Phylogenetic statistics and biological laws

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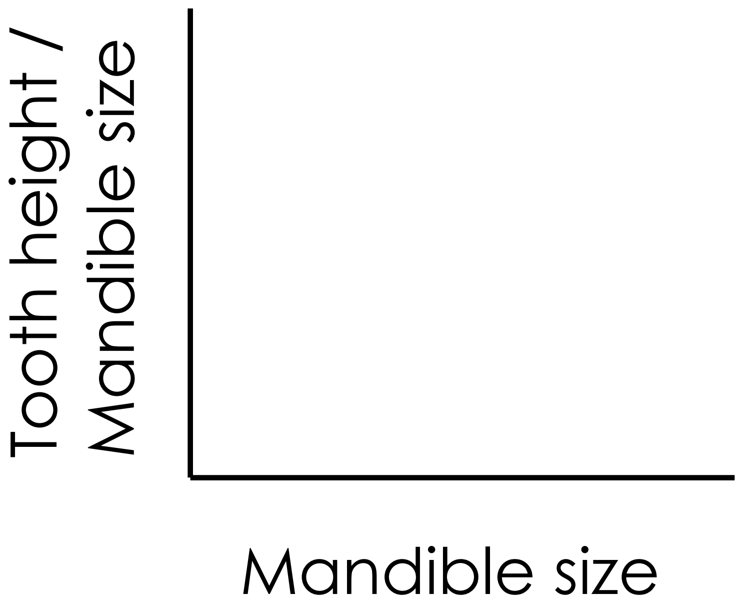
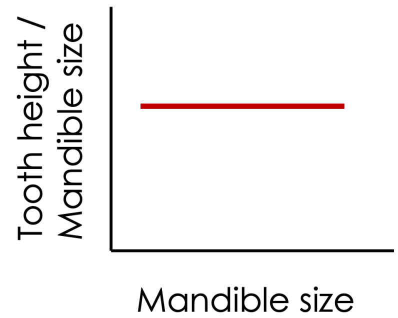
Simple maths reminder

whatever your question
– model possible answers

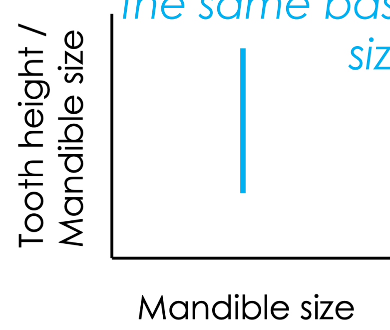
What will you plot ?

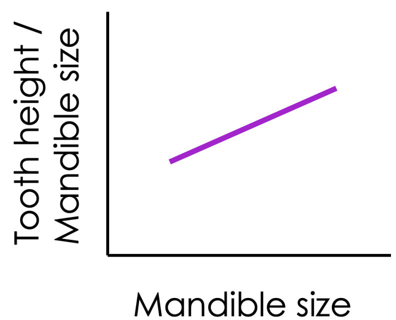
x = mandible size; y = tooth height

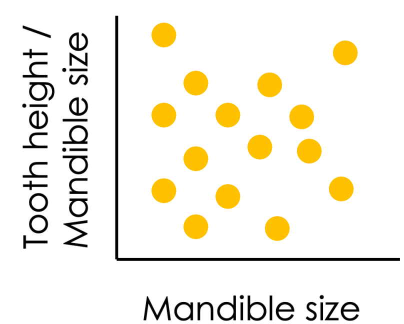




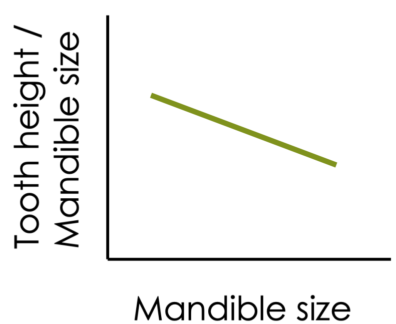
'everything has the same basic size'





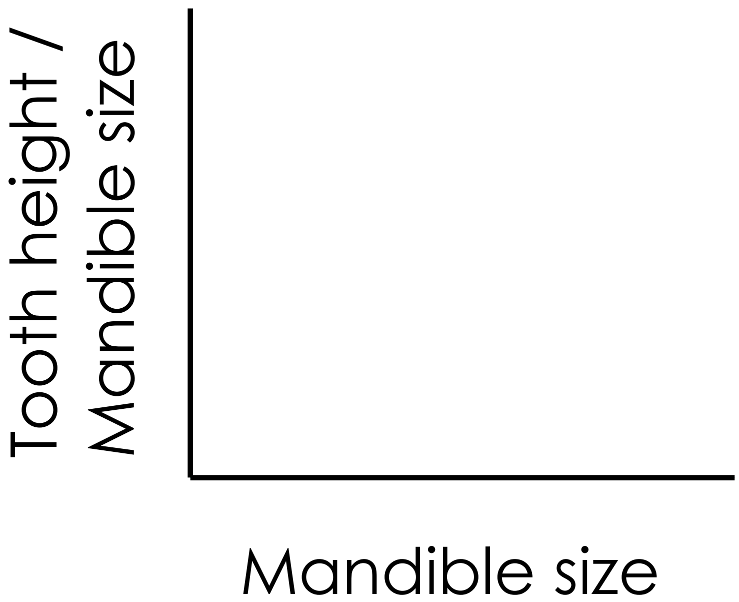


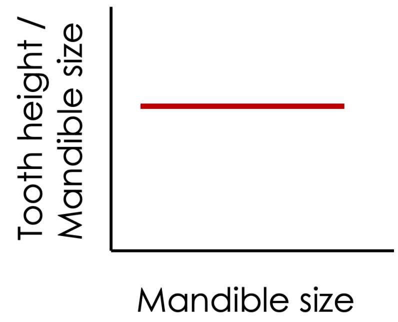
'there is no pattern'



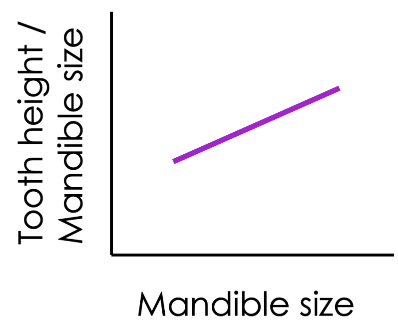
What will you plot ?

