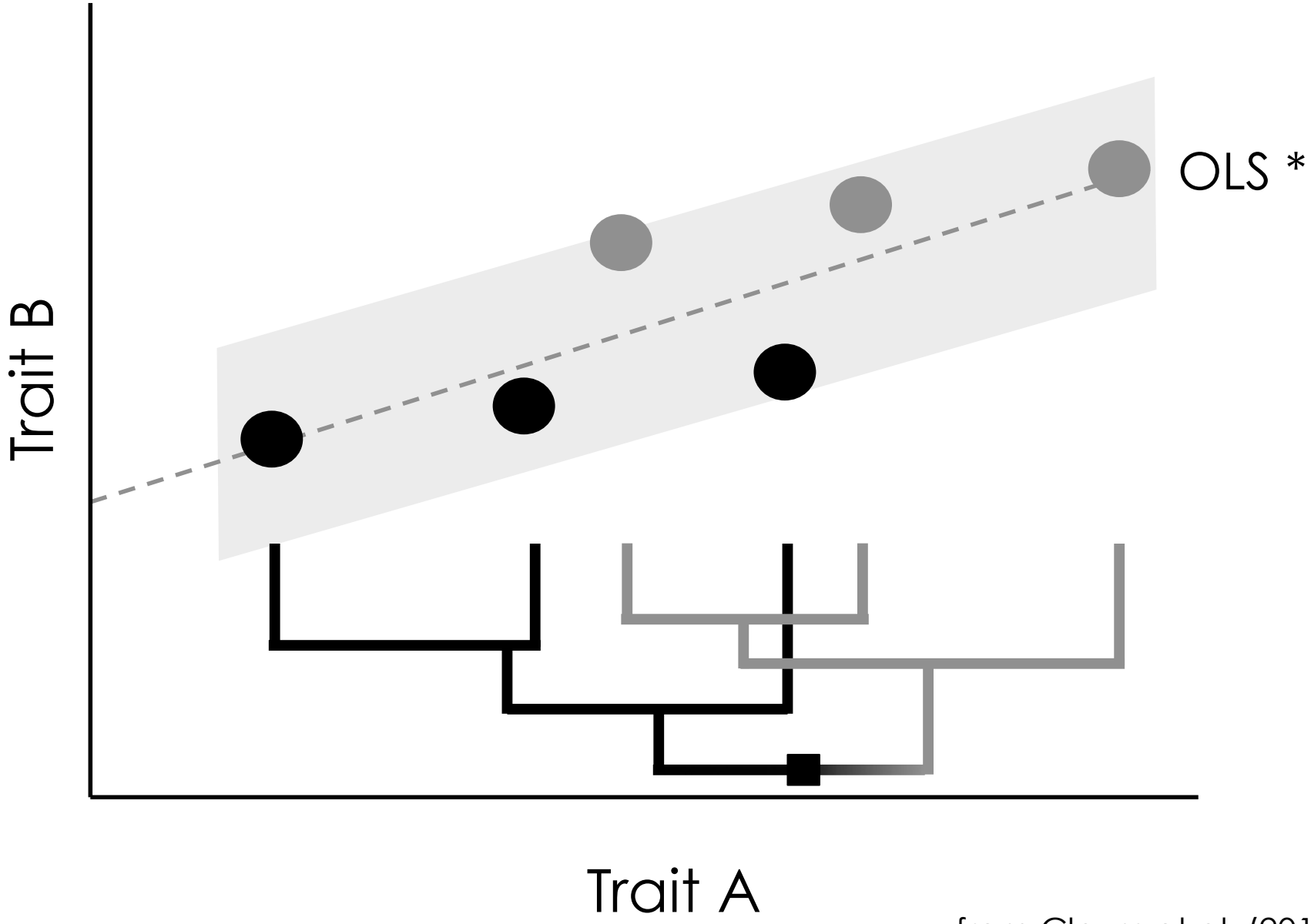

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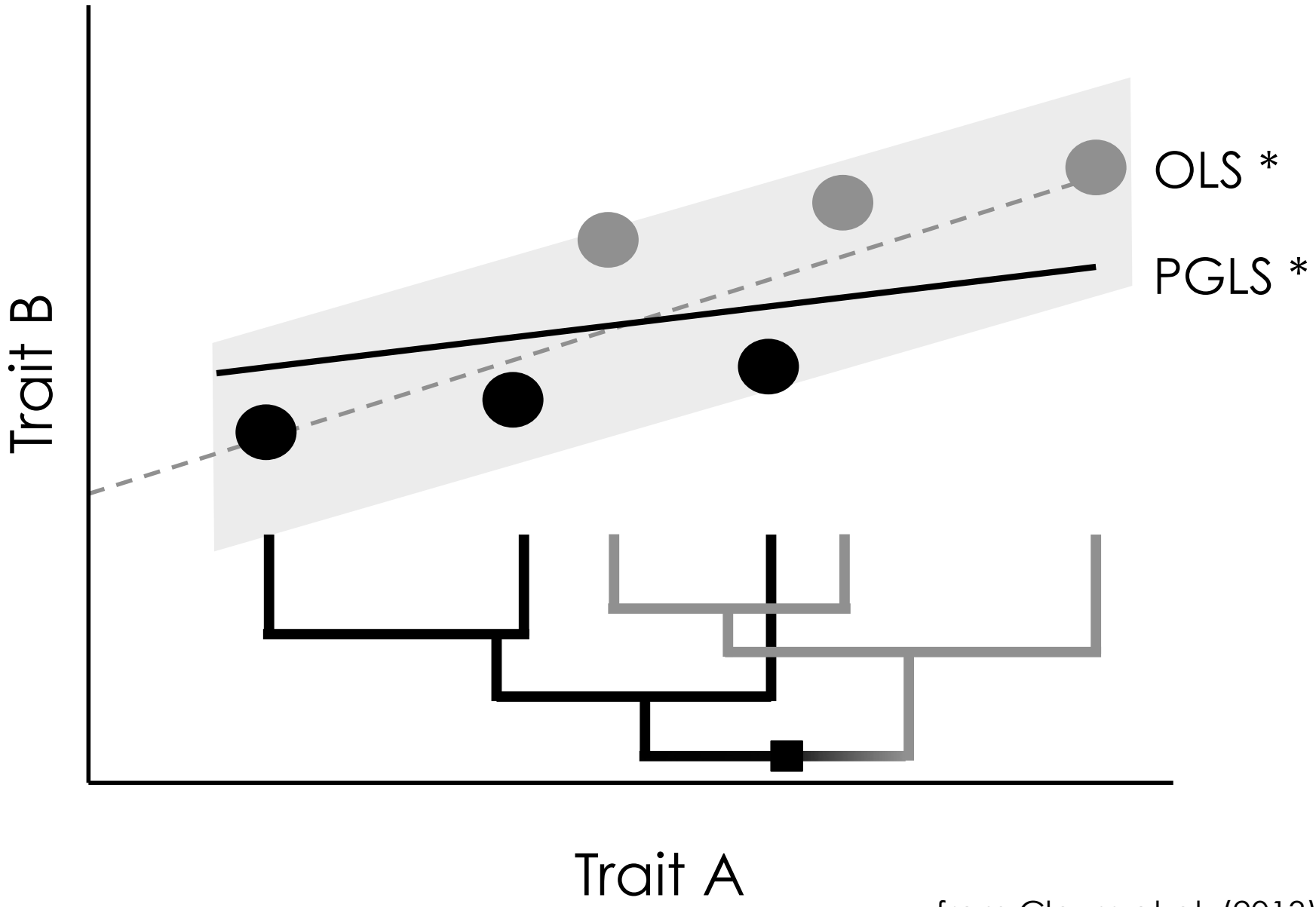

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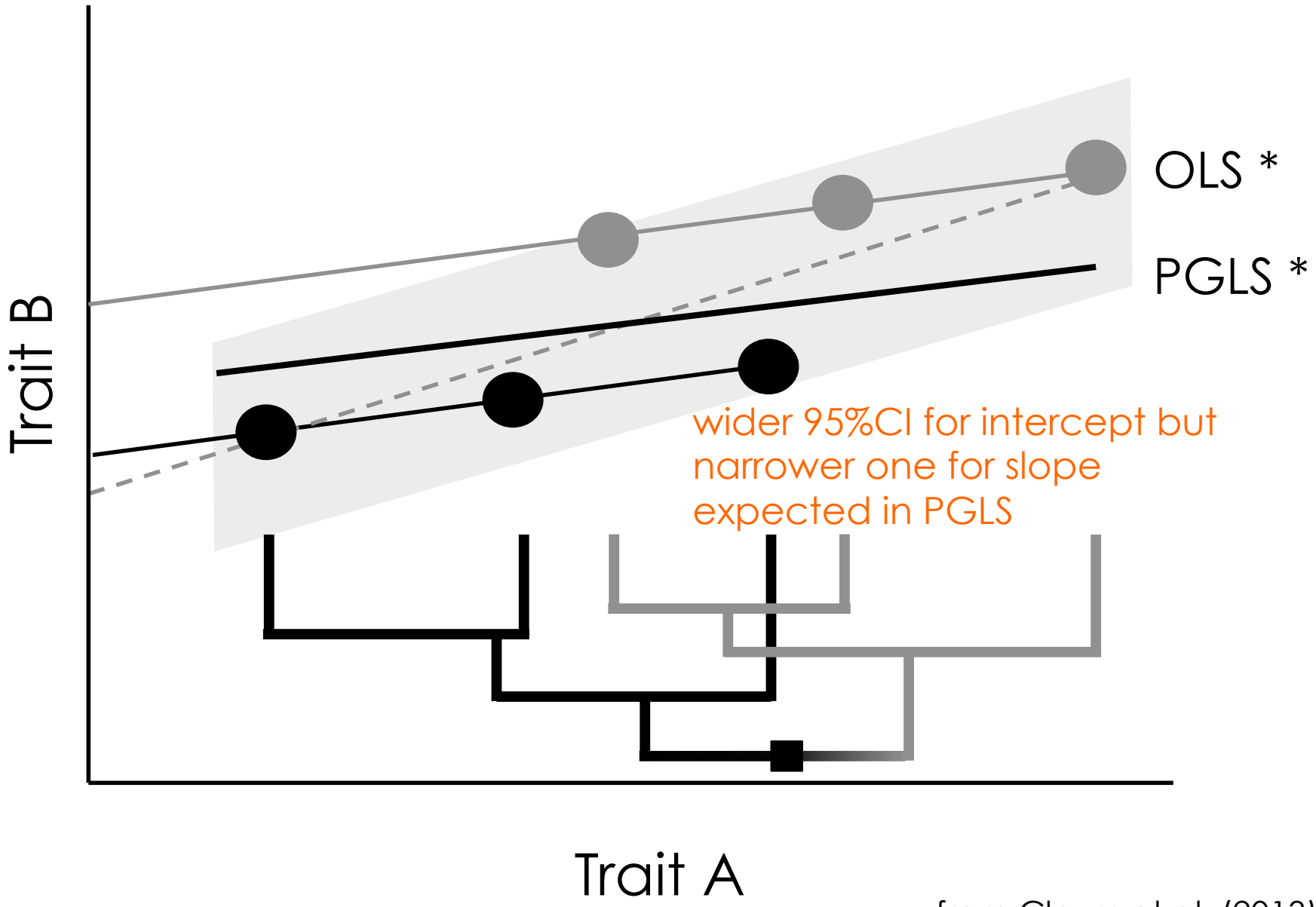

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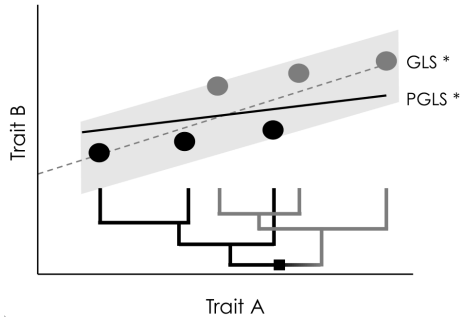

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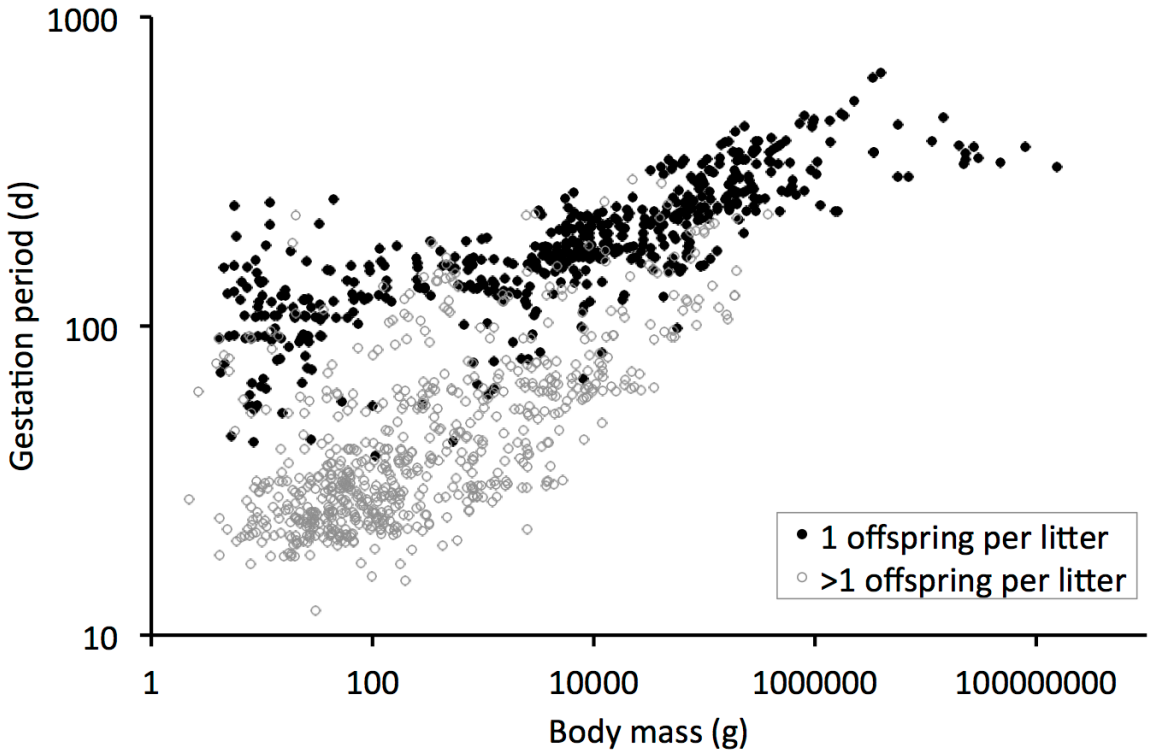

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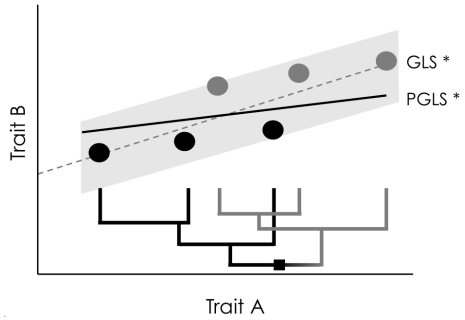

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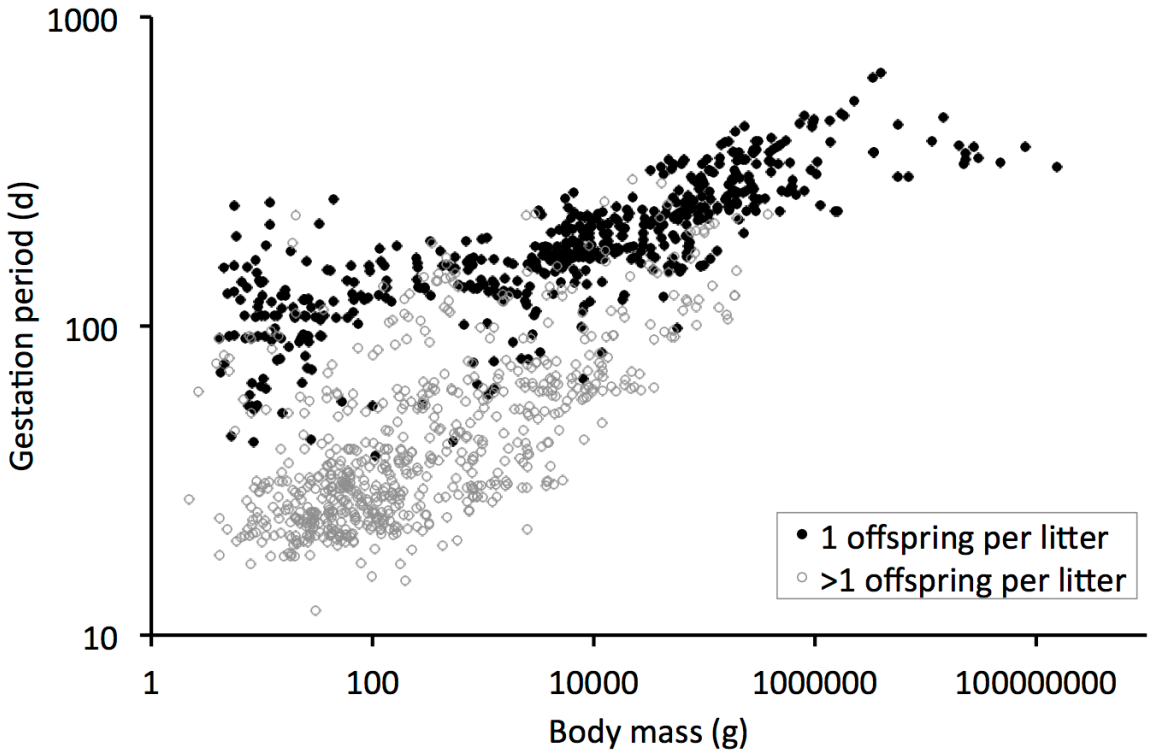

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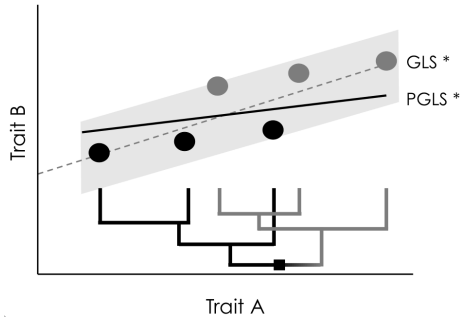

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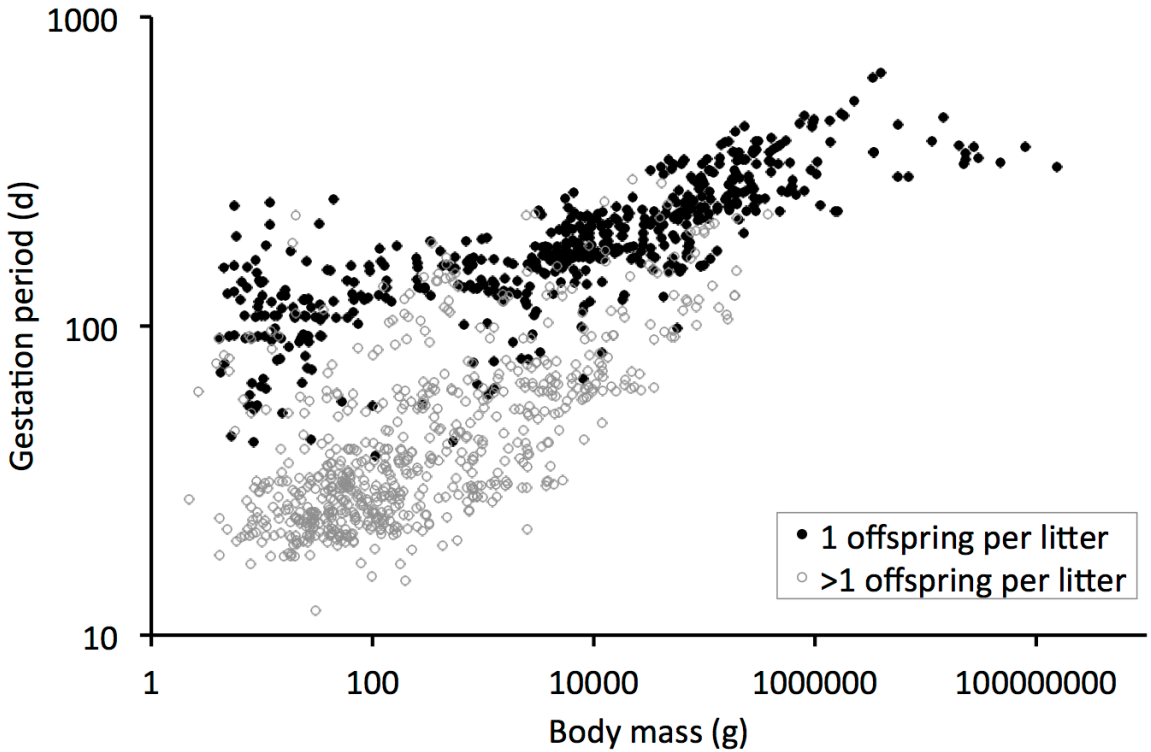

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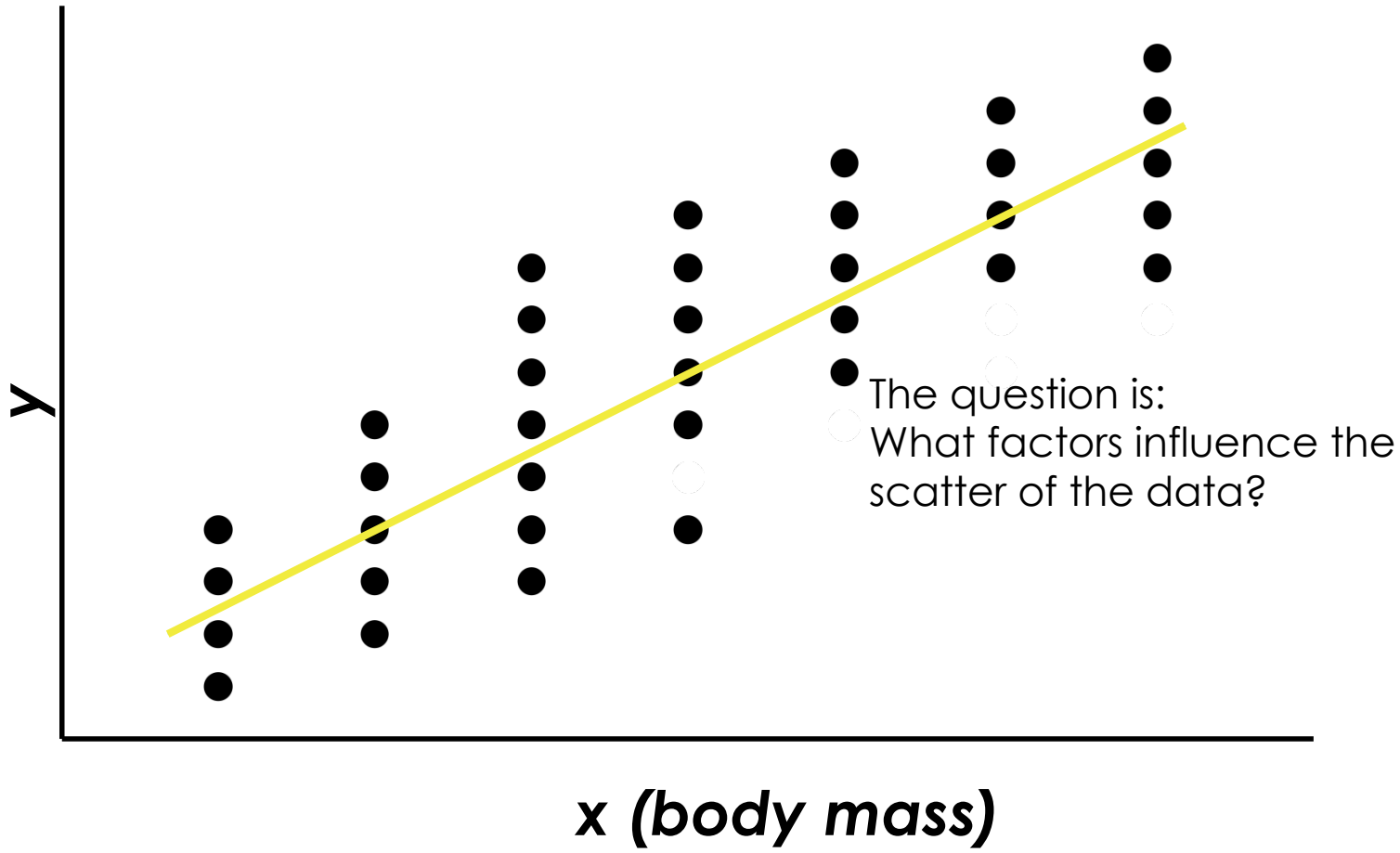
Allometries as snapshots in evolutionary time