x = mandible size; y = tooth height

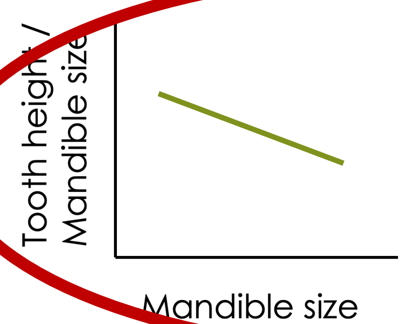




‘tooth height is constant across body size’



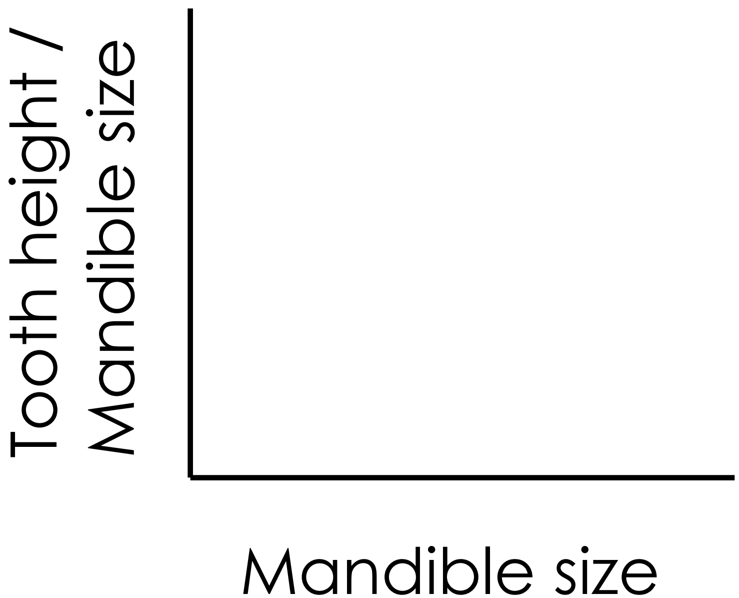
‘relative tooth height increases with body size’

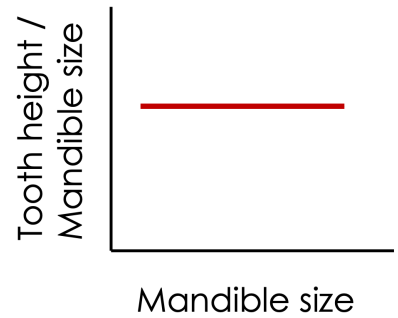


‘relative tooth height decreases with body size’

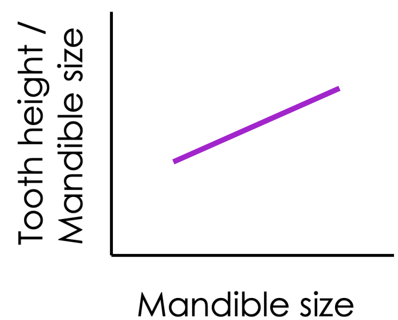
What will you plot ?

x = mandible size; y = tooth height

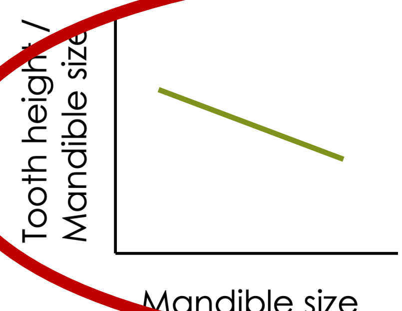




'tooth height is constant across body size'



'relative tooth height increases with body size'



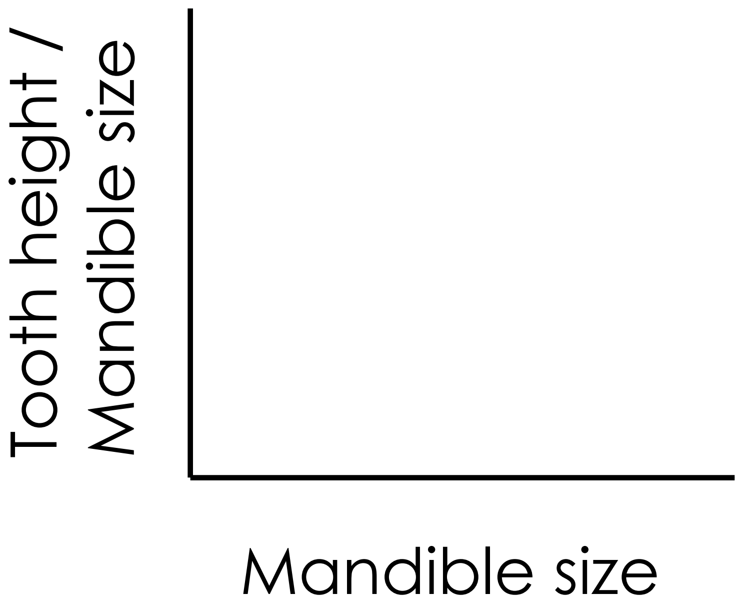
'there is no pattern'

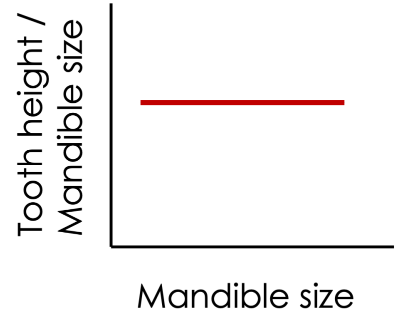
or

'relative tooth height decreases with body size'

What will you plot ?

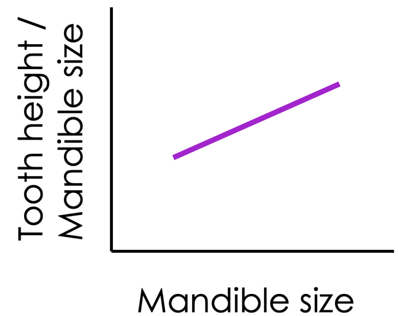
x = mandible size; y = tooth height





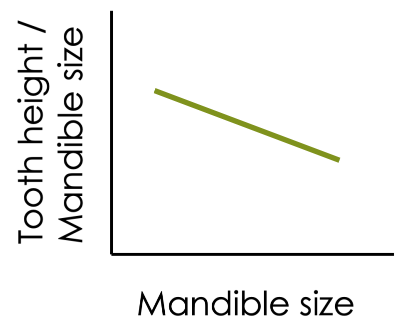
$$y = b\,x$$

'tooth height is constant across body size'



$$y = b\,x^{c}$$

$c > 1$
'relative tooth height increases with body size'



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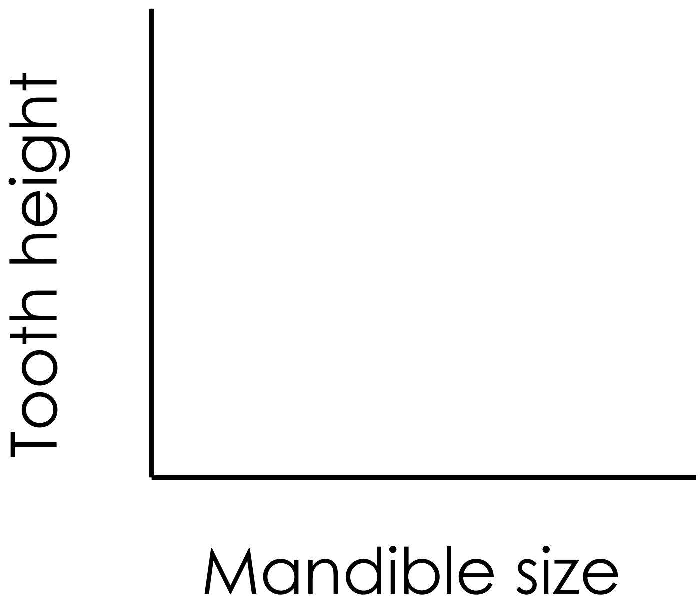

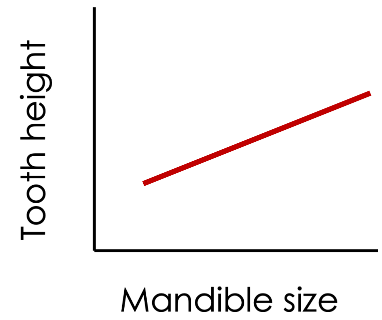

$y = b\,x$

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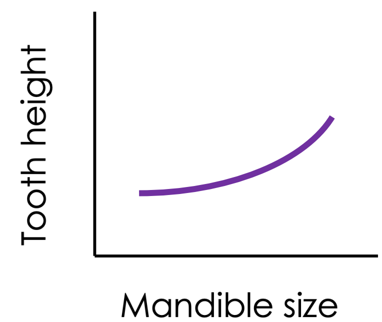

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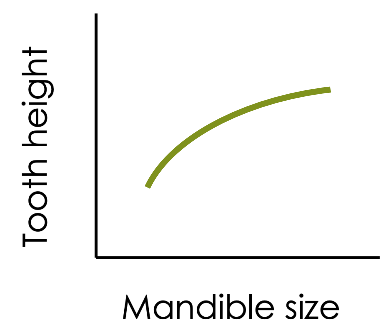

$y = b\,x^c$

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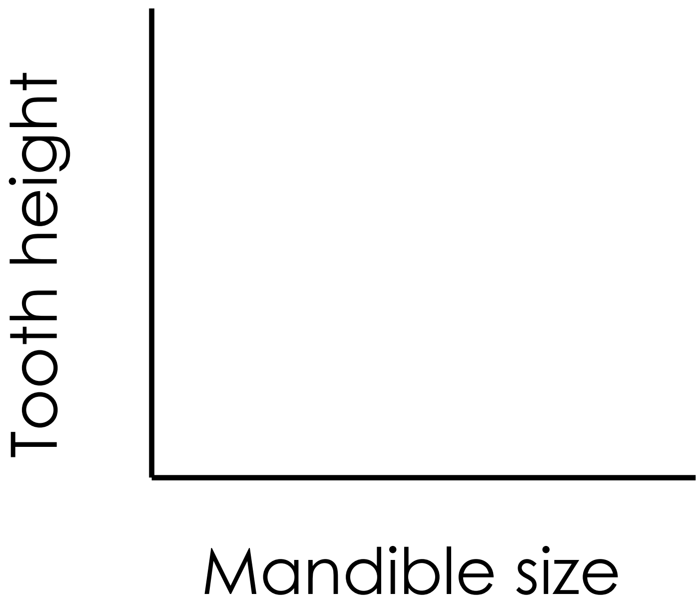
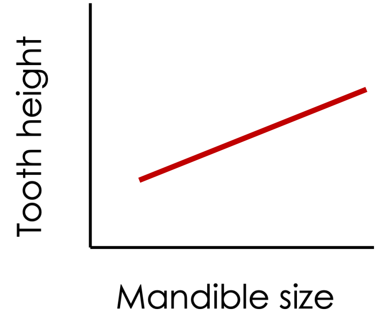
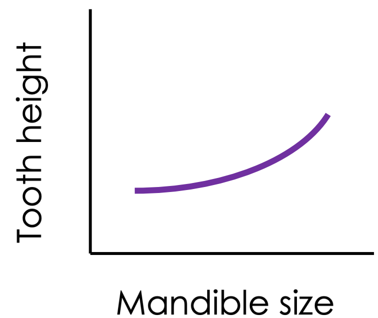




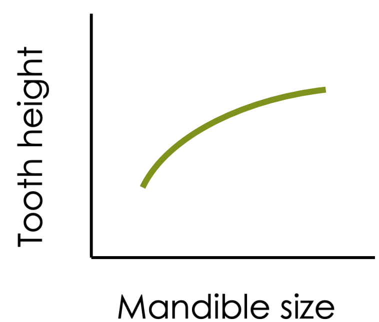
$y = b\,x^c$

$c = 1$
'tooth height is constant across body size'



$y = b\,x^c$

$c > 1$
'relative tooth height increases with body size'



$y = b\,x^c$

$c < 1$
'relative tooth height decreases with body size'