Interpreting allometries

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



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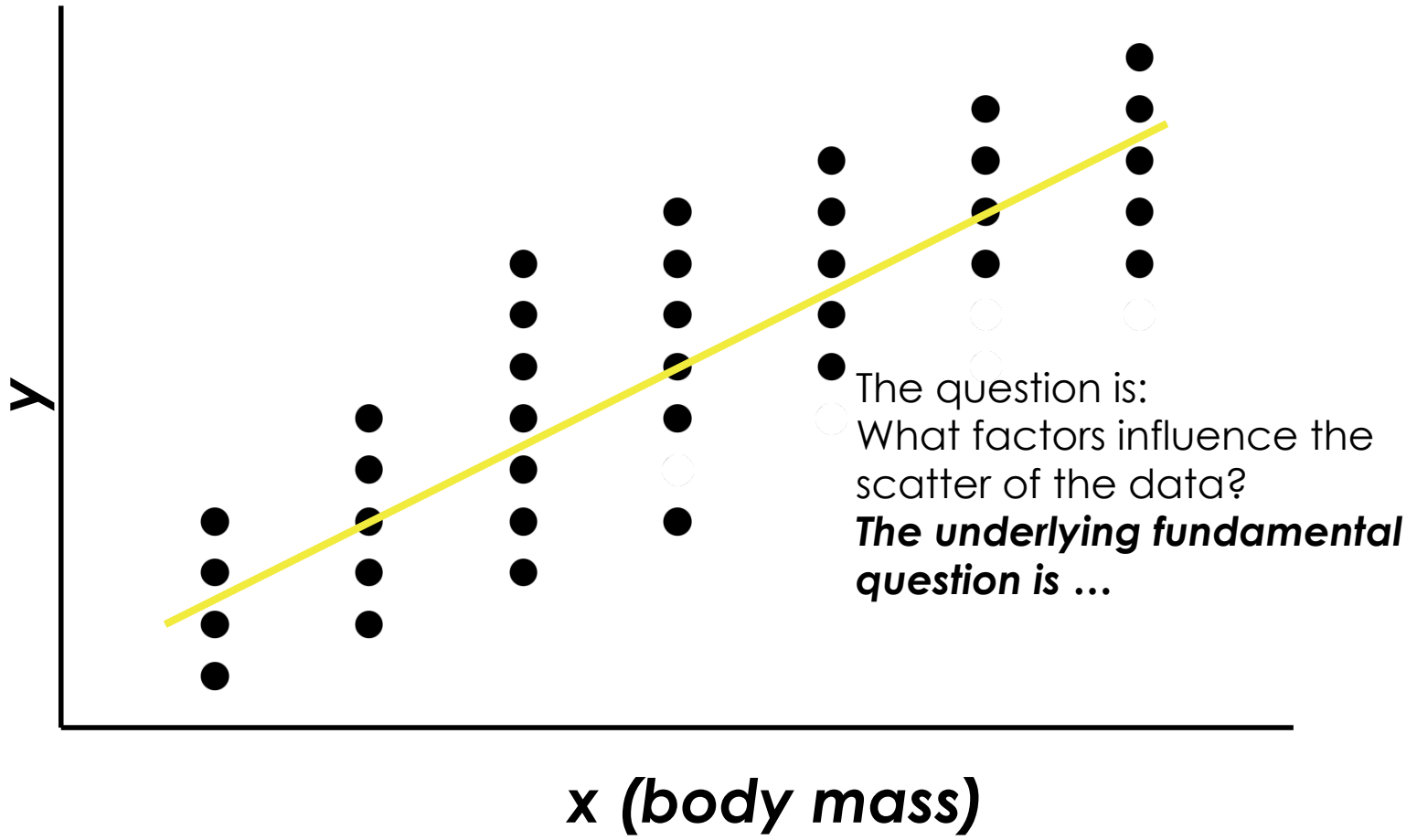

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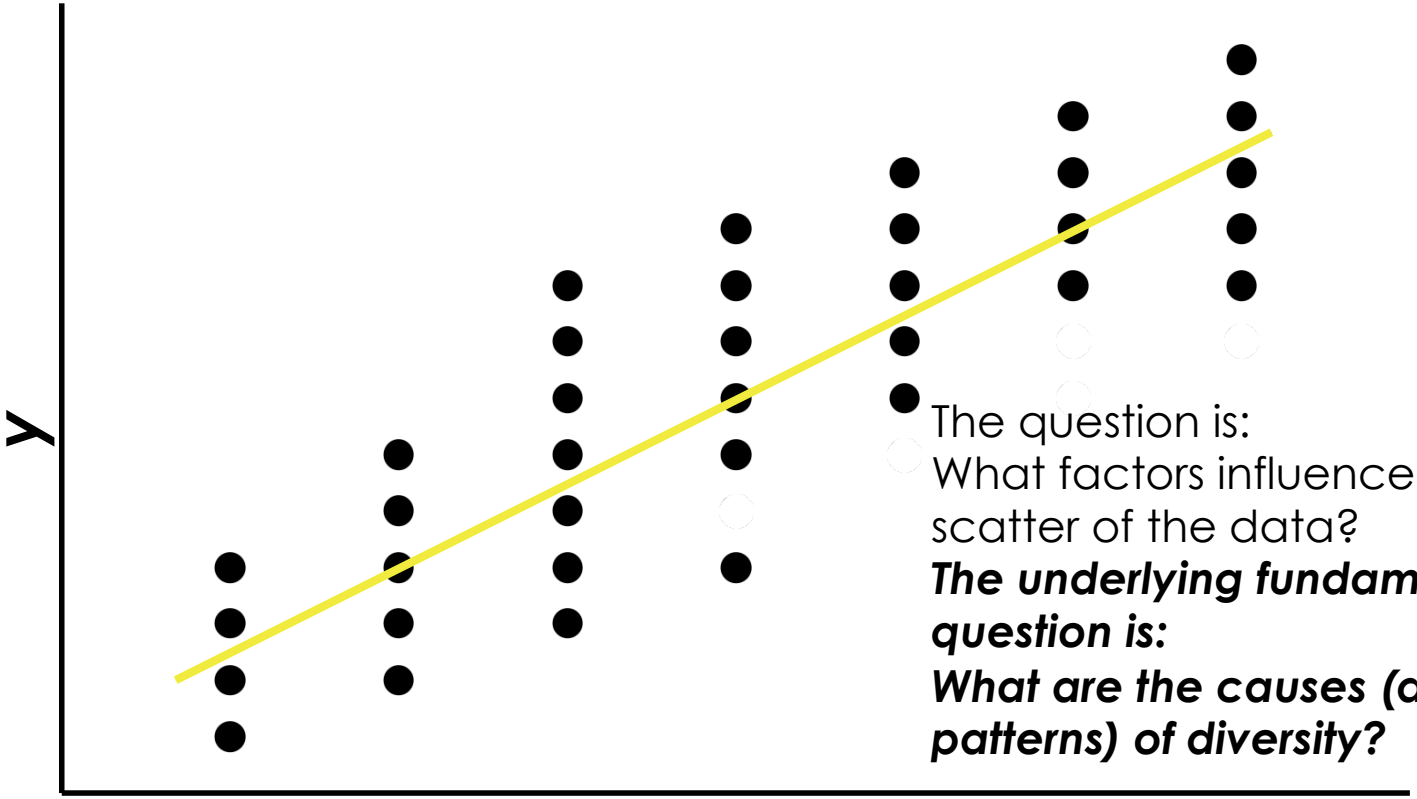

The question is:
What factors influence the scatter of the data?
The underlying fundamental question is:
What are the causes (and patterns) of diversity?

x (body mass)

Interpreting allometries

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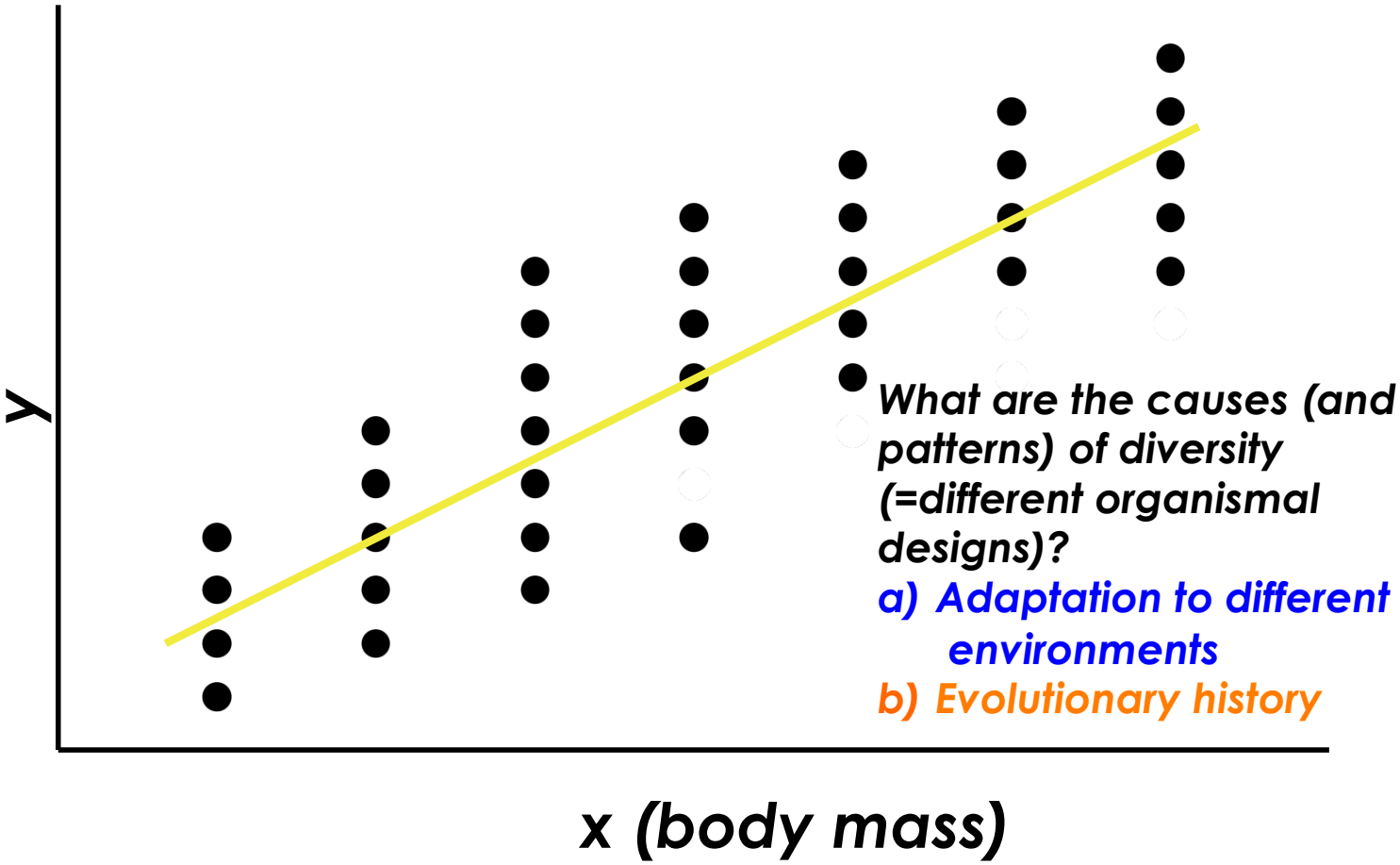

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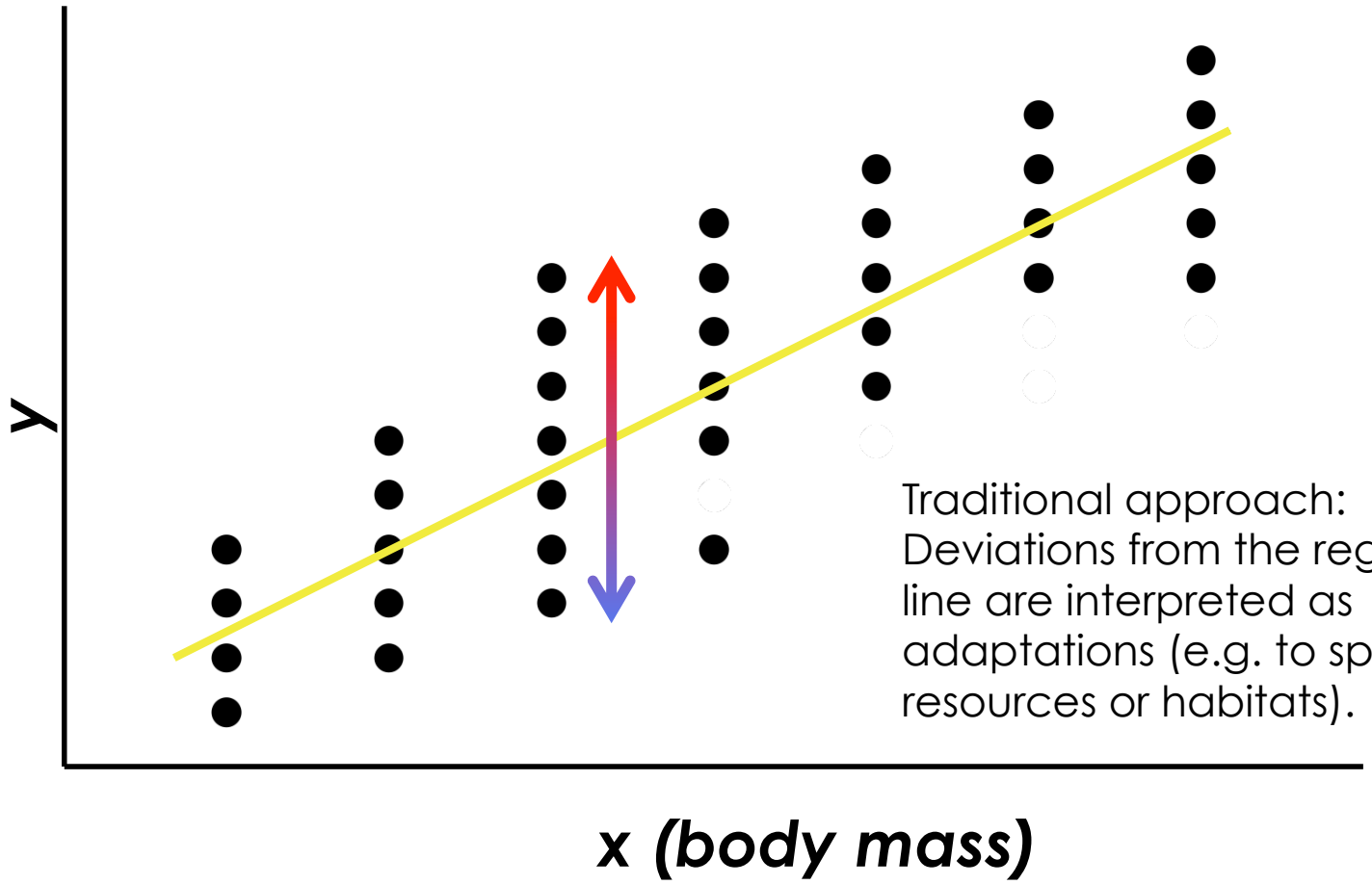

Traditional approach: Deviations from the regression line are interpreted as adaptations (e.g. to specific resources or habitats).

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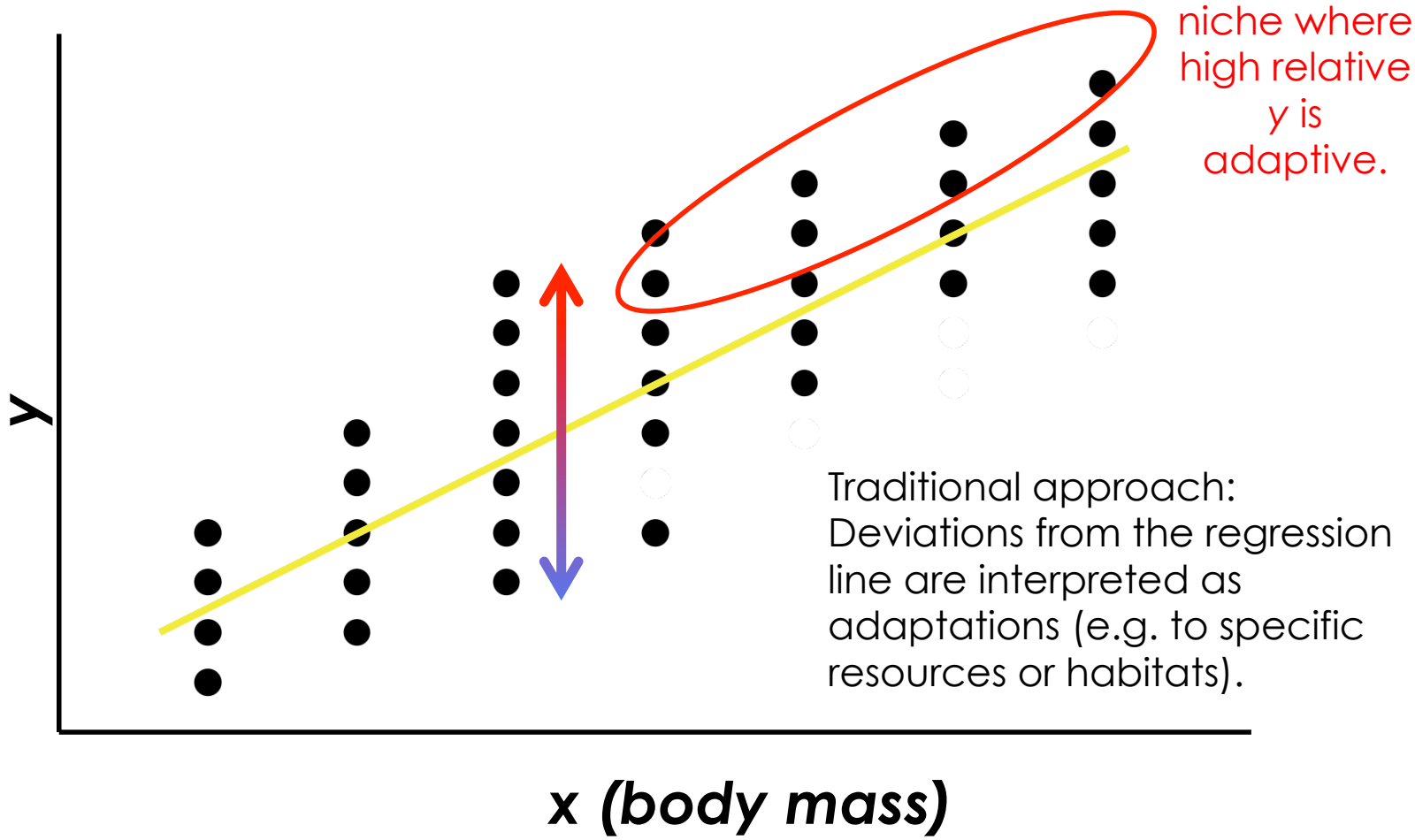