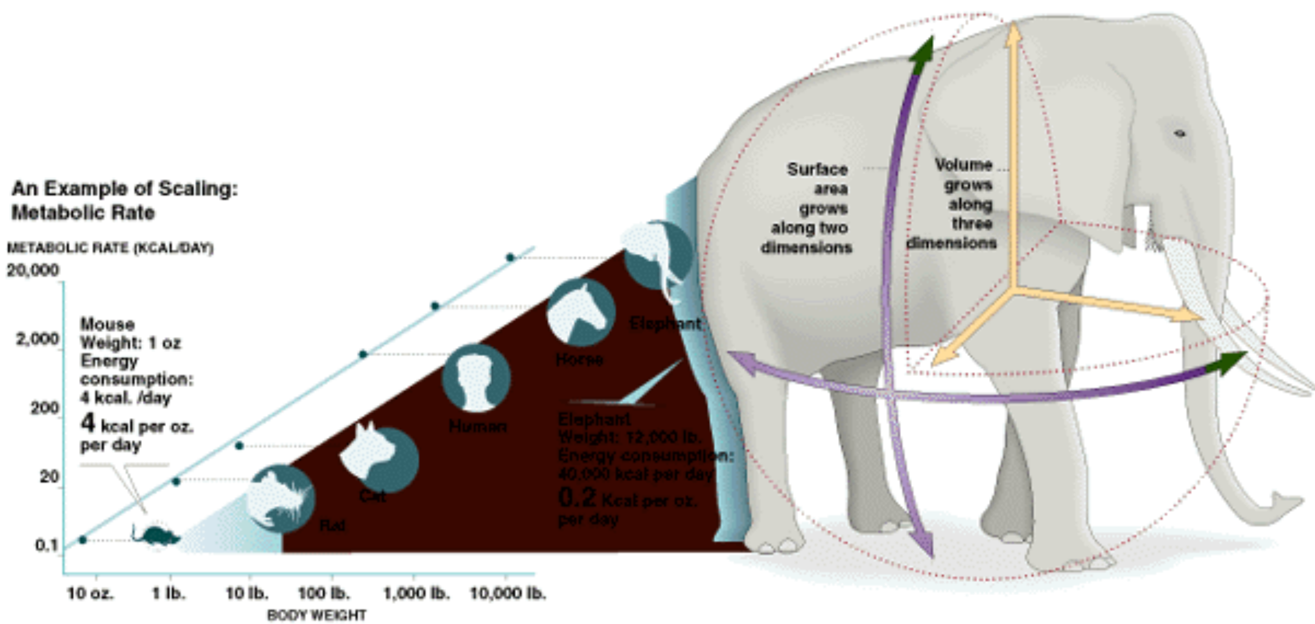
Allometry reminder

Scaling: fundamental (conceptual) relevance of body mass

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

All morphological and physiological traits scale somehow with body mass.

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



Allometries

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

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

Whenever you express something in % body mass, you imply (whether you know it or not) linear scaling !

Think before you express anything in % body mass!

If you express something in % body mass without having tested whether the underlying relation is linear, it is your fault!

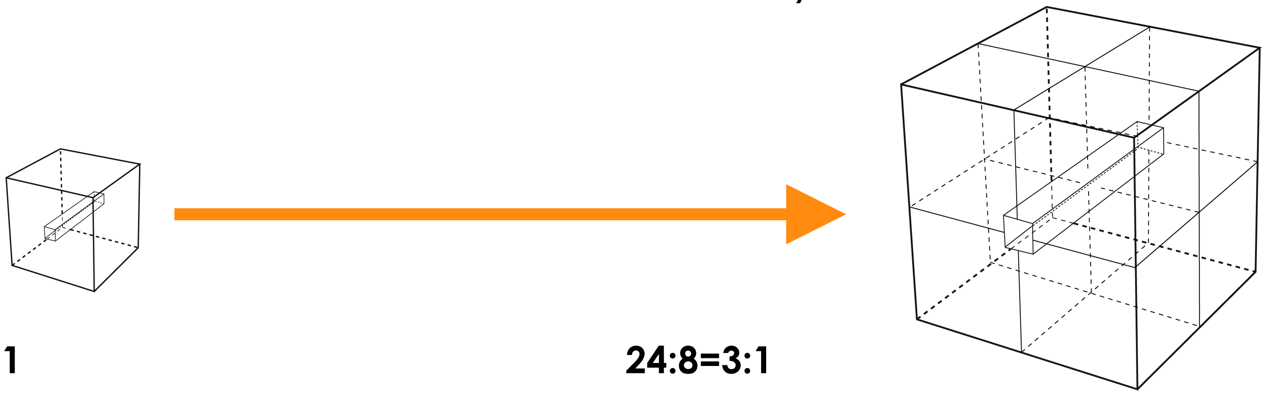
Allometries

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

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

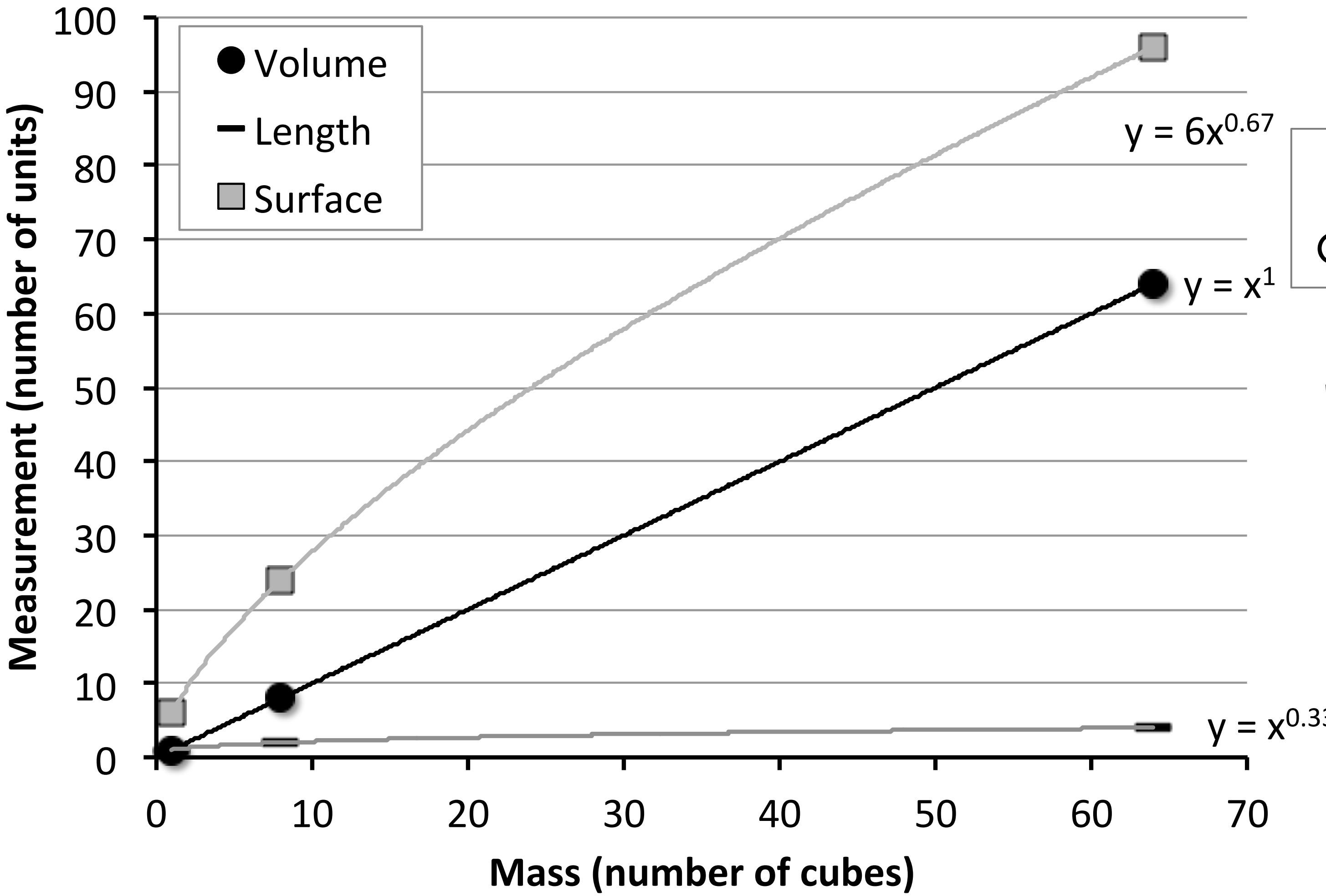
Allometric scaling: $y = a\ \mathrm{BM}^{b}$ or $\log y = \log a + b \log \mathrm{BM}$

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

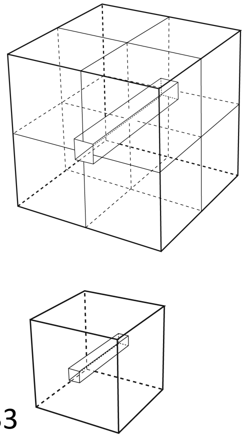


6:1 **24:8=3:1**

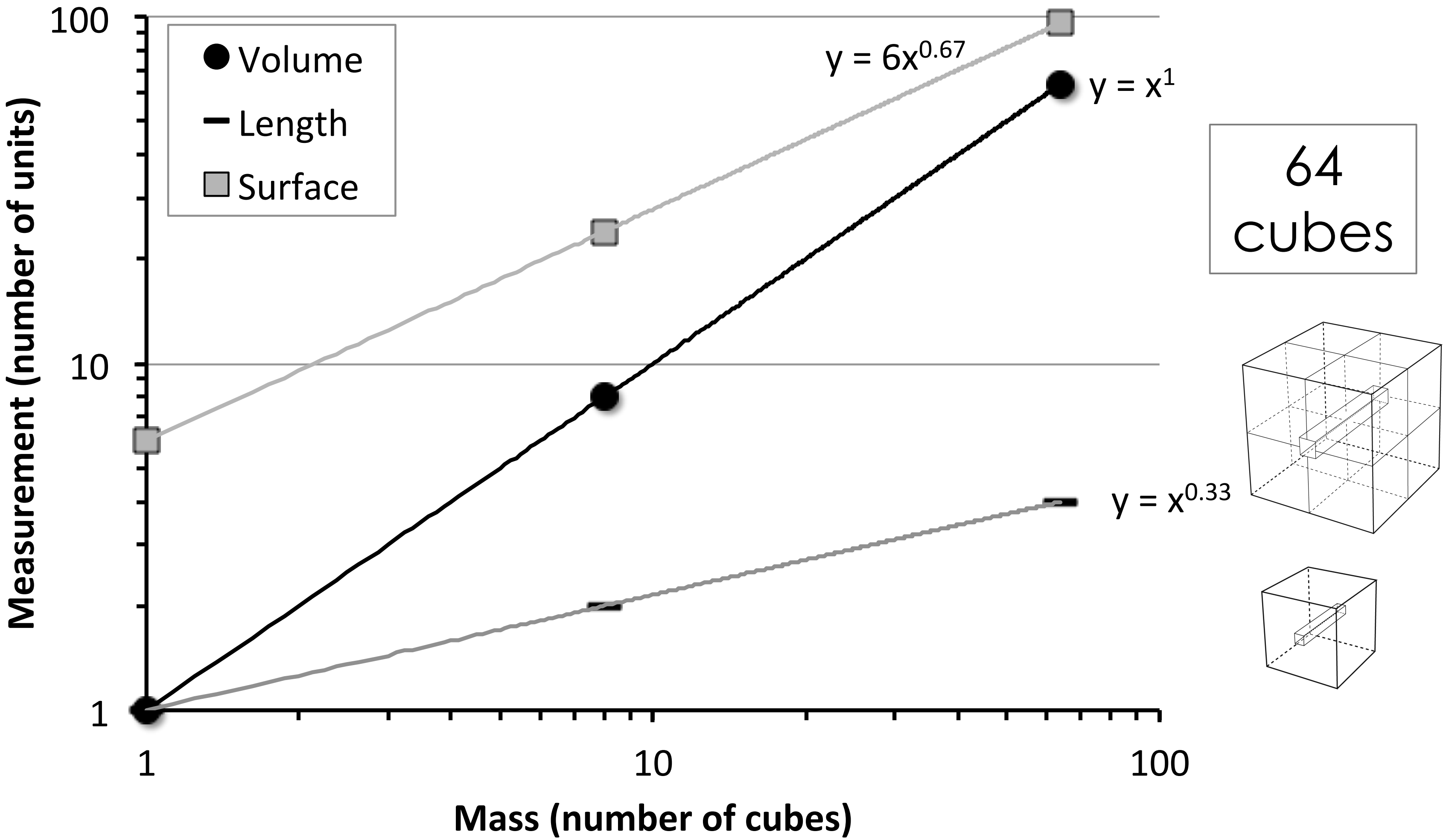
Geometric scaling



64 cubes

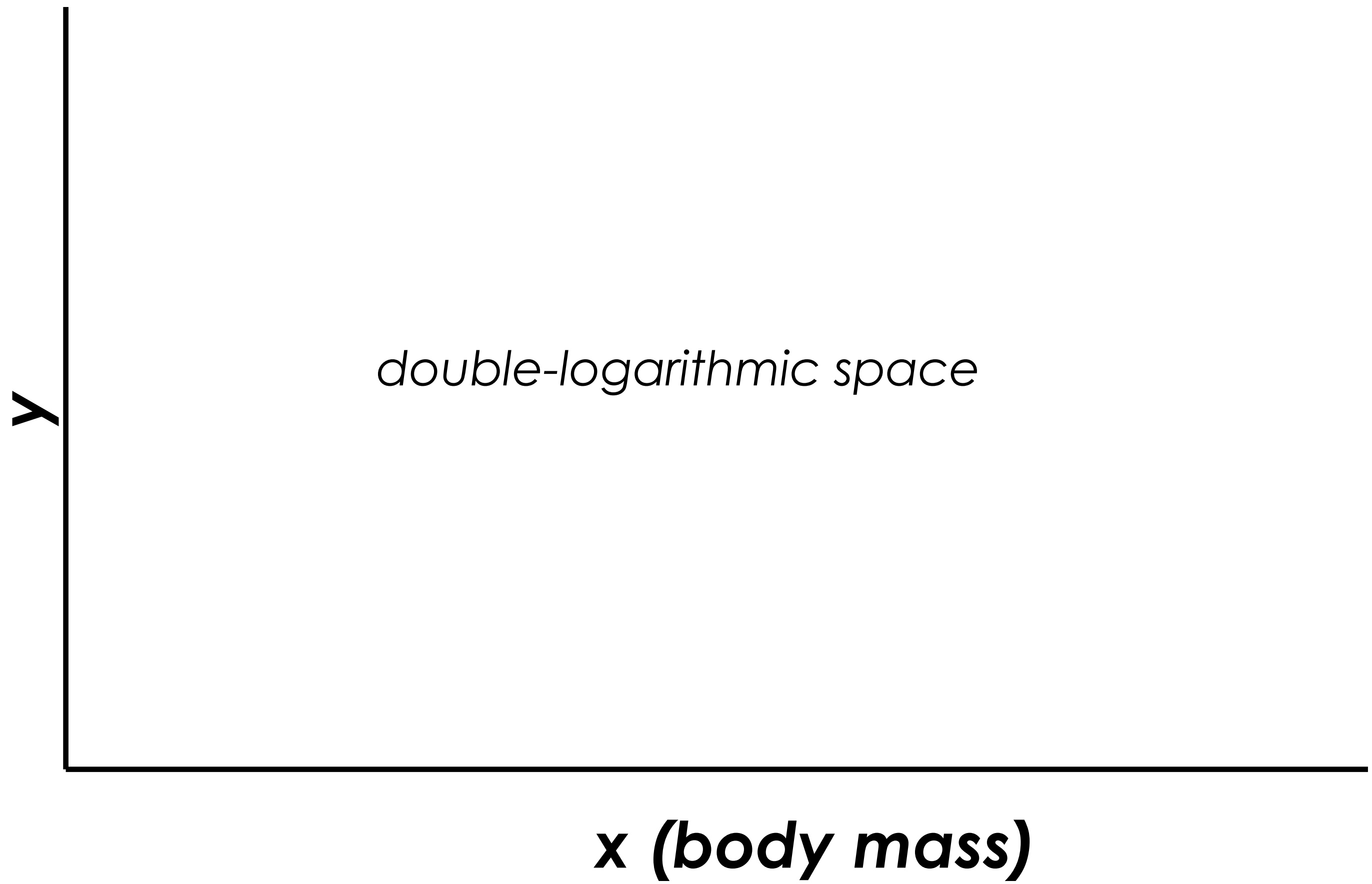