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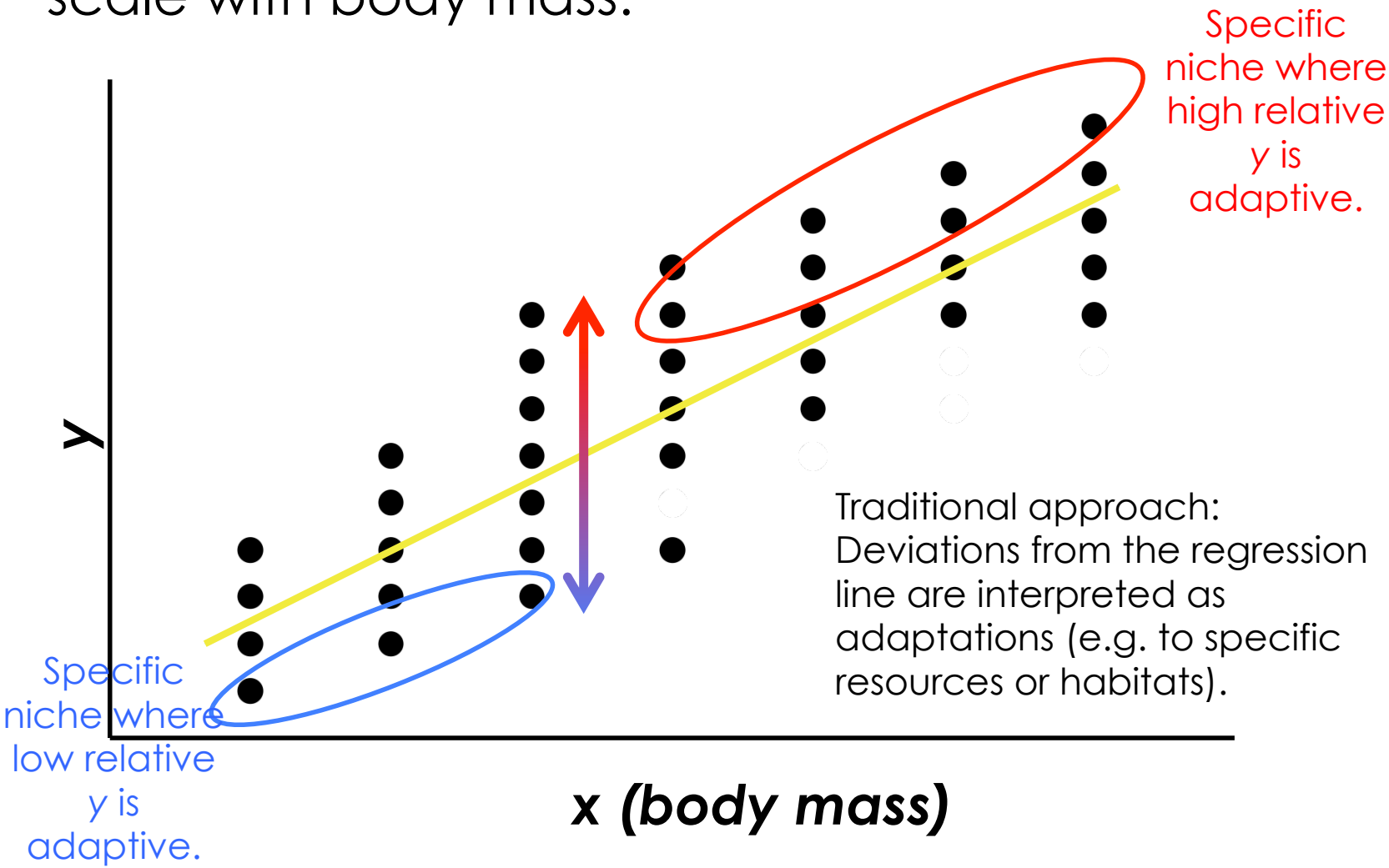
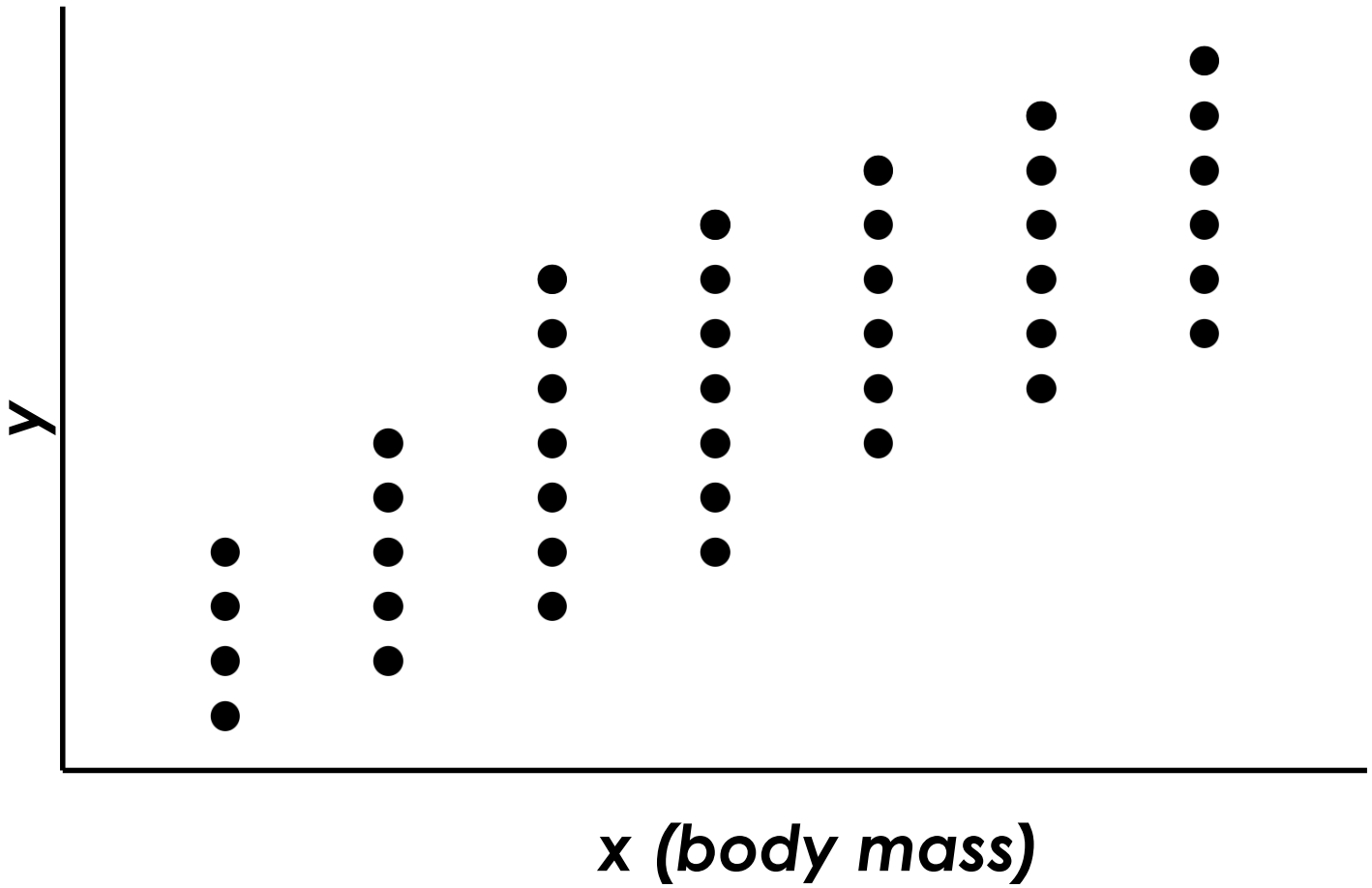


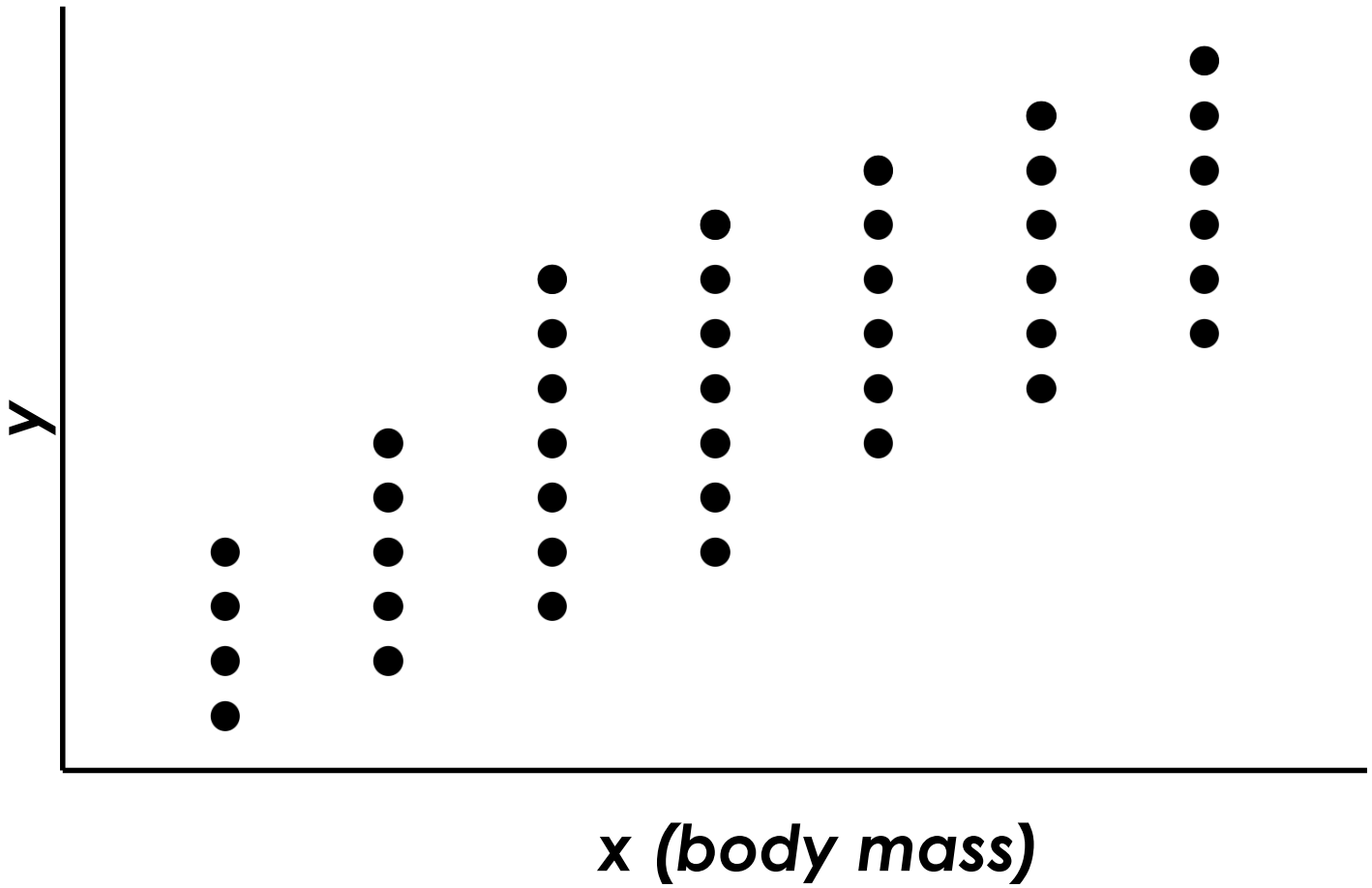
Interpreting allometries

But is it that simple – and are allometries really such 'laws' around which adaptation works?



Interpreting allometries

Is there a systematic phylogenetic structure in the dataset?



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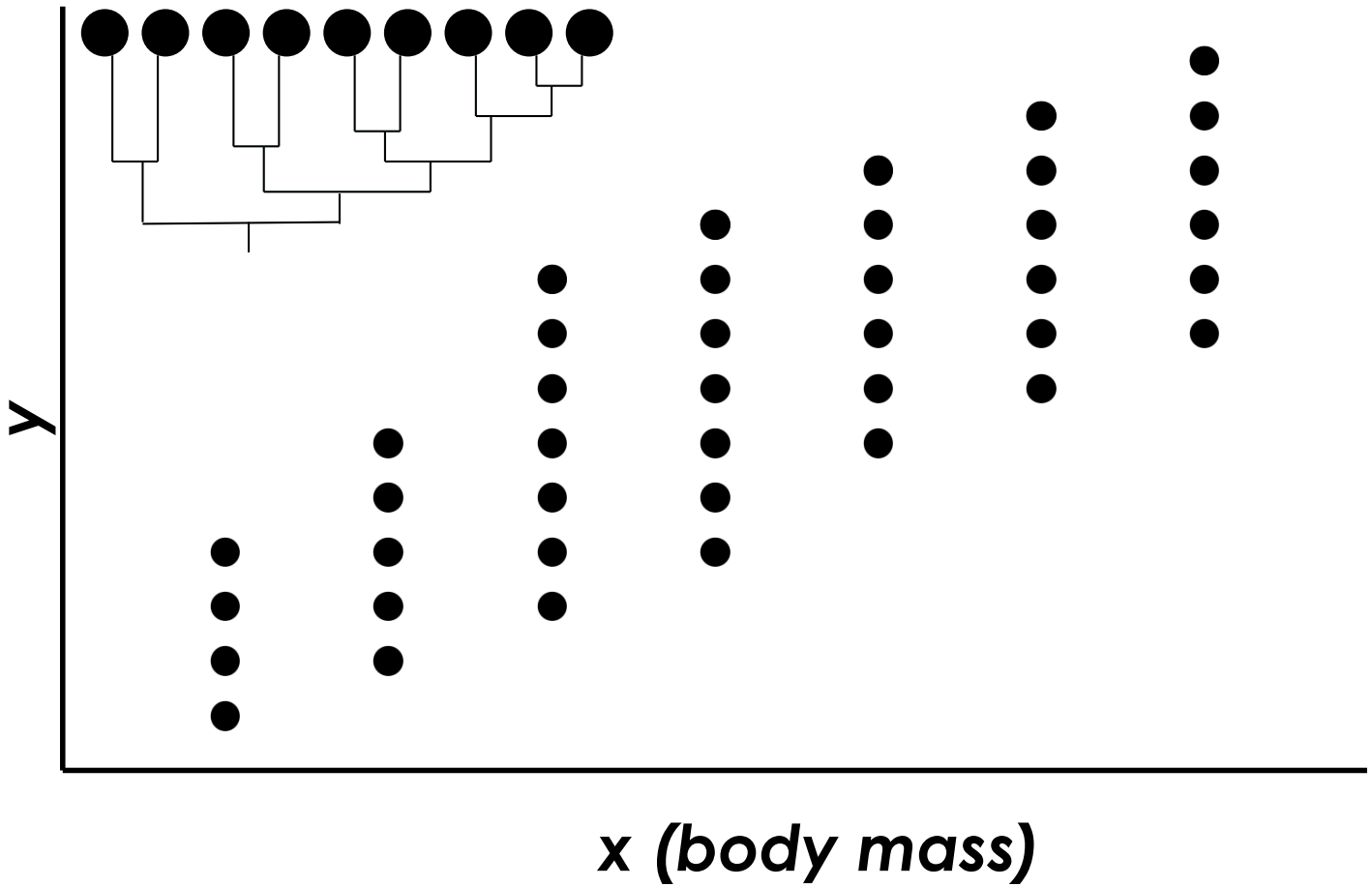

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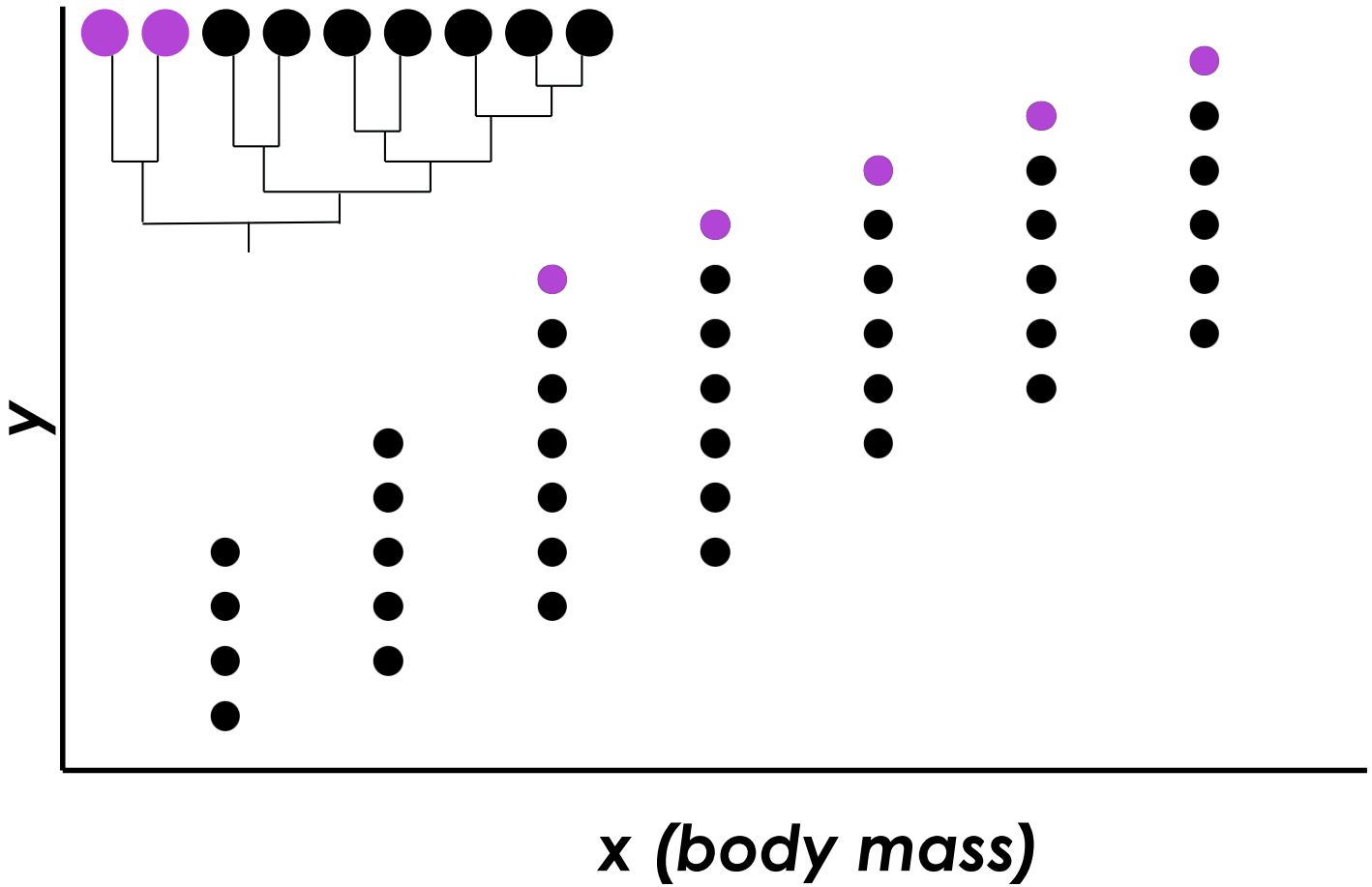

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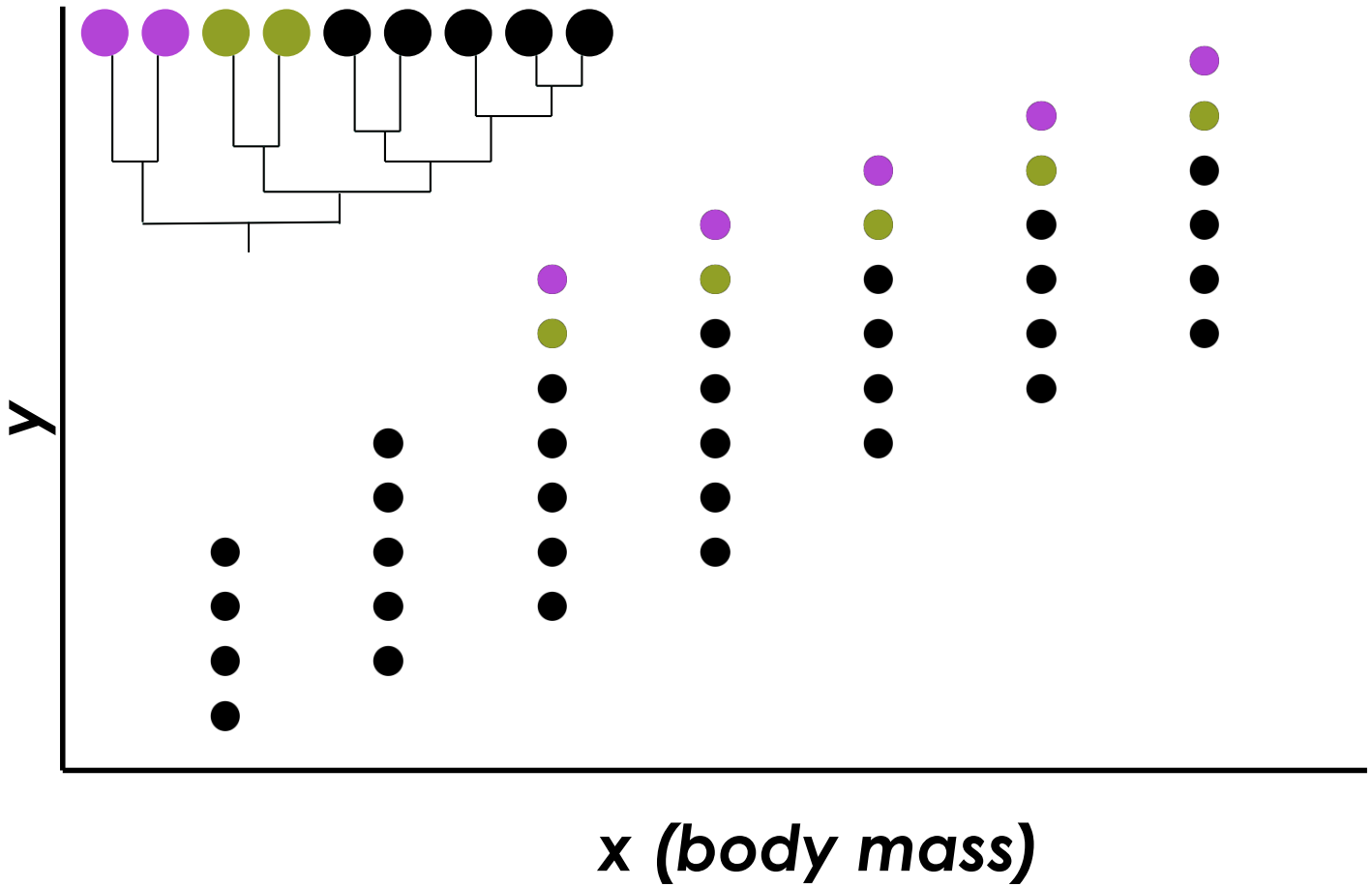

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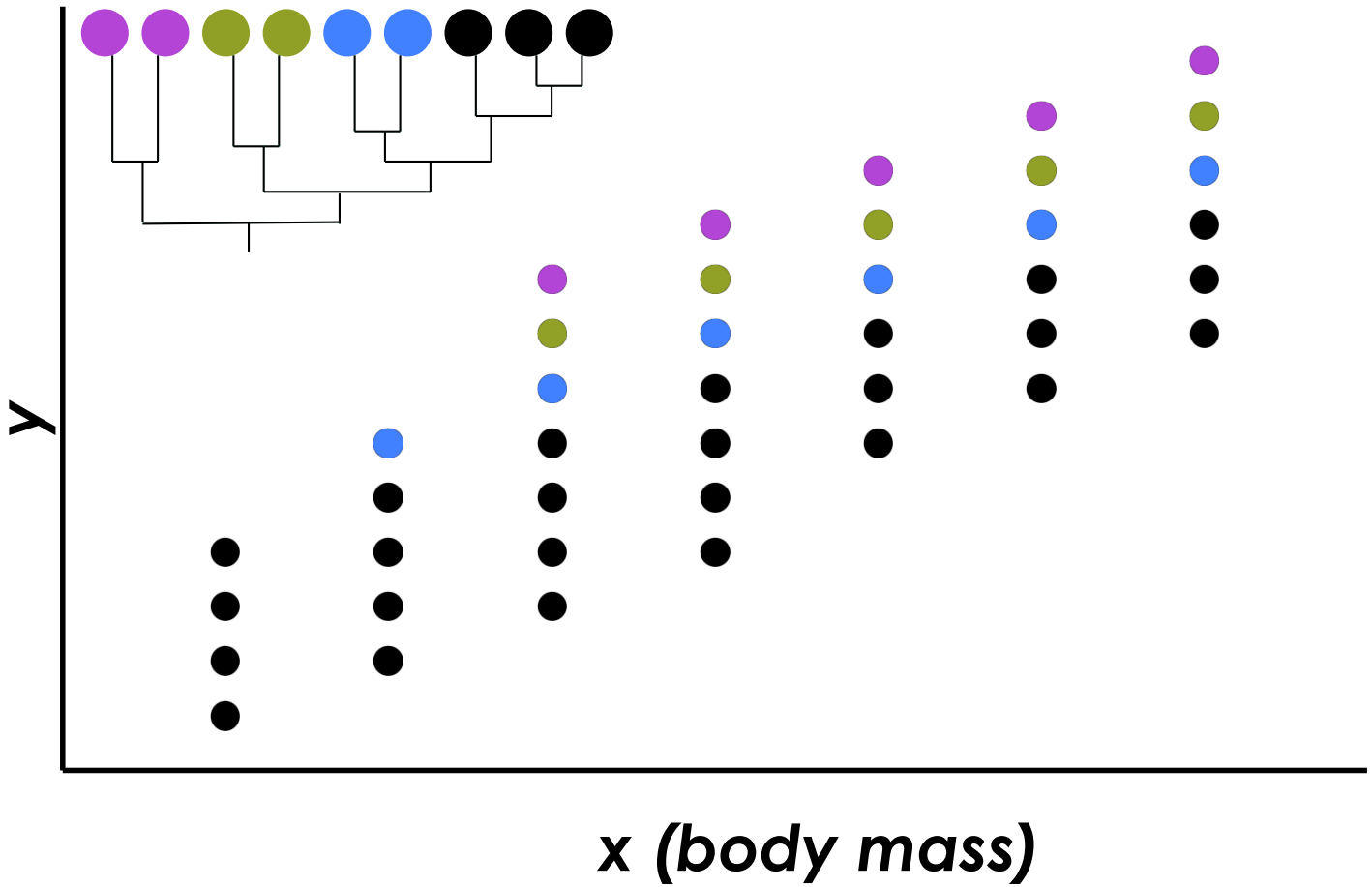