Geometric scaling



Allometries

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



Allometries

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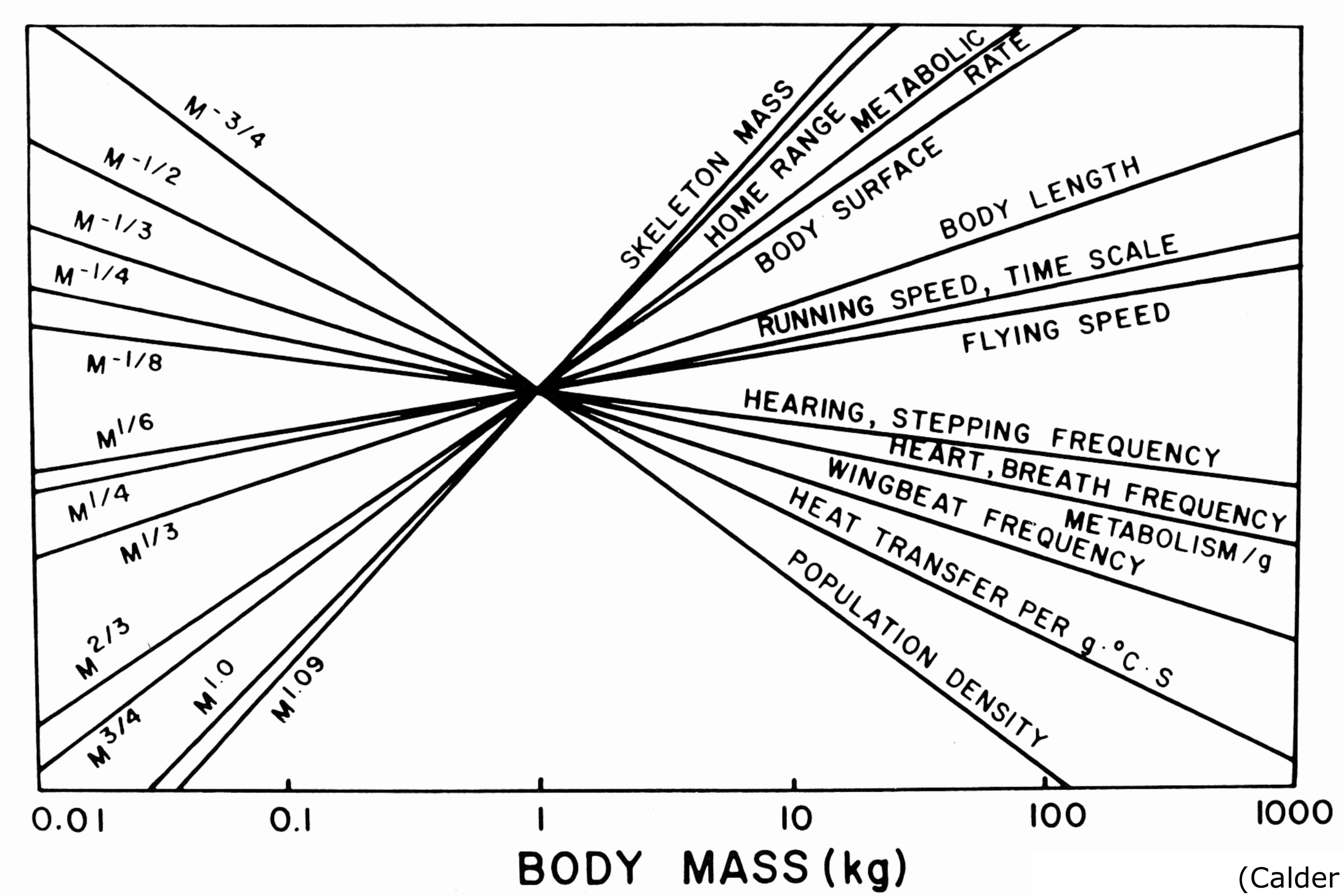