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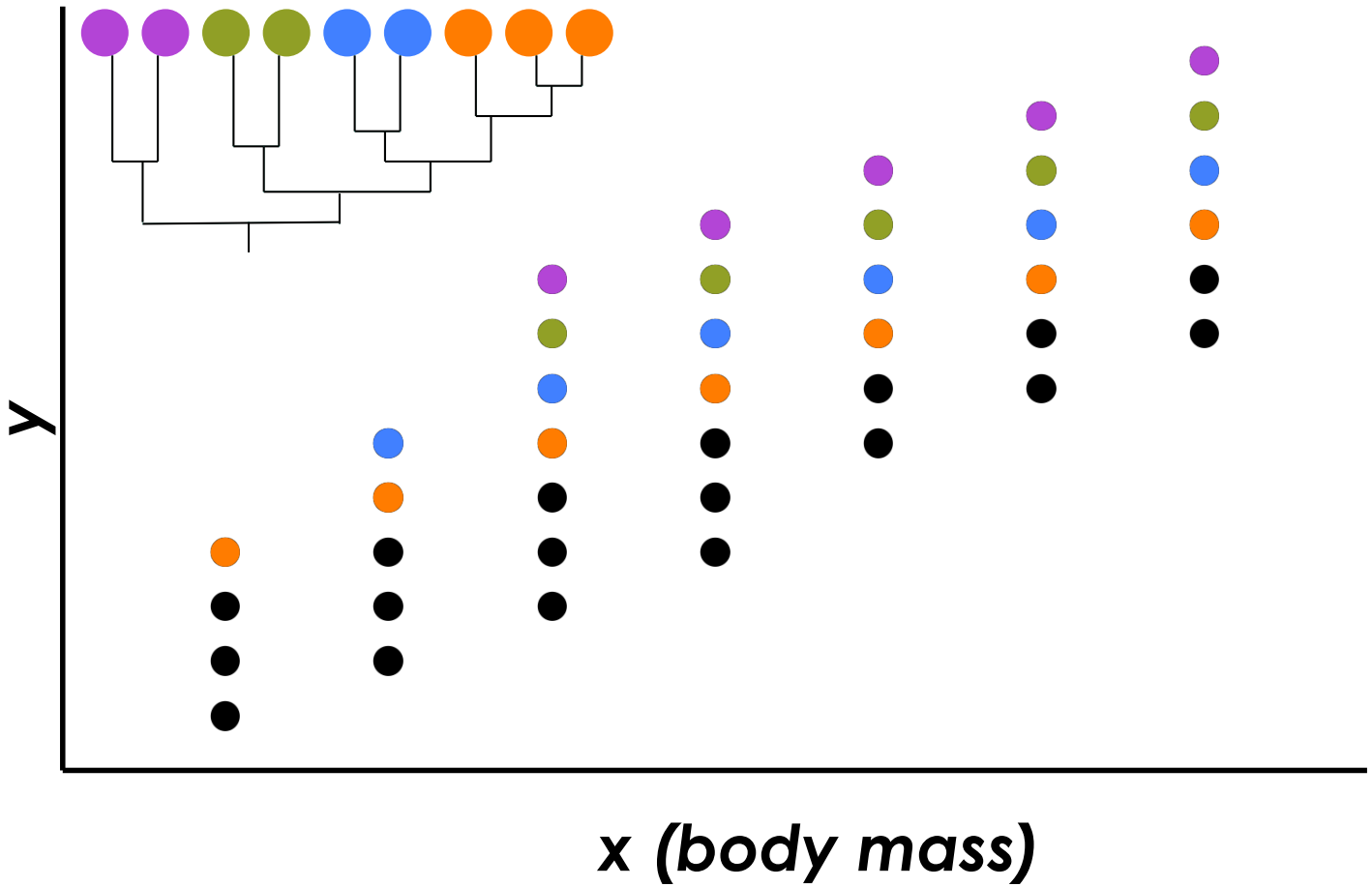

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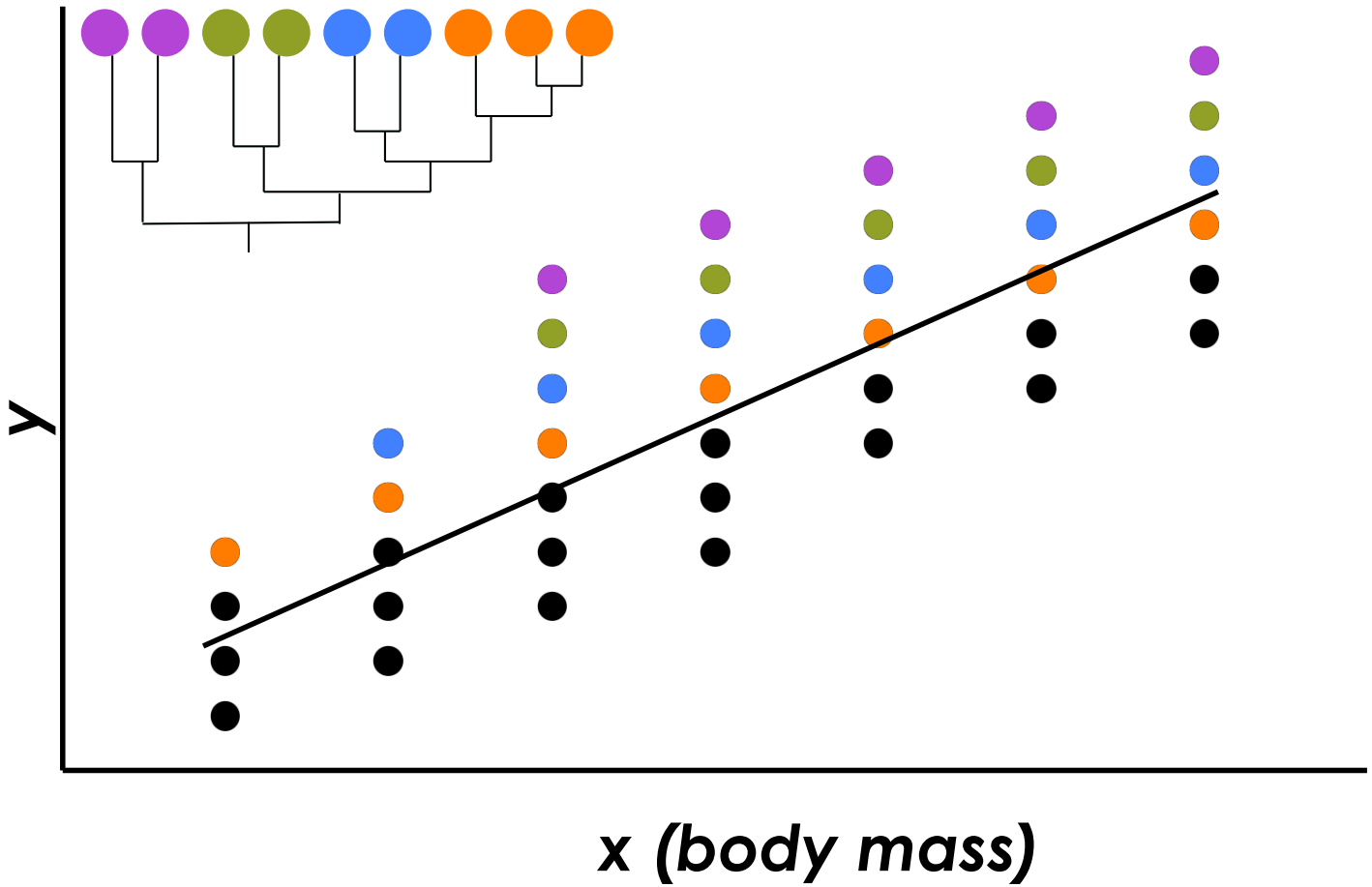

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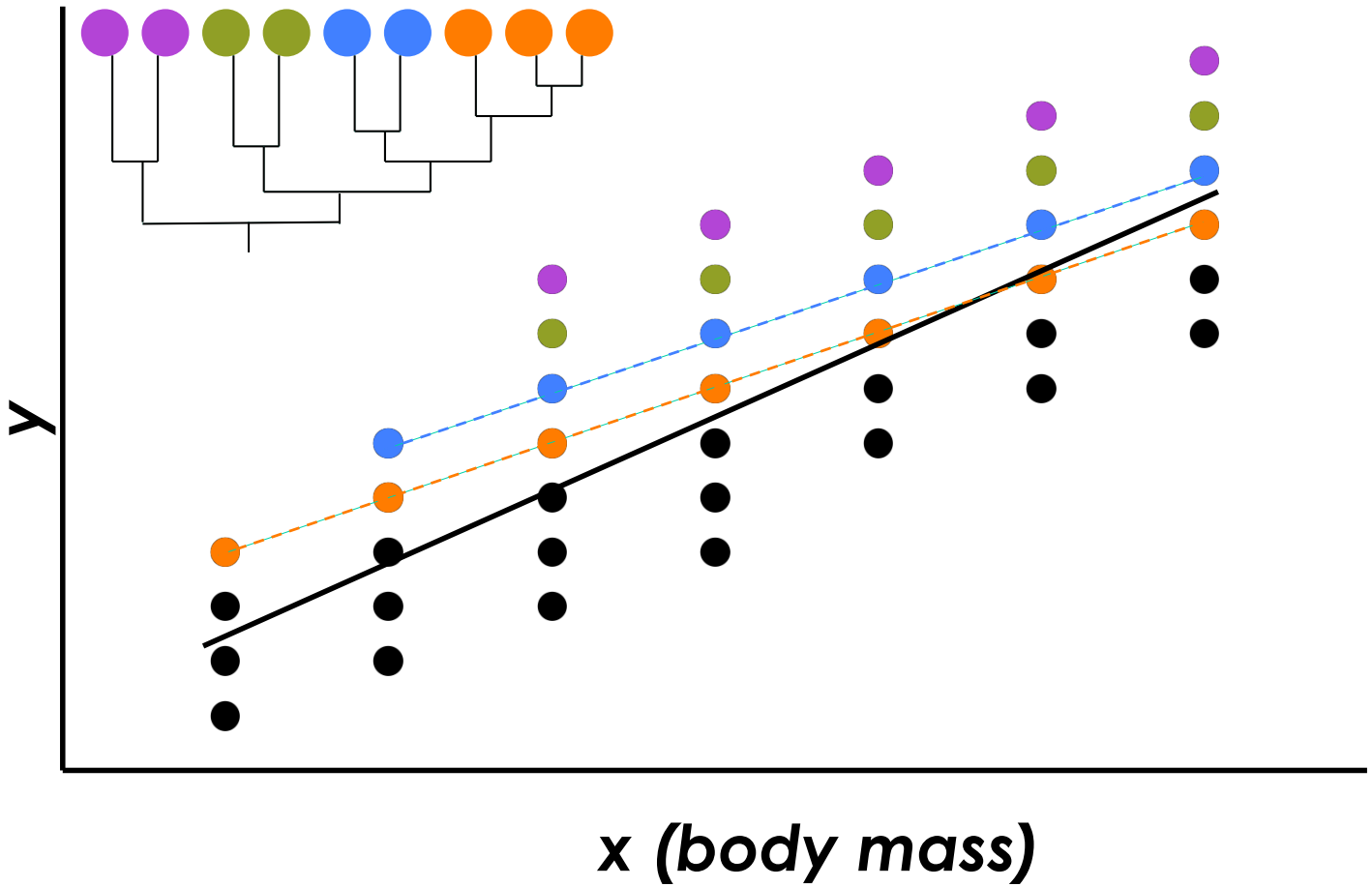

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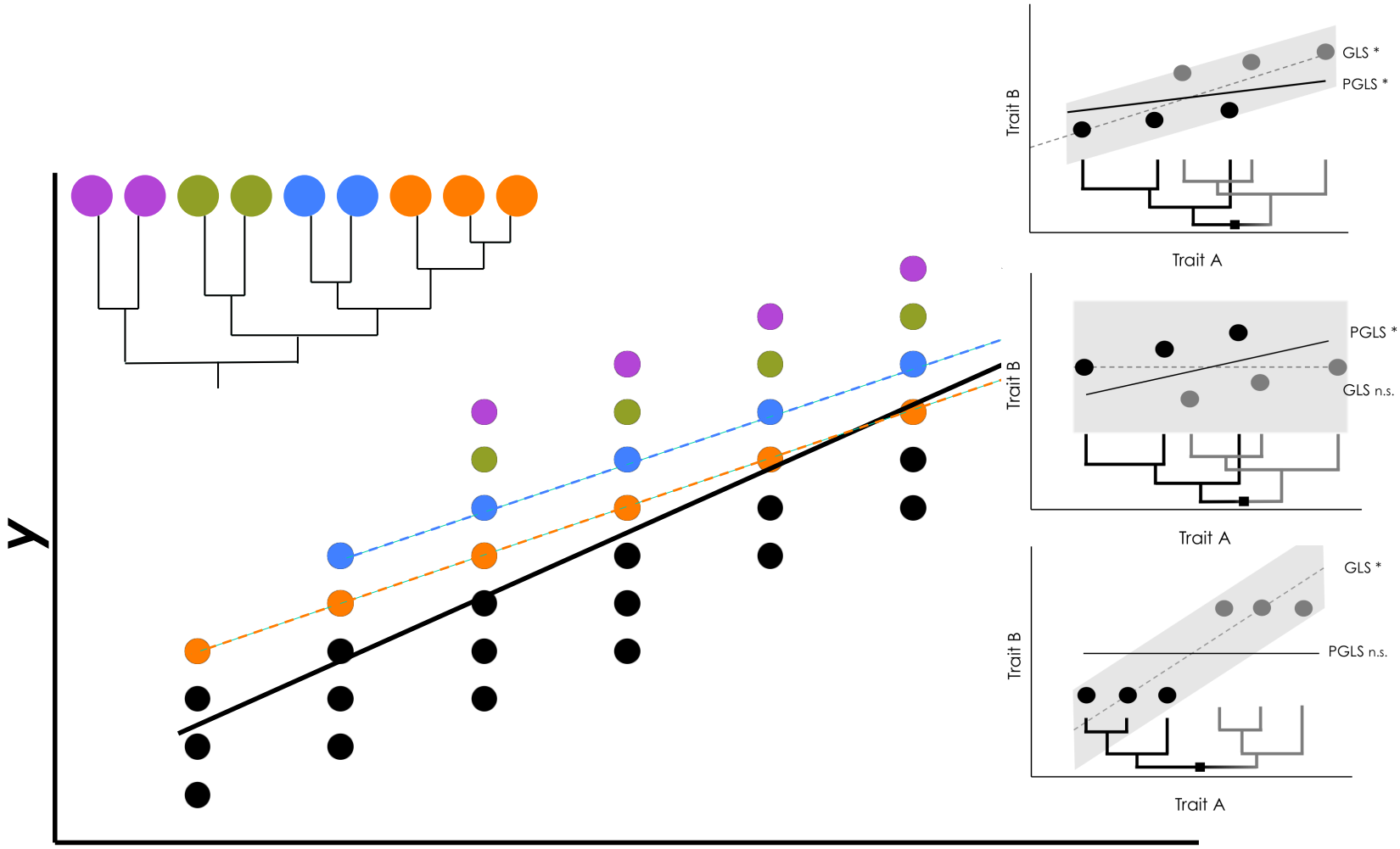
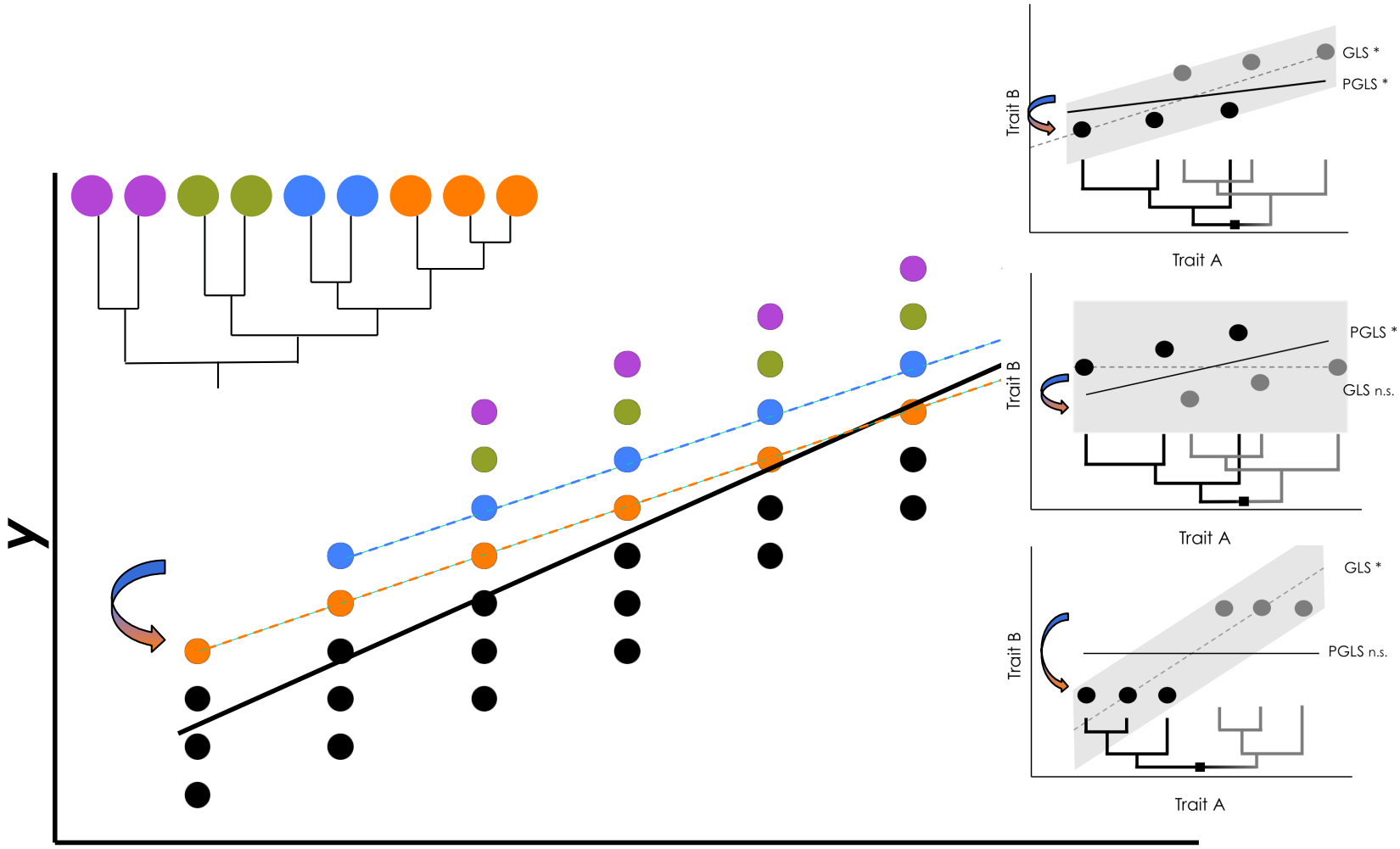
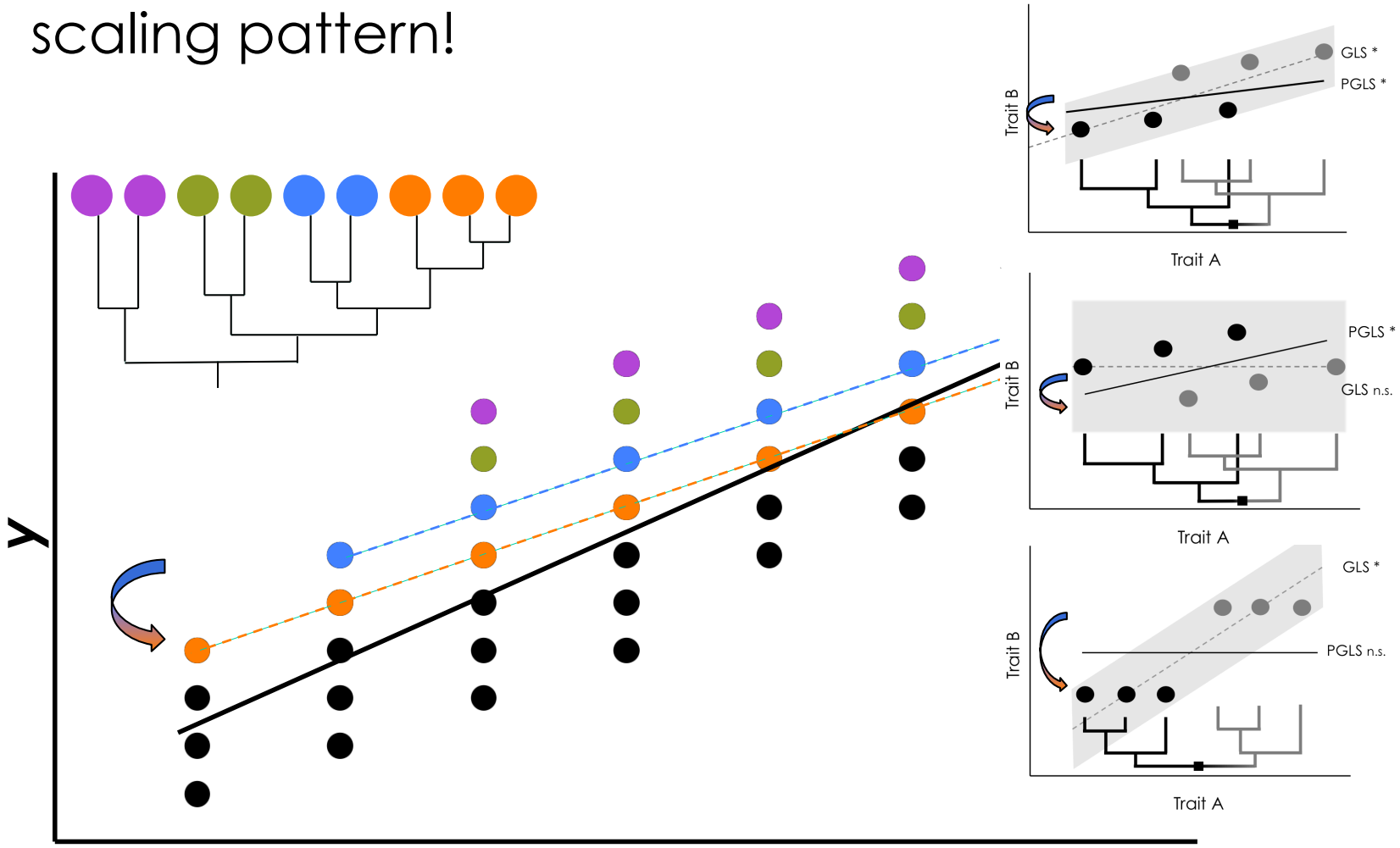


Changing the intercept



Changing the intercept

These changes are unrelated to the underlying scaling pattern!



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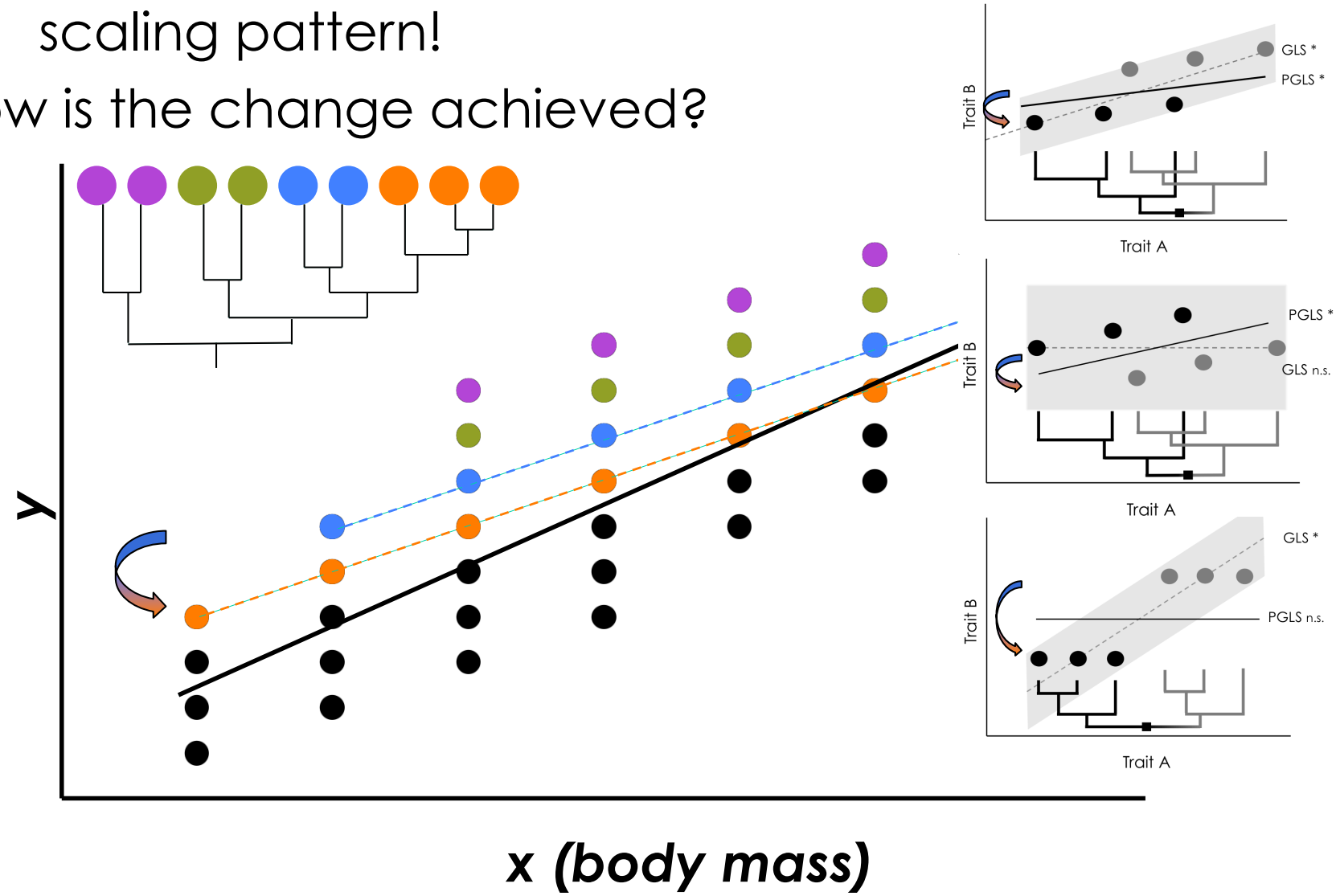
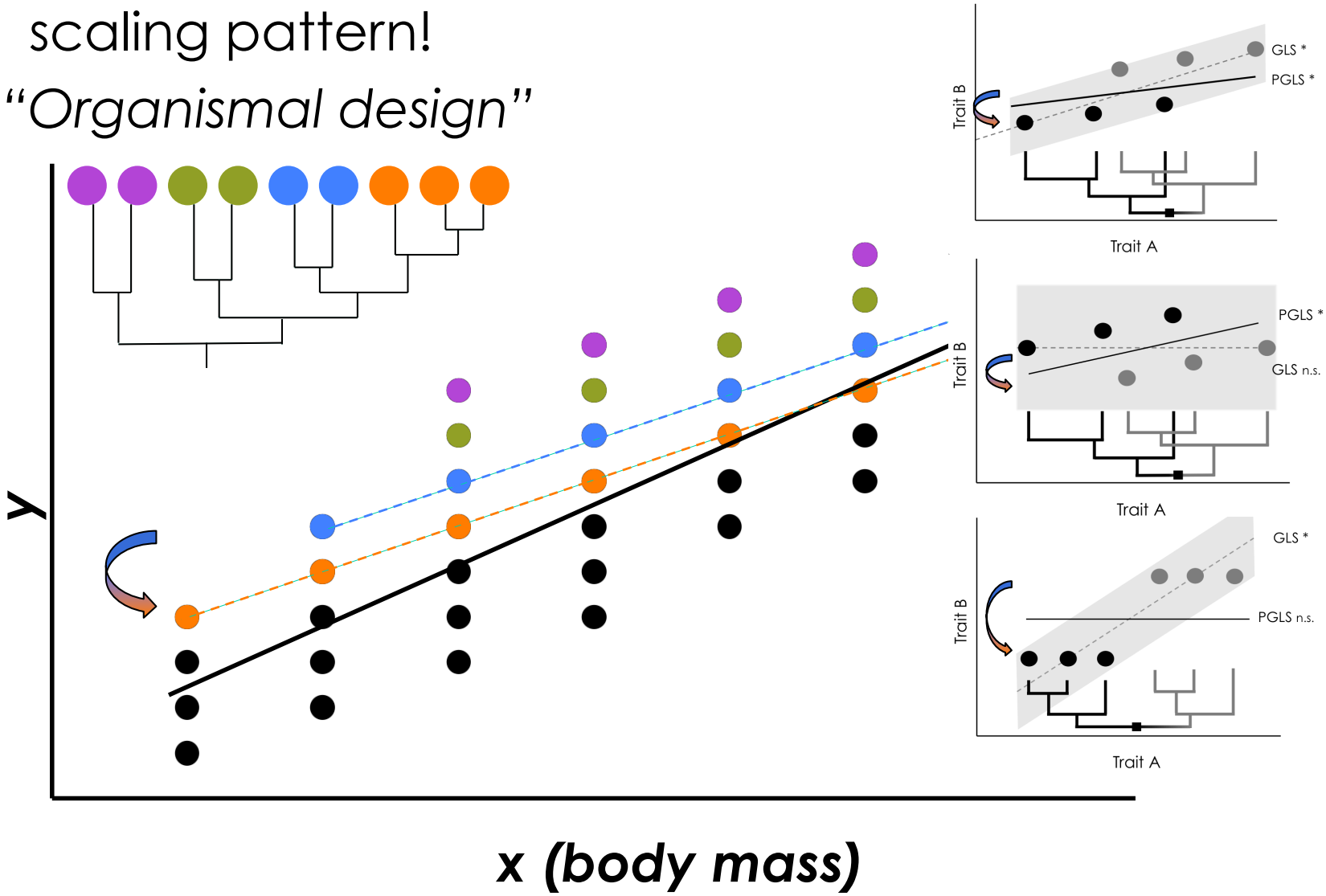
How is the change achieved?



Changing the intercept

These changes are unrelated to the underlying scaling pattern!

=> *"Organismal design"*



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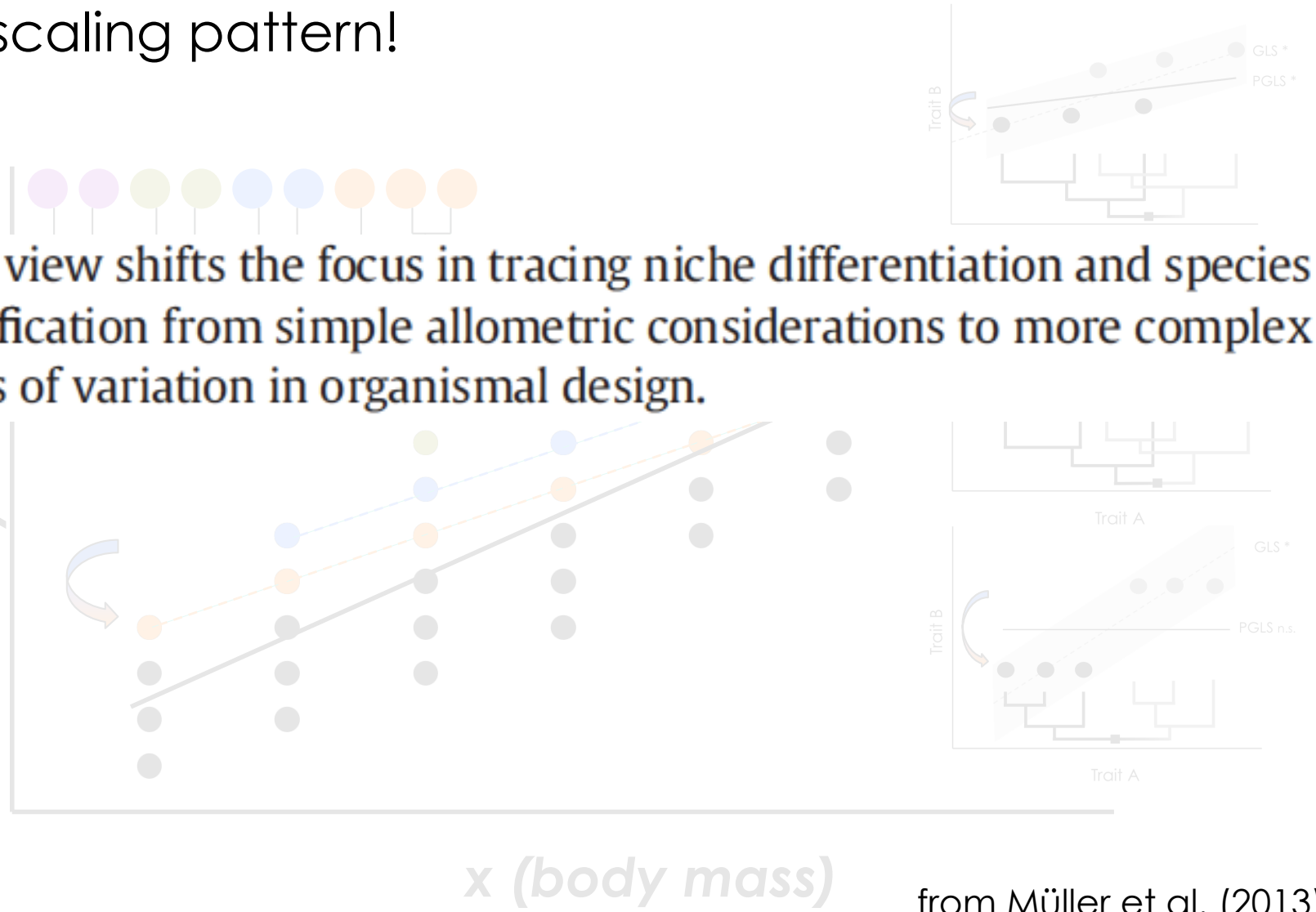


Such a view shifts the focus in tracing niche differentiation and species diversification from simple allometric considerations to more complex aspects of variation in organismal design.

from Müller et al. (2013)

Changing the intercept

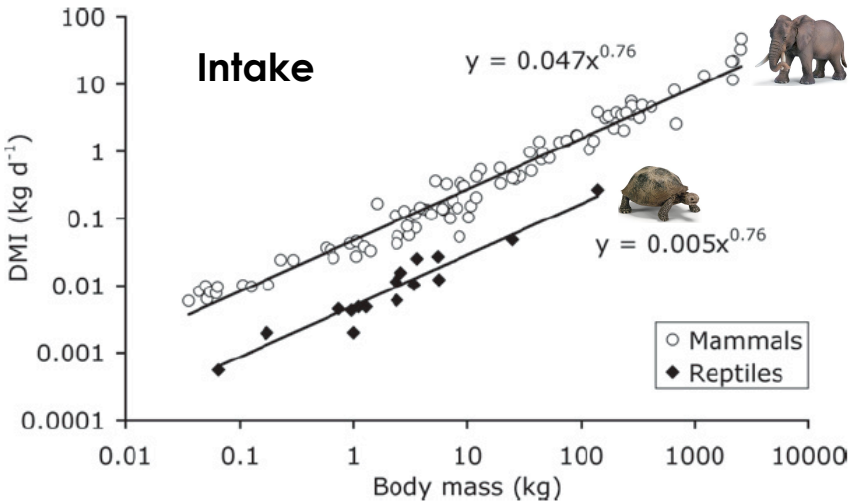
=> "*Organismal design*"

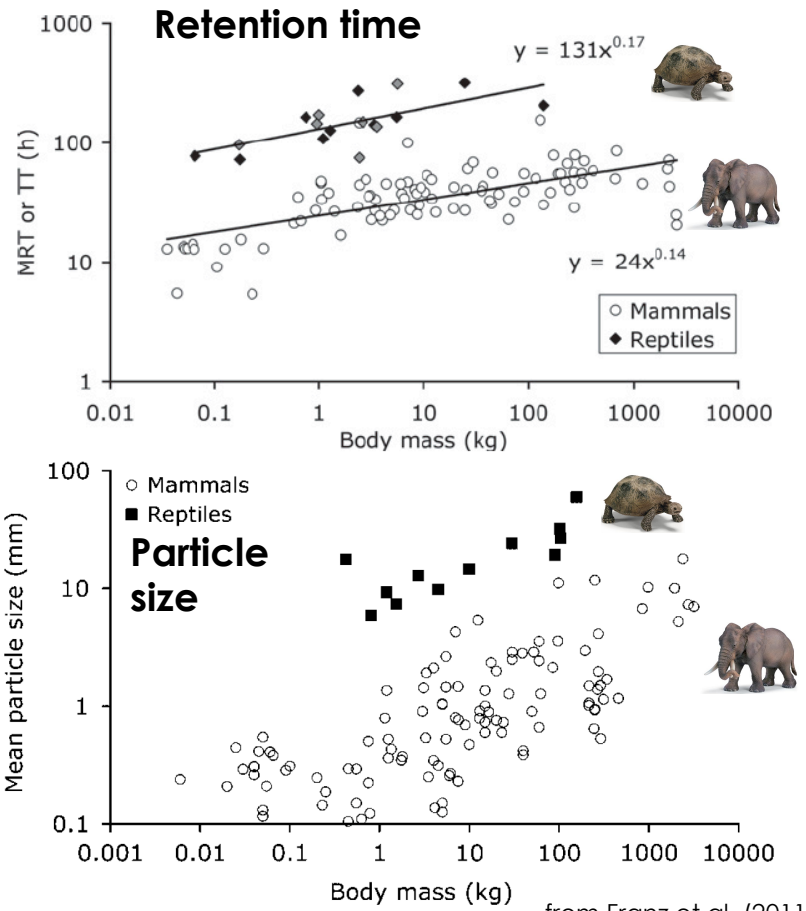
Easy to understand at low taxonomic level

Changing the intercept

=> "*Organismal design*"

Easy to understand at low taxonomic level





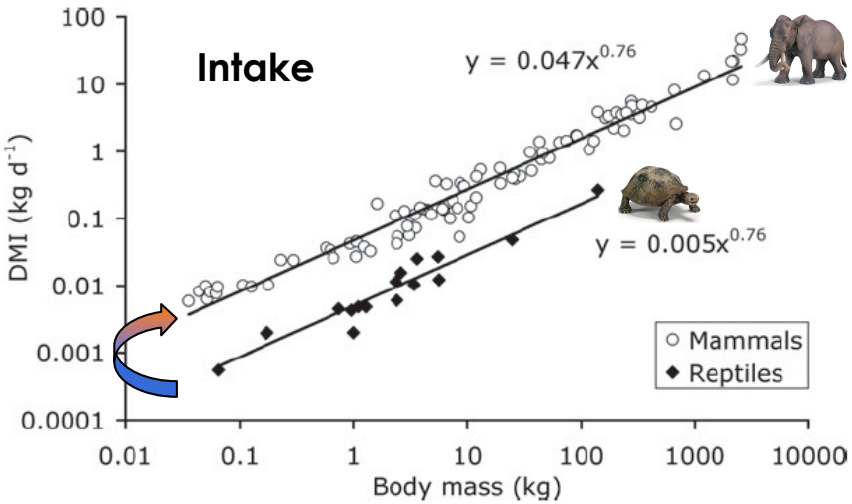
from Franz et al. (2011) CBP A

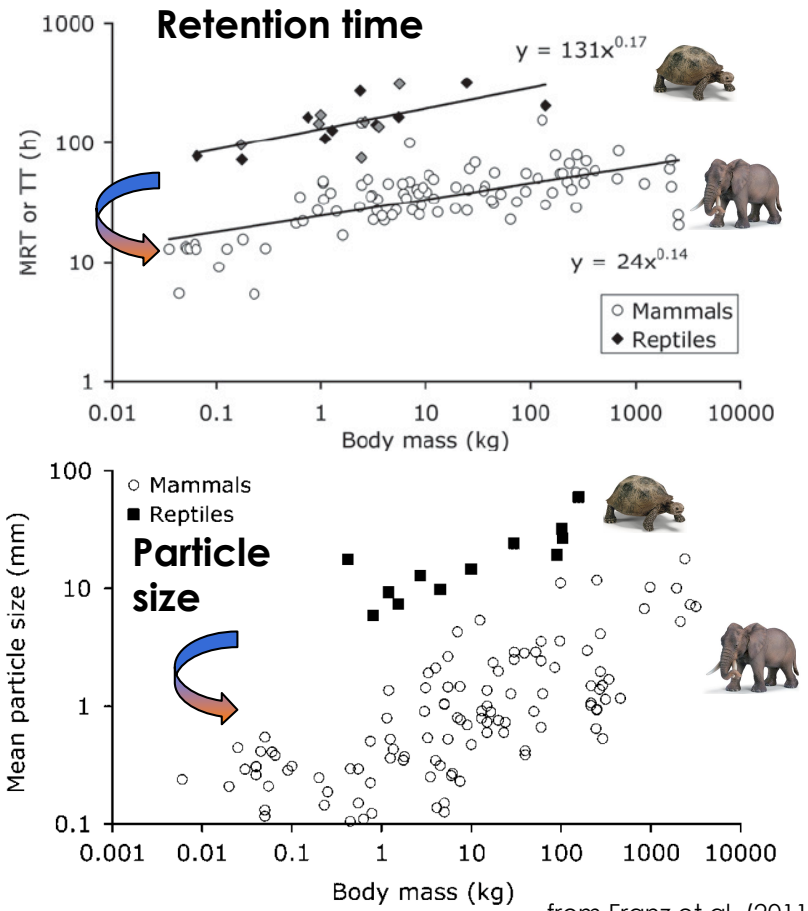
from Franz et al. (2011) CBP A
and Fritz et al. (2010) JExpZool

Changing the intercept

Easy to understand at low taxonomic level

e.g. ectotherm vs. endotherm





from Franz et al. (2011) CBP A

from Franz et al. (2011) CBP A
and Fritz et al. (2010) JExpZool

Changing the intercept

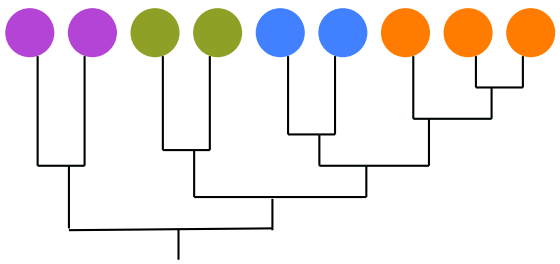
Easy to understand at low taxonomic level

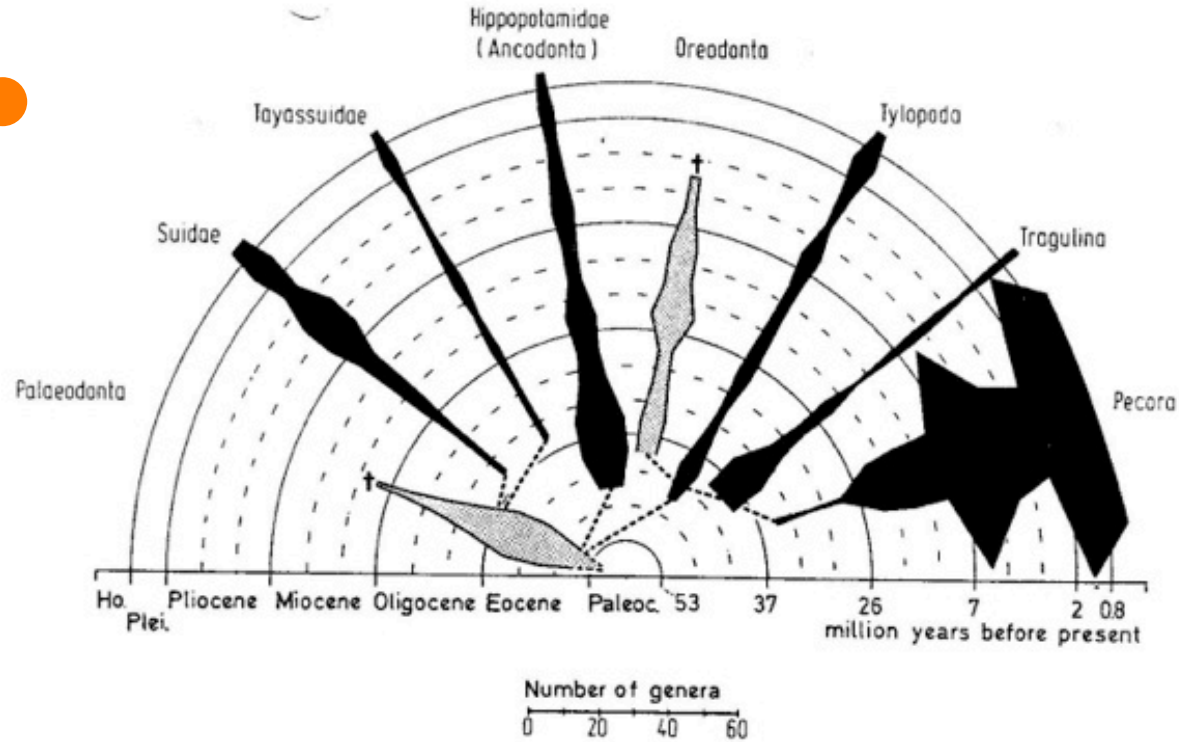
e.g. ectotherm vs. endotherm

… but at higher taxonomic levels, e.g. within mammals, within ruminants …?