(Calder 1983)

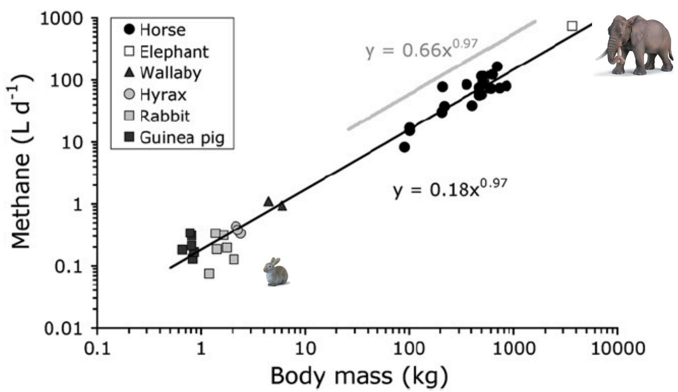
Using allometries

Using allometric relationships to extrapolate data for other species.

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



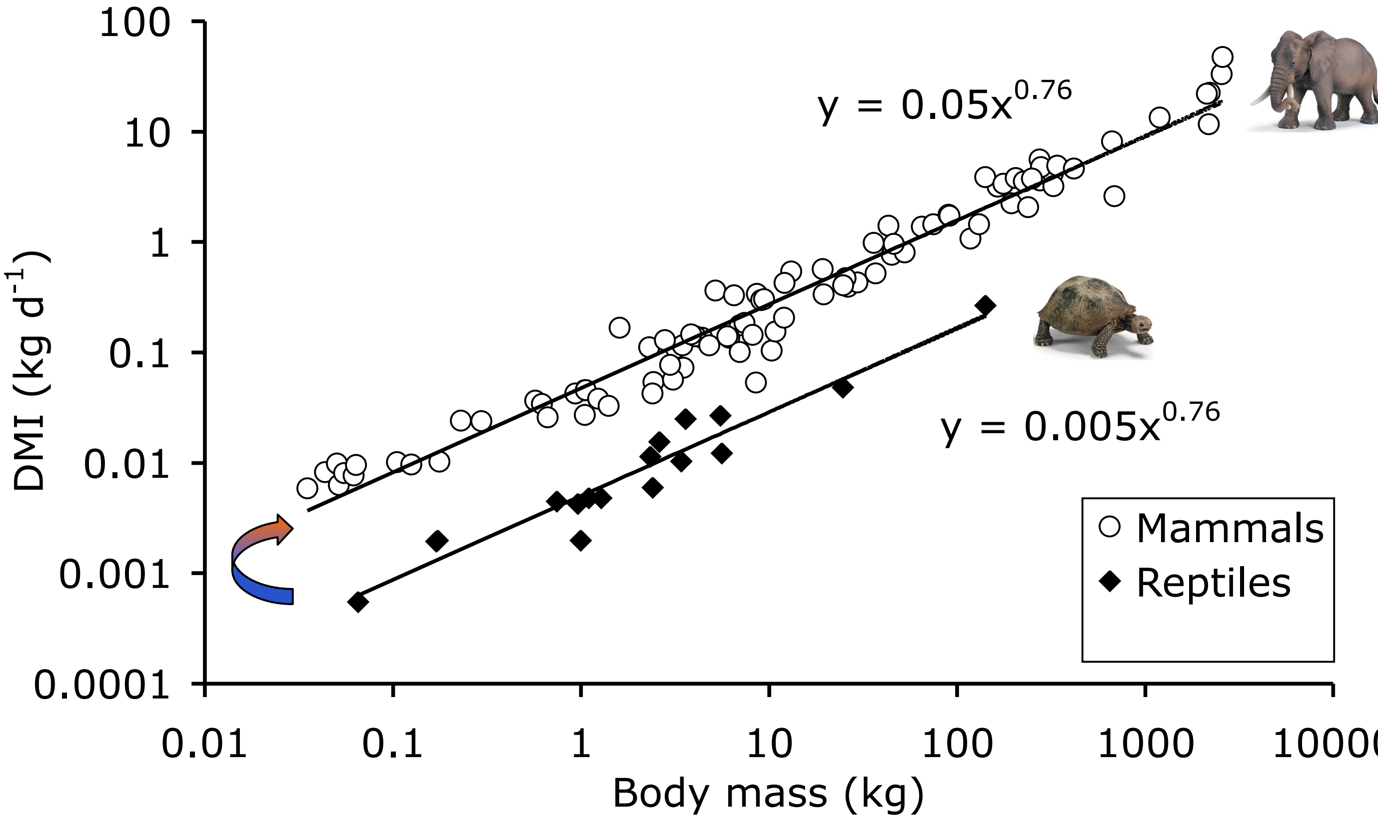
Could methane produced by sauropod dinosaurs have helped drive Mesozoic climate warmth?

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

Current Biology Vol 22 No 9 R292

Using allometries

Using allometric relationships to compare different animal groups.



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

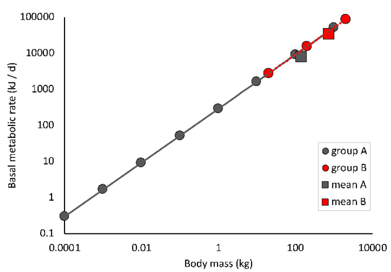
Using allometries: a call for caution

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

This can be expressed in three different ways:

Using allometries: a call for caution

1



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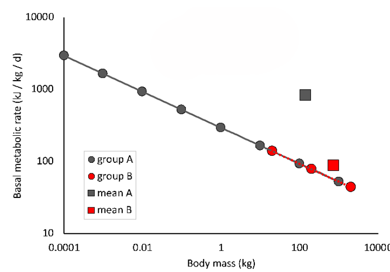
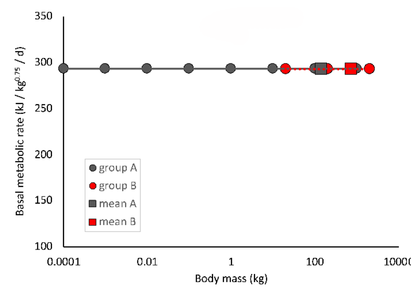


3



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.