Interpreting allometries

Phylogenetic structure represents not only taxonomy but also evolutionary time (incl. radiation events)

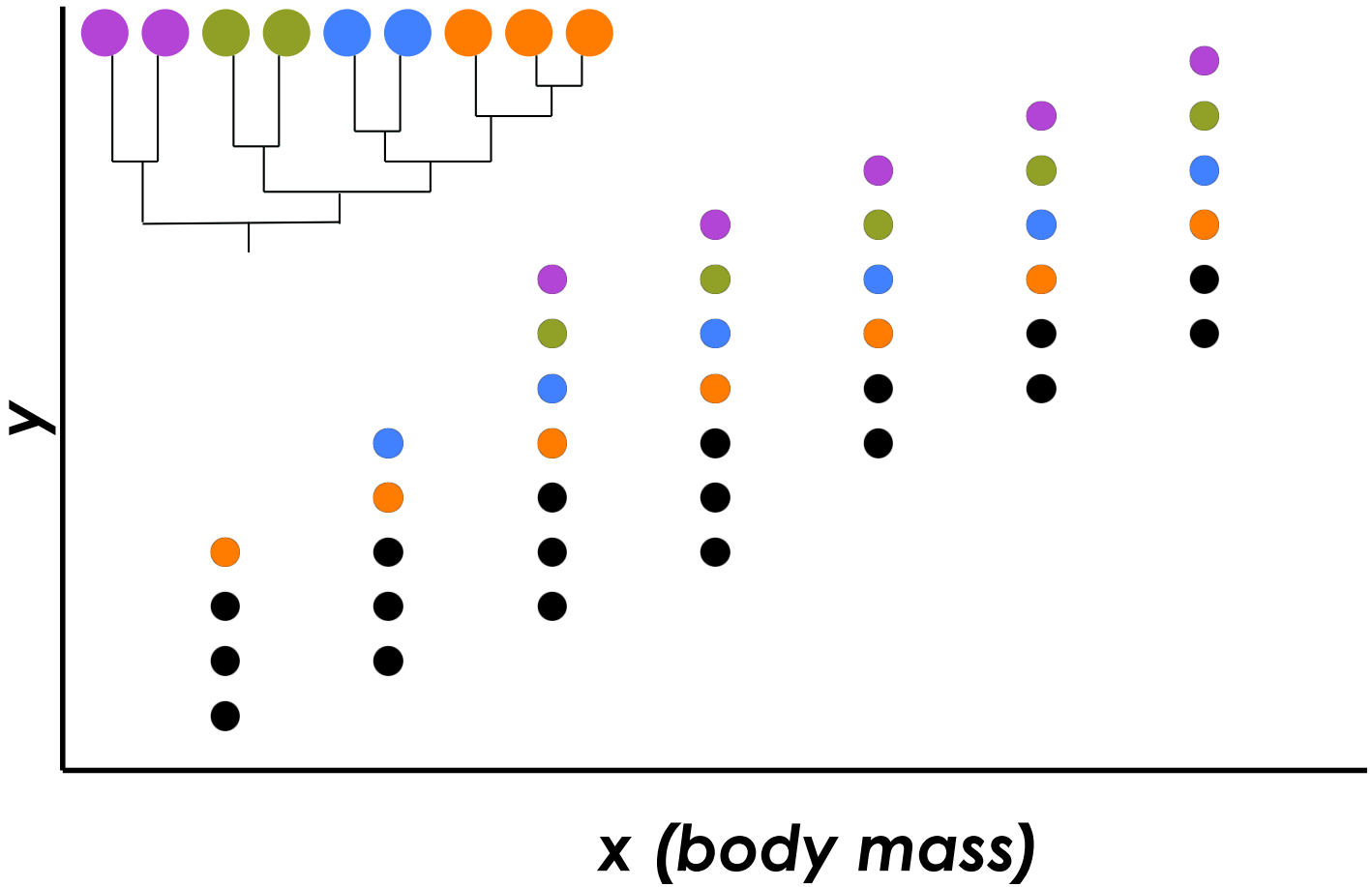




from Langer (1994)

Interpreting allometries

Is there a systematic phylogenetic structure in the dataset?



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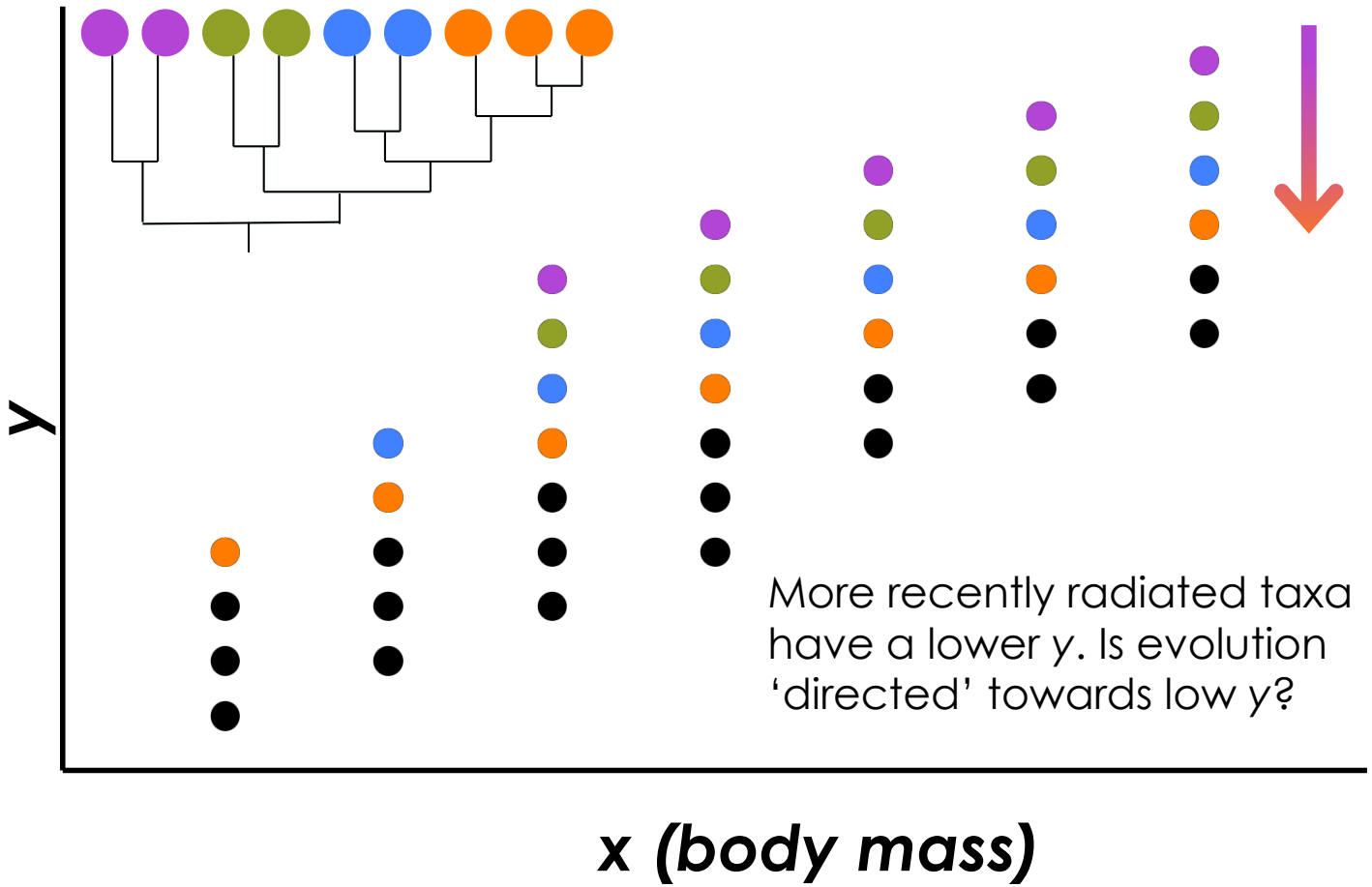

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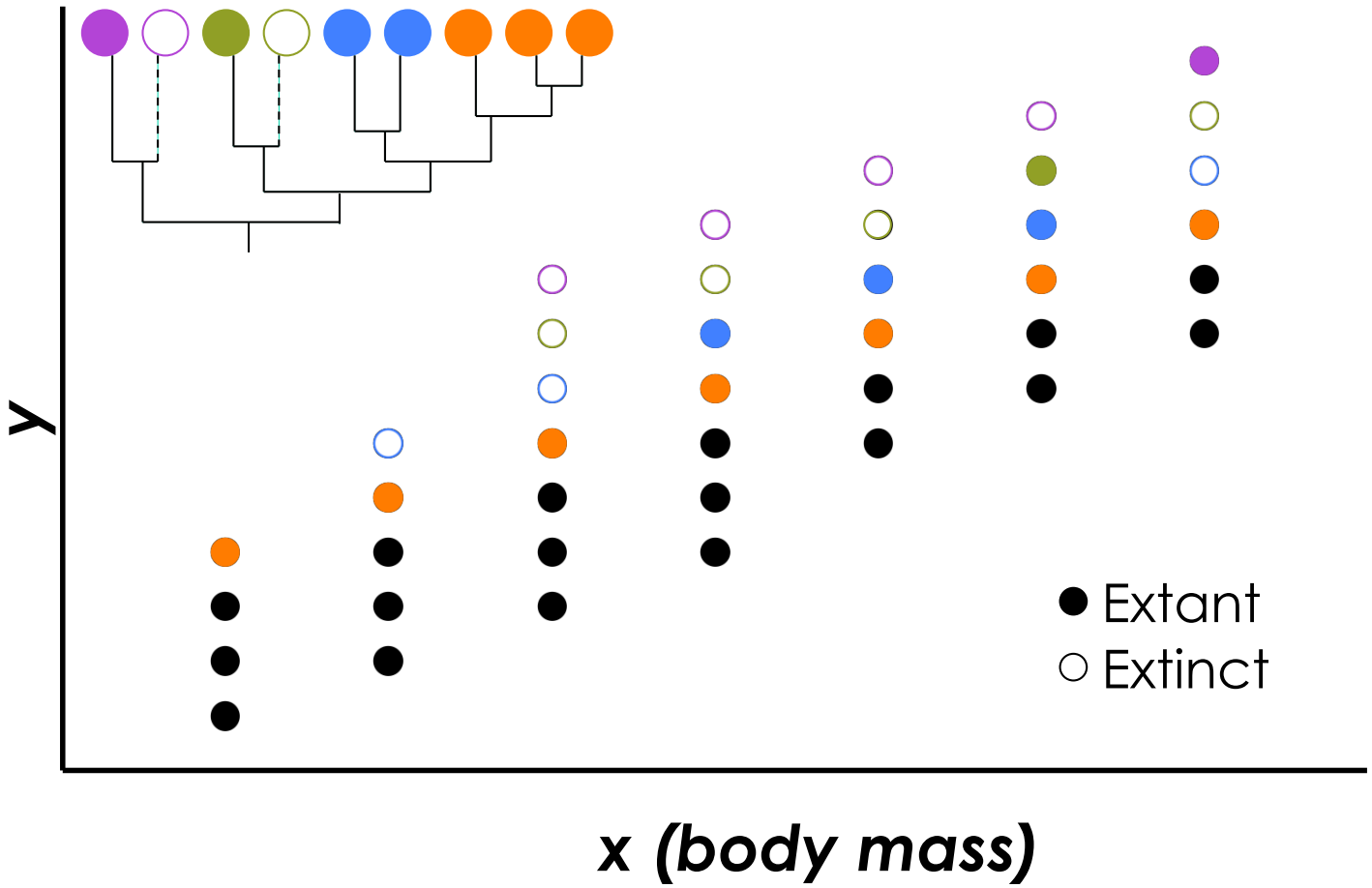

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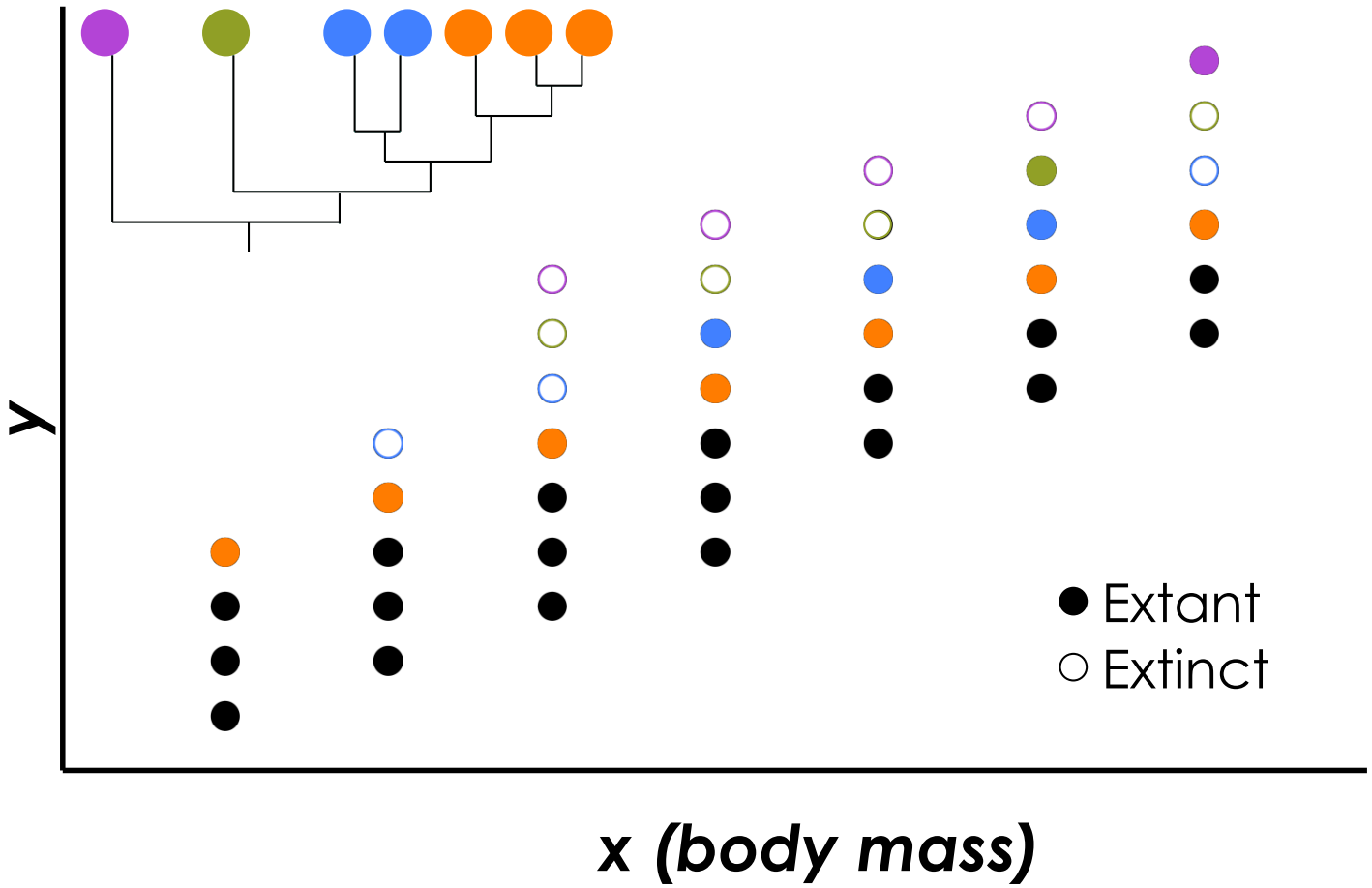

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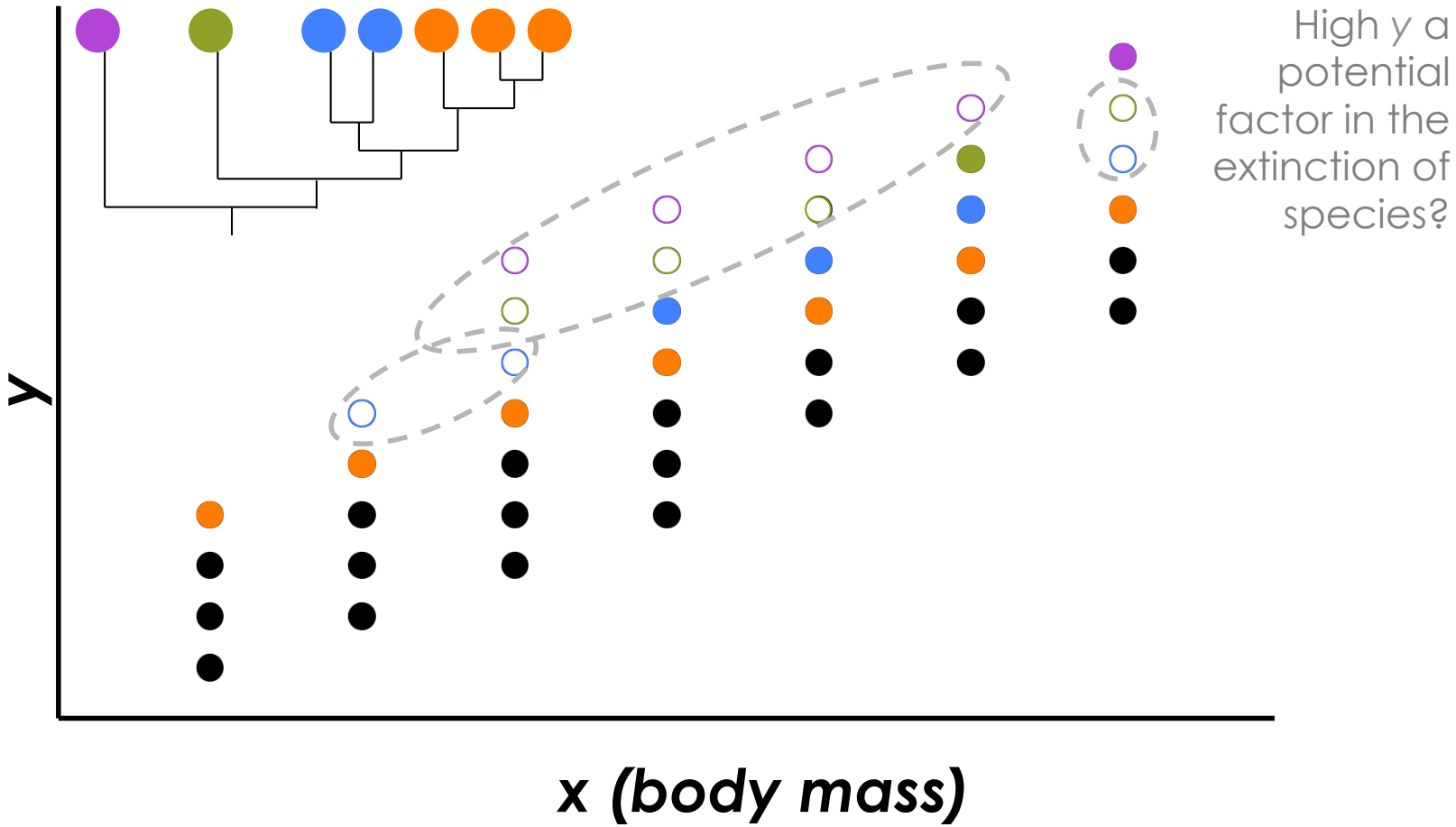

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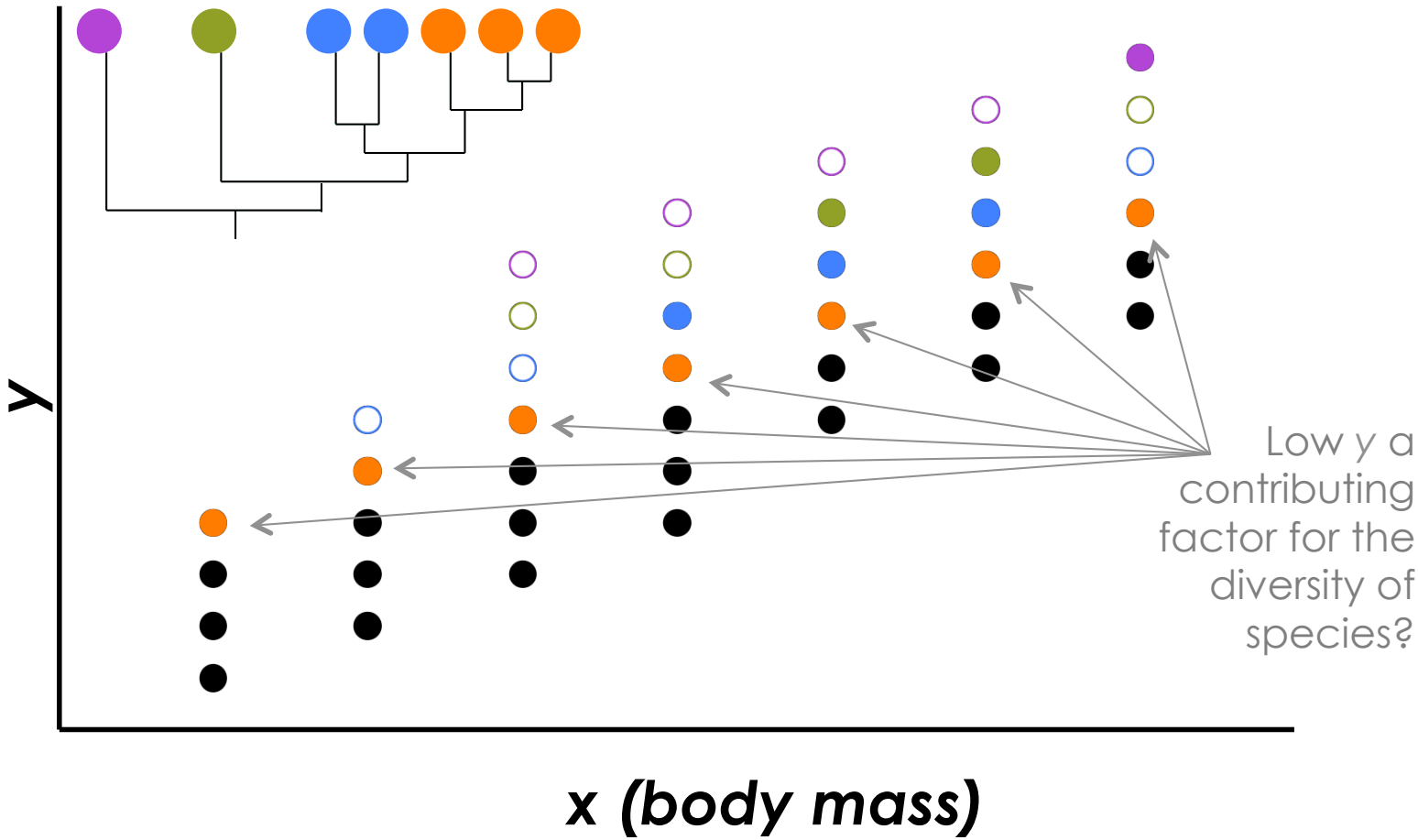

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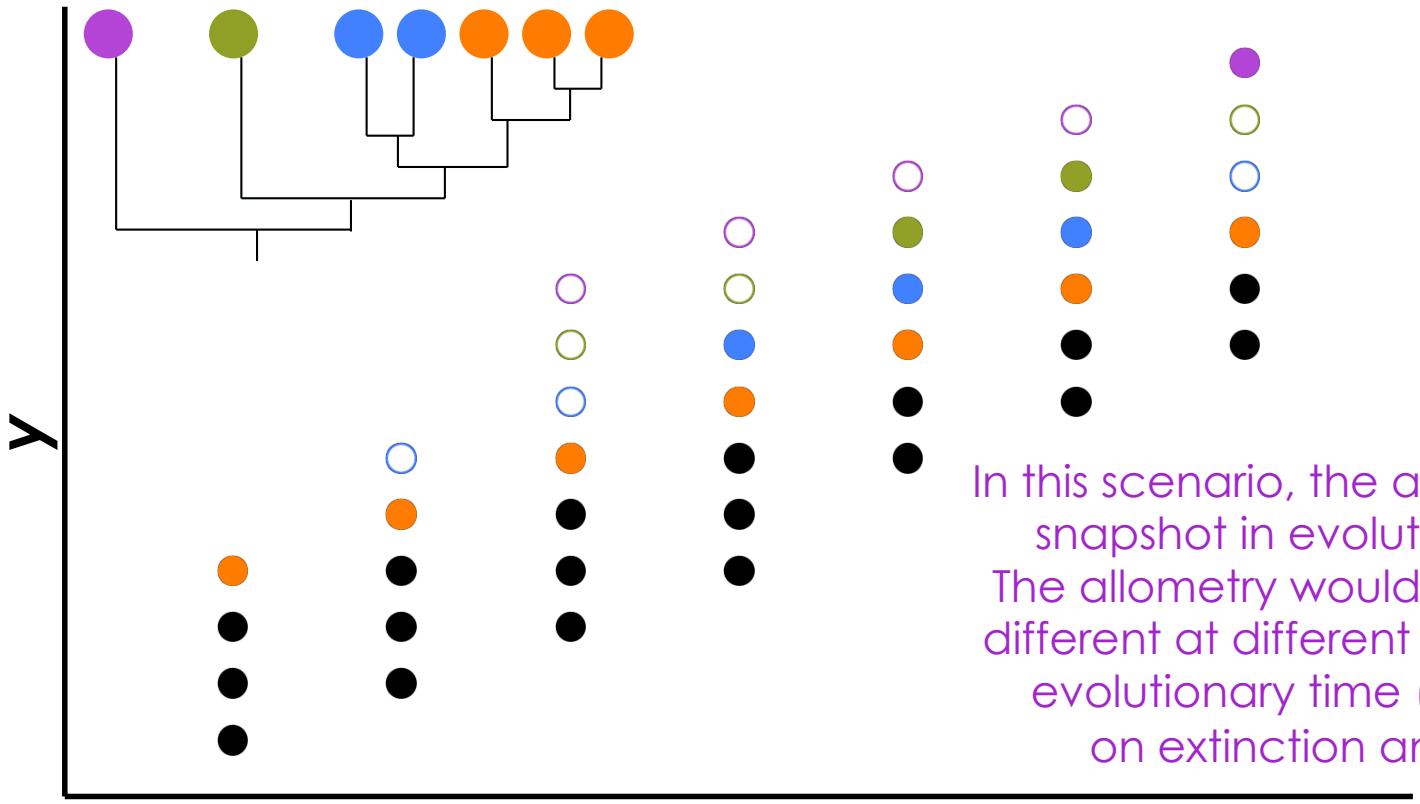

In this scenario, the allometry is a snapshot in evolutionary time. The allometry would have been different at different moments in evolutionary time (depending on extinction and radiation events)

x (body mass)

‘Evolutionary progress’ – directed evolution

Conceptualizing evolution as ‘directed’ in terms of a sequence of innovations means assuming that some characteristics are advantageous for basically all animals in a particular niche range.

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Conceptualizing evolution as ‘directed’ in terms of a sequence of innovations means assuming that some characteristics are advantageous for basically all animals in a particular niche range.

Because niche space is less diverse at larger body sizes, large herbivores may be a particularly fruitful area of research for ‘directed evolution’.

Herbivore basic™

Herbivore 2.0™

Herbivore professional™

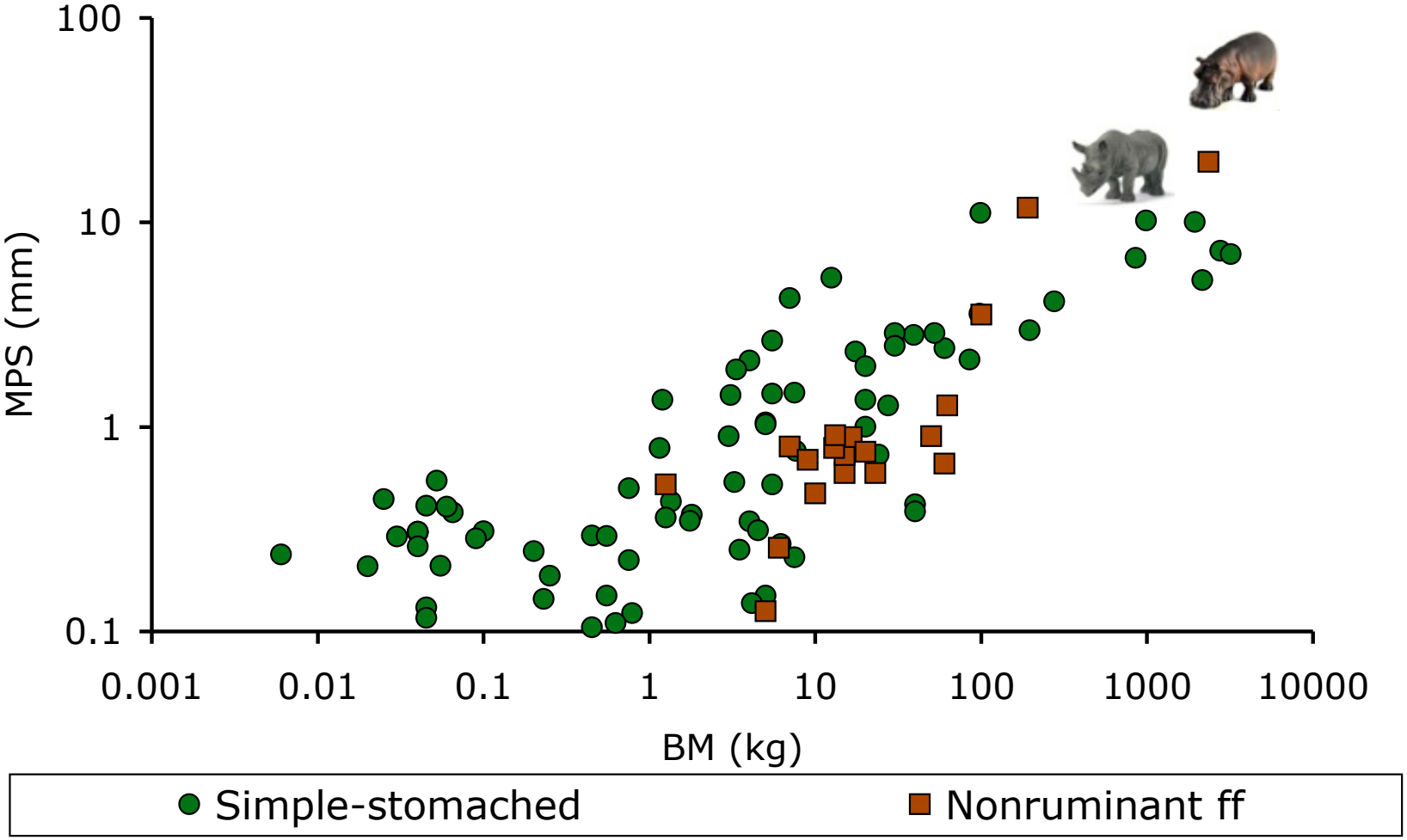
Herbivore ultimate™

Example I: Mammal chewing efficiency

For any herbivore, increasing chewing efficiency – if not associated with higher costs – should be advantageous (higher feeding efficiency due to higher digestibility).

We would predict that herbivore group with the highest chewing efficiency should be particularly 'successful' (e.g. in terms of species diversity).

Example I: Mammal chewing efficiency



from Fritz et al. (2009)

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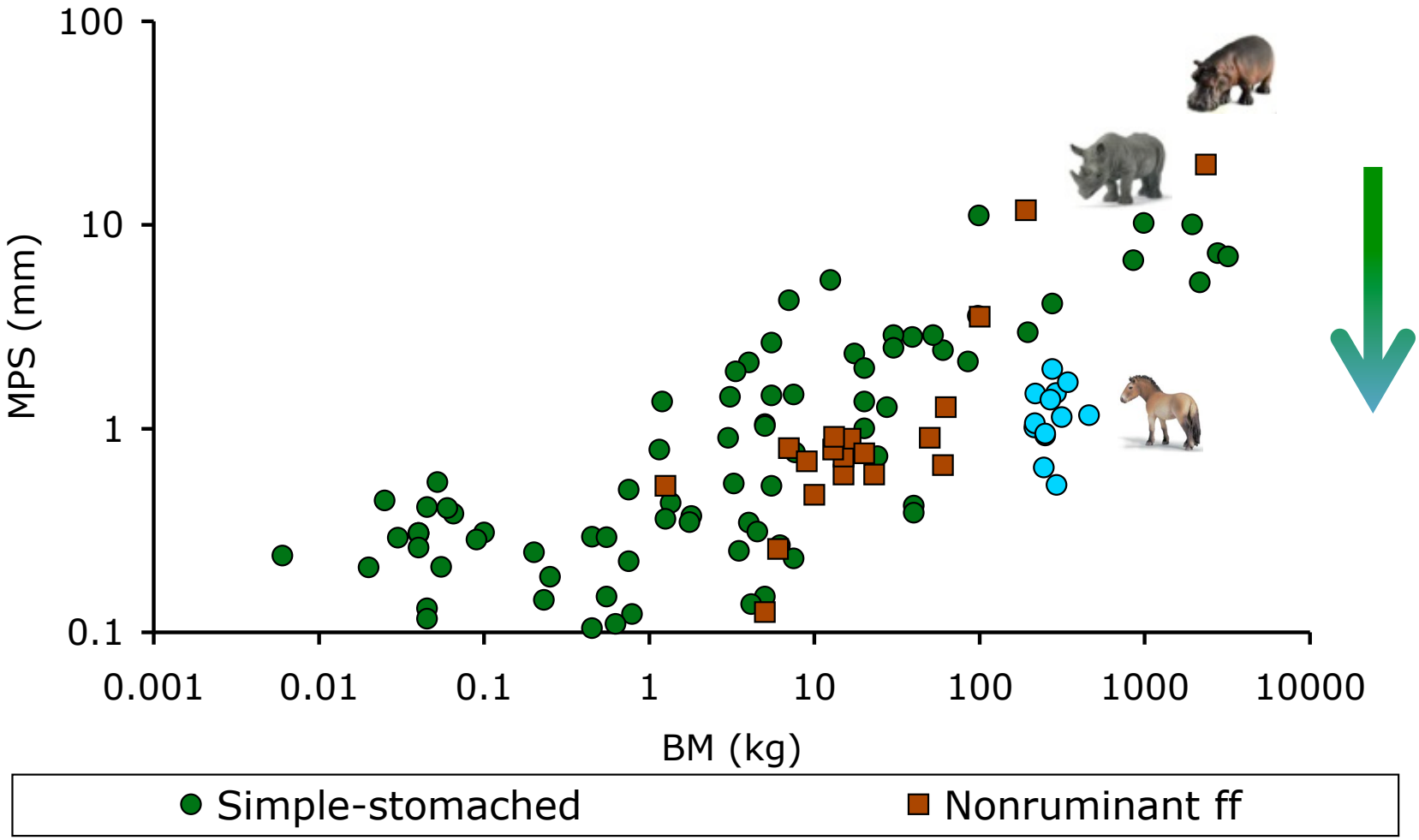

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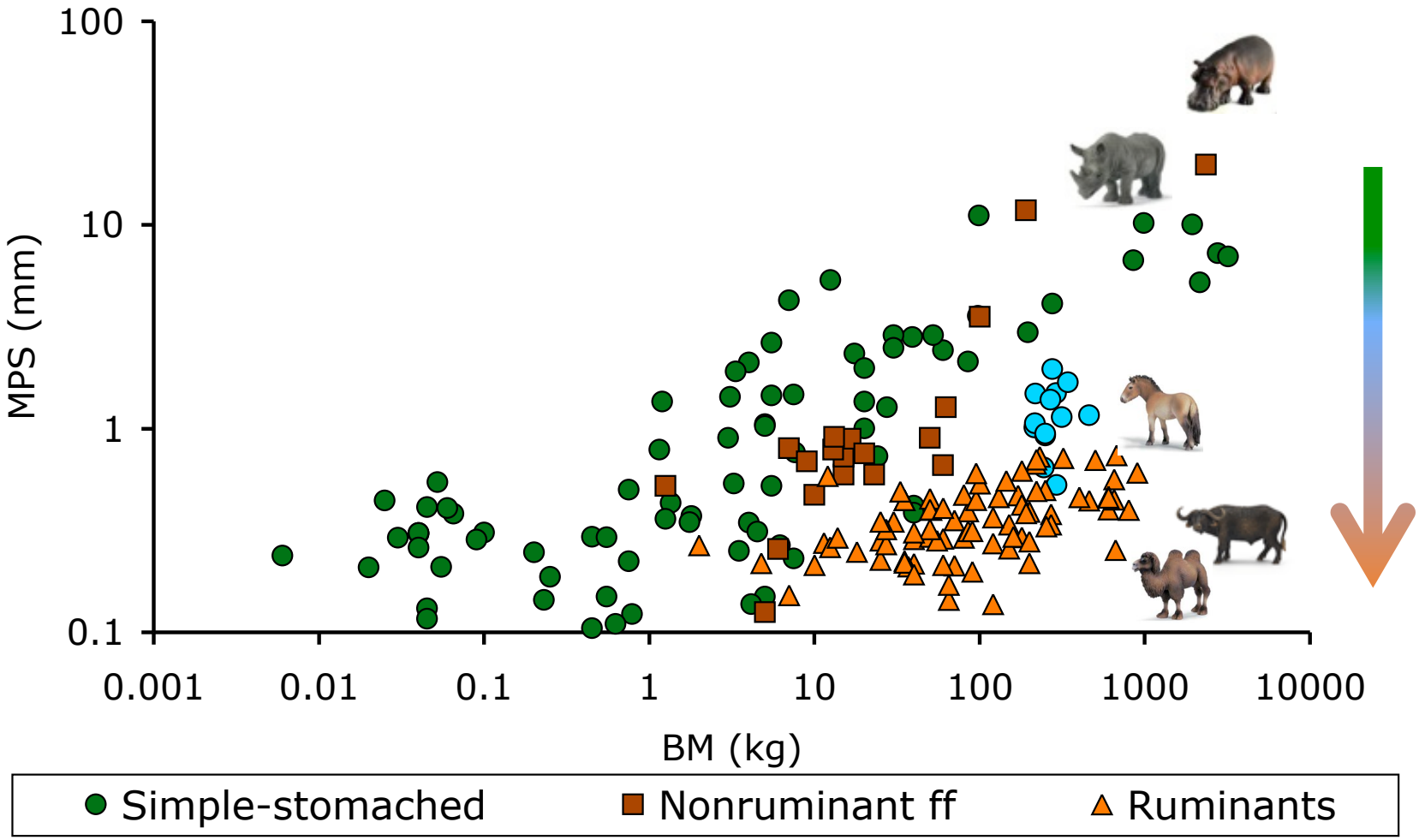

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Example II: (Precocial) Mammal gestation period

For any mammal, achieving the same degree of neonatal development in a shorter gestation period – if not associated with higher costs – should be advantageous (higher fecundity due to shorter generation times).

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Days of gestation period (to apparently similar level of precociality)

Cattle:	app. 280 days
Horse:	app. 340 days
Dromedary:	app. 390 days
Okapi:	app. 440 days

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The difference cannot be due to body size!

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nearly extinct in a very limited geographical range

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only in extreme, resource-poor habitats

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rule the world !!

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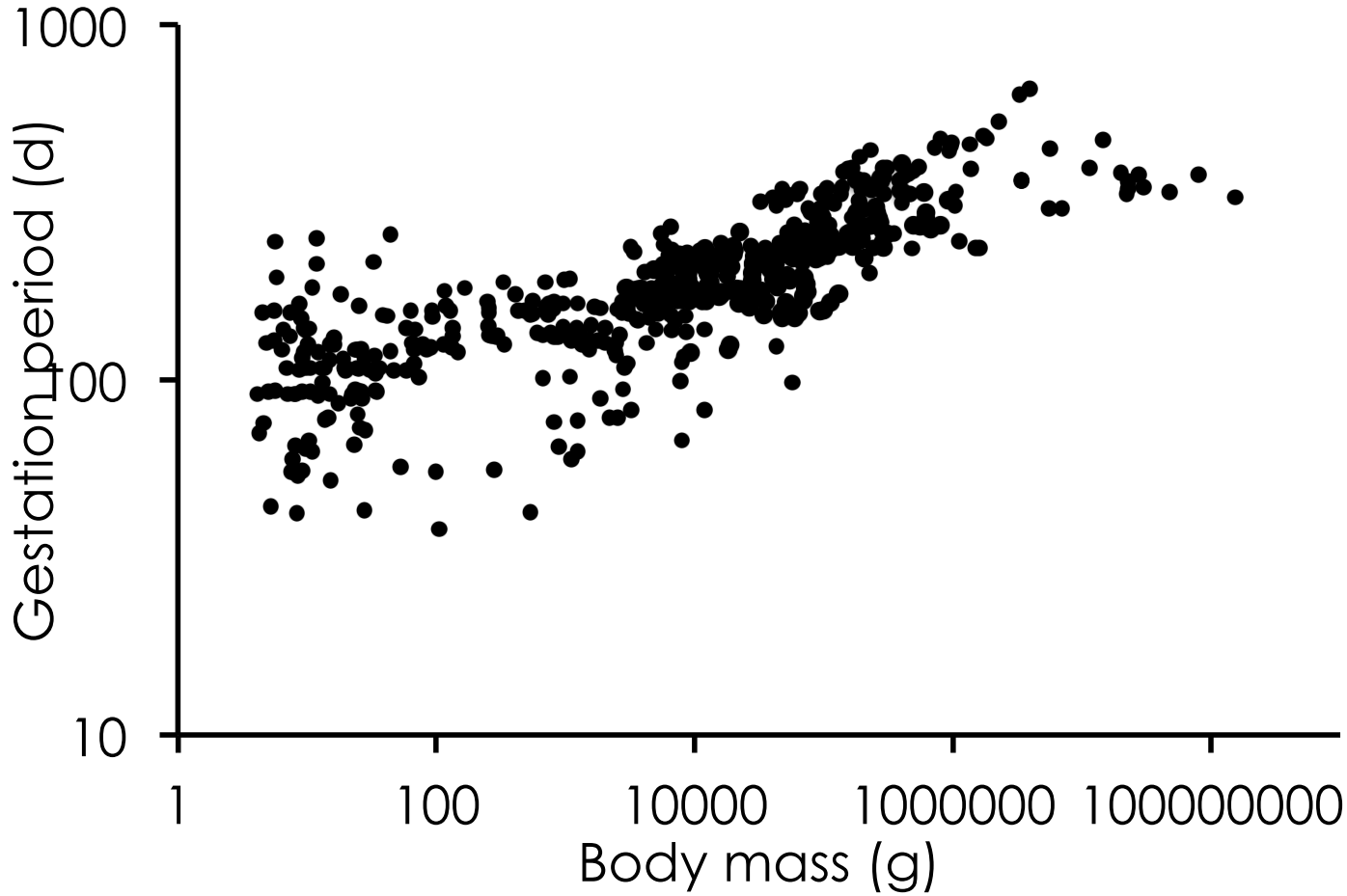

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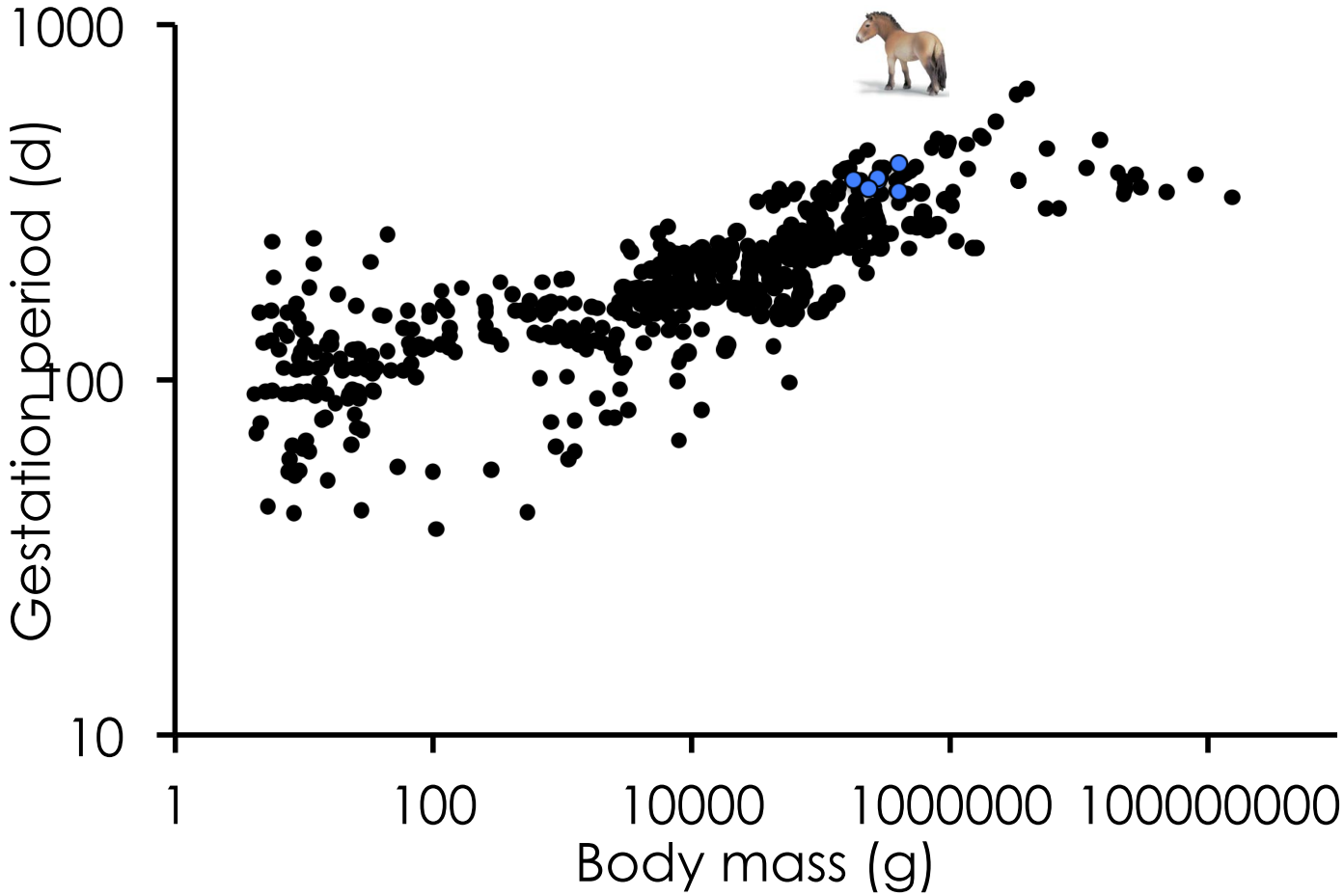

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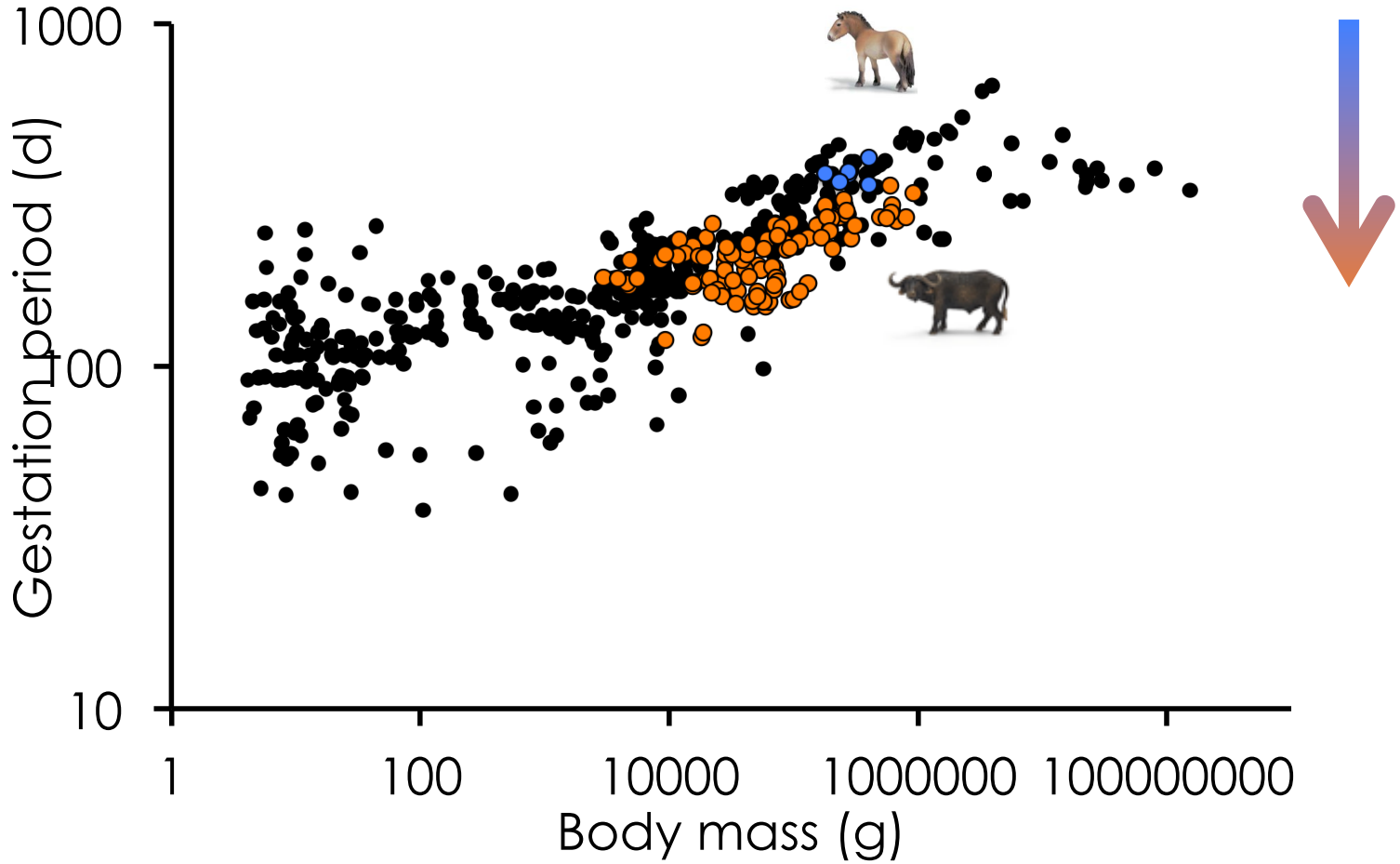

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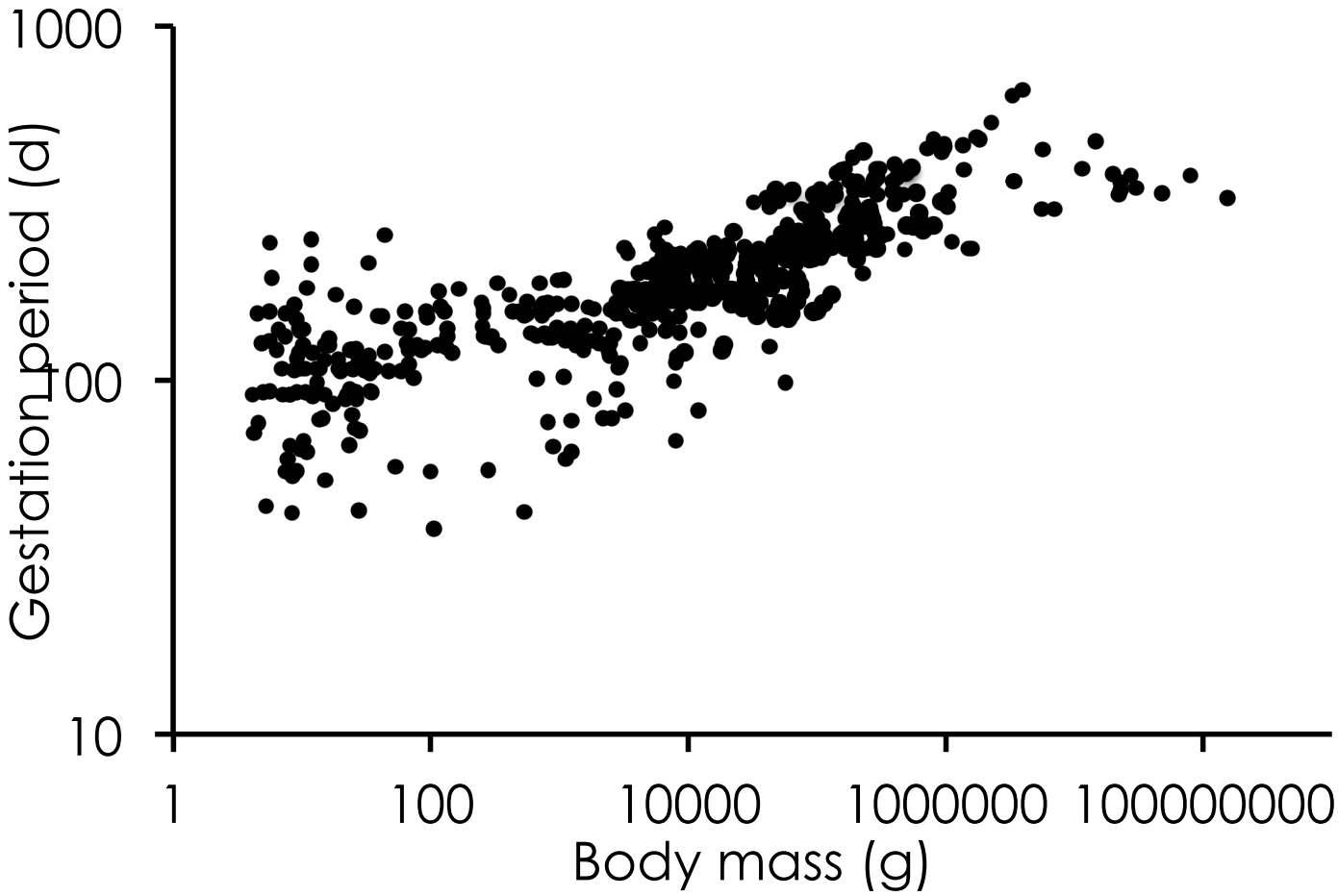

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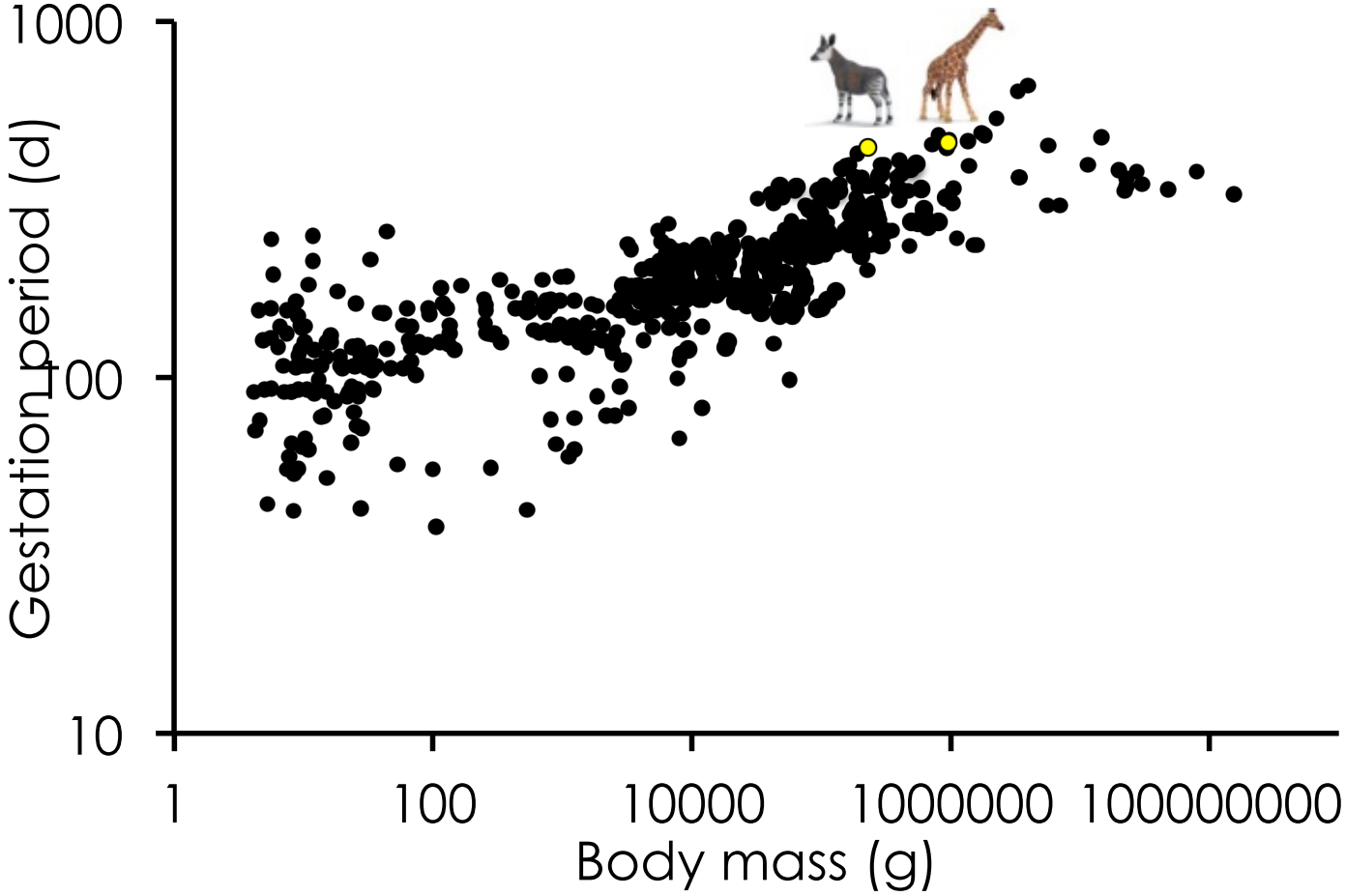

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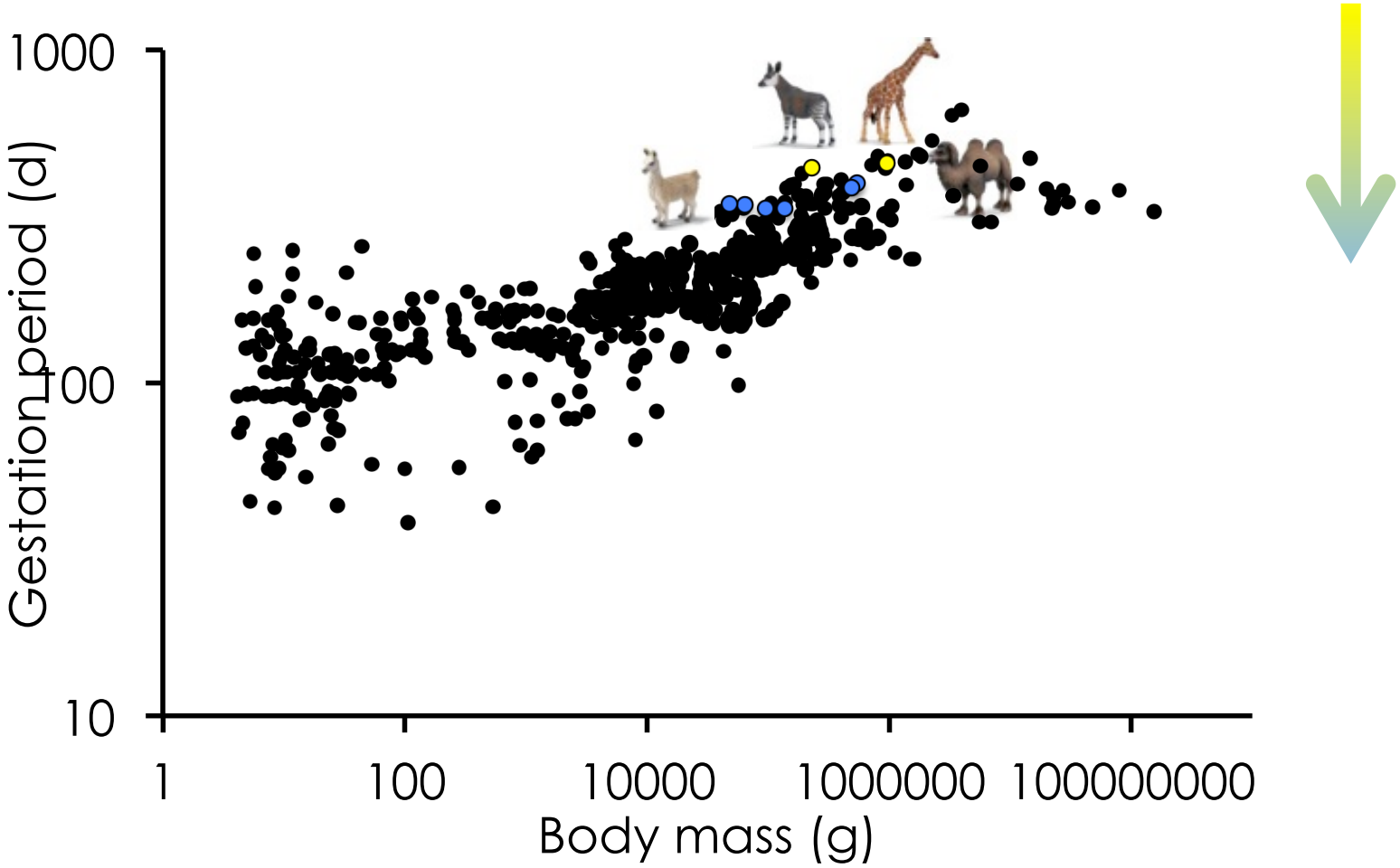

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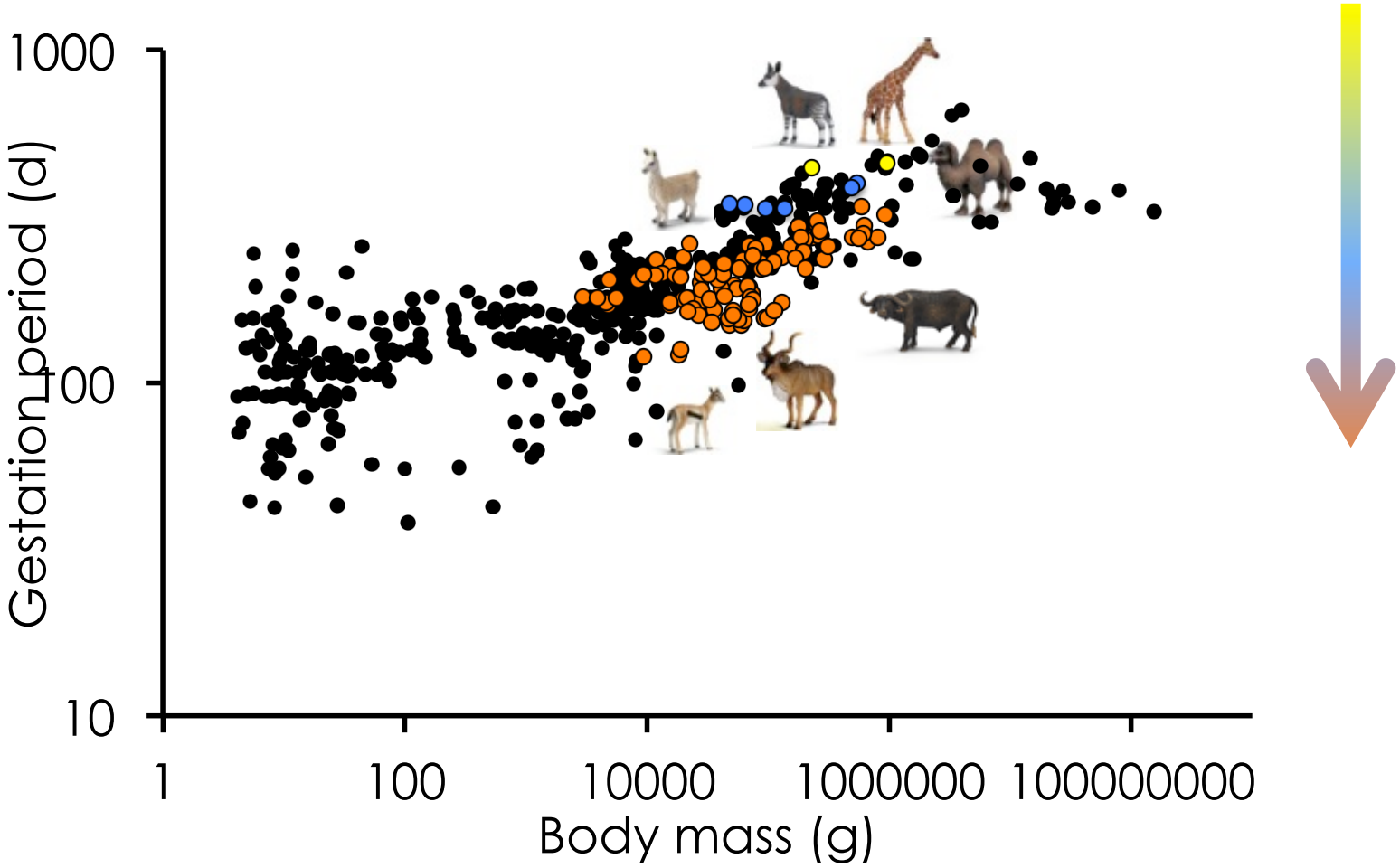

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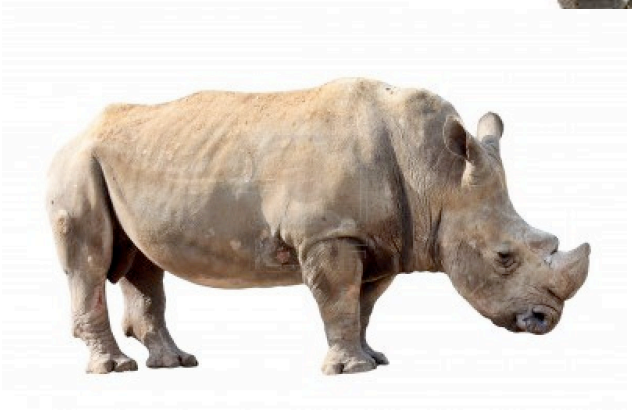
The interesting question …

… what allowed the remaining extant species of the 'disadvantaged' species to survive?






Final words

Allometries are useful tools for comparing, extrapolating and explaining differences between or among animal groups.

Final words

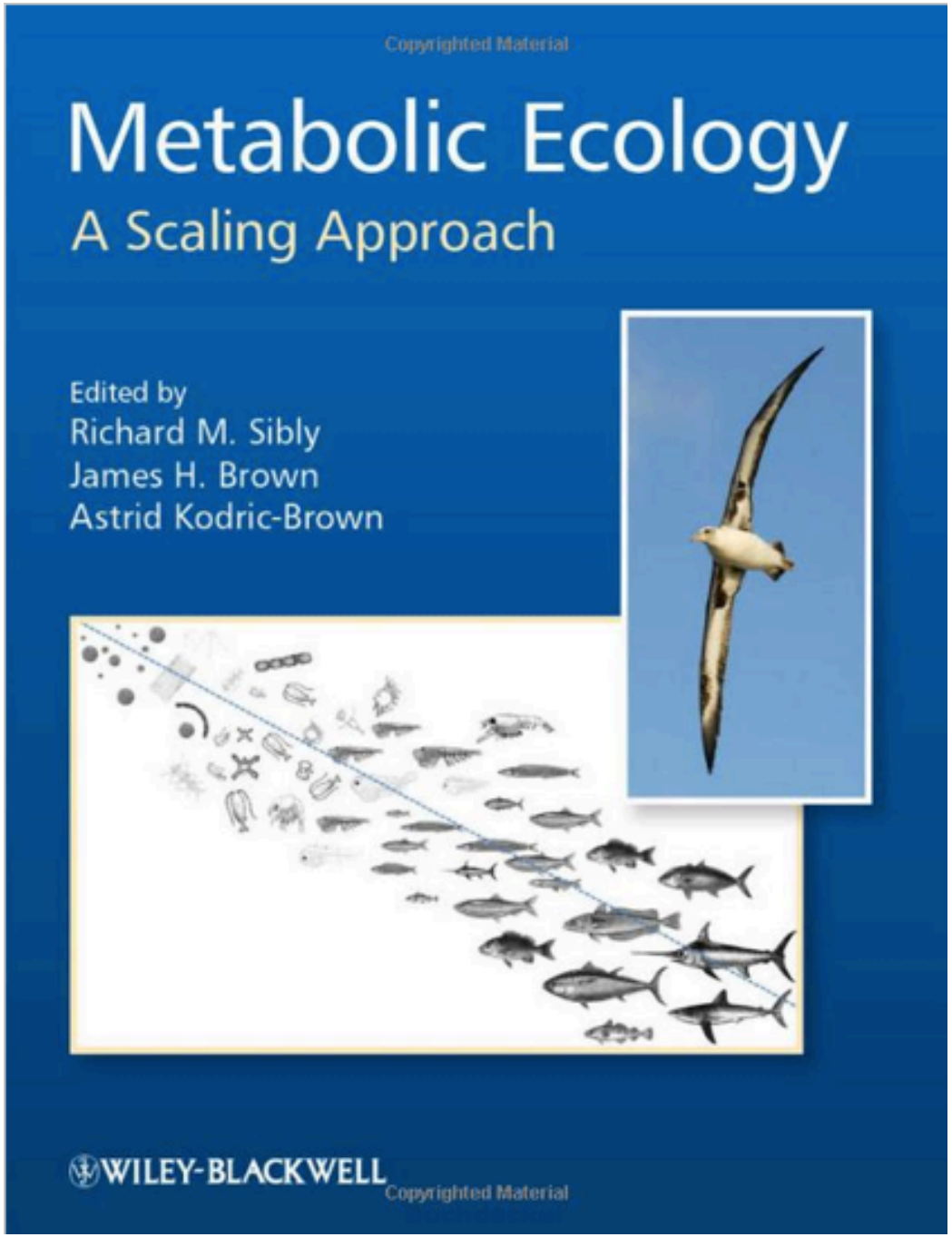
Statements based on allometries should be checked for congruence with empirical data and conceptual soundness.

Do not trust one-scaling statements.

Final words

Comparative datasets, combined with information on phylogeny and diversification history, have enormous potential for the generation of hypotheses on evolutionary constraints and innovations – mainly 'changes in the intercept'.

Finding patterns / mechanisms in 'changes in the intercept' may be a fruitful area of future research.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