ARTICLES
https://doi.org/10.1038/s41559-018-0690-4

nature ecology & evolution

Phylogenetic patterns and phenotypic profiles of the species of plants and mammals farmed for food

Rubén Milla[1*], Jesús M. Bastida[1], Martin M. Turcotte[2], Glynis Jones[3], Cyrille Violle[4], Colin P. Osborne[5], Julia Chacón-Labella[1,19], Ênio E. Sosinski Jr[6], Jens Kattge[7,8], Daniel C. Laughlin[9], Estelle Forey[10], Vanessa Minden[11,12], Johannes H. C. Cornelissen[13], Bernard Amiaud[14,20], Koen Kramer[15], Gerhard Boenisch[7], Tianhua He[16], Valério D. Pillar[17] and Chaeho Byun[18]

The origins of agriculture were key events in human history, during which people came to depend for their food on small numbers of animal and plant species. However, the biological traits determining which species were domesticated for food provision, and which were not, are unclear. Here, we investigate the phylogenetic distribution of livestock and crops, and compare their phenotypic traits with those of wild species. Our results indicate that phylogenetic clustering is modest for crop species but more intense for livestock. Domesticated species explore a reduced portion of the phenotypic space occupied by their wild counterparts and have particular traits in common. For example, herbaceous crops are globally characterized by traits including high leaf nitrogen concentration and tall canopies, which make them fast-growing species and proficient competitors. Livestock species are relatively large mammals with low basal metabolic rates, which indicate moderate to slow life histories. Our study therefore reveals ecological differences in domestication potential between plants and mammals. Domesticated plants belong to clades with traits that are advantageous in intensively managed high-resource habitats, whereas domesticated mammals are from clades adapted to moderately productive environments. Combining comparative phylogenetic methods with ecologically relevant traits has proven useful to unravel the causes and consequences of domestication.

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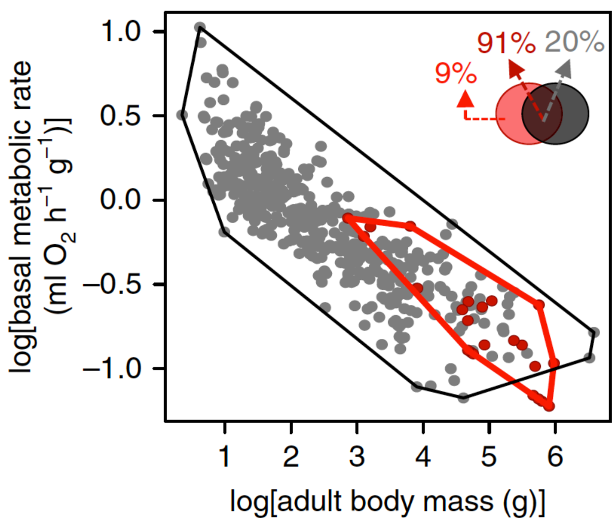

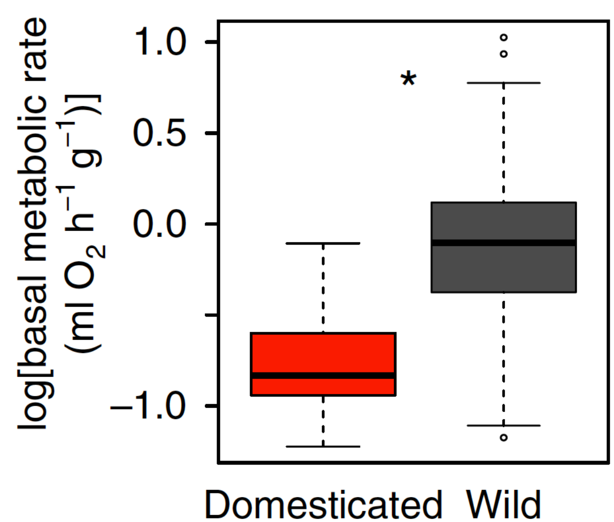

correspondence

No evidence for different metabolism in domestic mammals

Recently, Milla et al.[1] concluded that "livestock species are relatively large mammals with low basal metabolic rates, which indicate moderate to slow life histories". While this claim may appear counterintuitive—production animals should be characterized by fast growth, a feature of a comparatively fast pace of life—the analyses performed in that study do not allow any claims to be made with respect to the comparative level of metabolism in domestic species.

When comparing one measurement that depends on another between two groups of organisms, such as absolute or mass-specific metabolism, which depends on body mass, it is the nature of the relationship between the measurements that must be investigated (for example, in a linear model in which 'group' is used as a co-variable), not the differences between measurement averages of the two groups.

Figure 1a,b shows two idealized groups that vary in the body mass range of their individuals, but not in the level of metabolism, arbitrarily set to 293 kJ per kg$^{0.75}$ per day (as in ref. [2]). In log–log space, both the slope and the intercept of their respective regression lines are identical (as indicated by the gray and dotted red regression lines). However, owing to the difference in body mass range in these groups, they distinctly differ in the average level of metabolism that is calculated as the mean of all individual group data points (the squares in Fig. 1a,b; Fig. 1b corresponds to Fig. 3a in Milla et al., and the squares represent the boxplots of Fig. 4b in Milla et al.). Comparing these averages when detached from the underlying body mass is meaningless. Therefore, any conclusions drawn by Milla et al. as to whether livestock species are characterized by a low or high level of metabolism are premature.

When dealing with the phenomenon of metabolism, one can use three different units: absolute metabolic rates (joules per day, refer to Fig. 1a), 'mass-specific' metabolic rates (joules per body mass and day, refer to Fig. 1b), and relative metabolic rates (joules per metabolic body weight and day, refer to Fig. 1c). Note that the reference frame can be chosen to facilitate any possible statement[3]: large animals have higher absolute metabolic rates (Fig. 1a), larger animals have lower 'mass-specific' metabolic rates (Fig. 1b), or relative metabolic rates do not change with body mass (Fig. 1c).

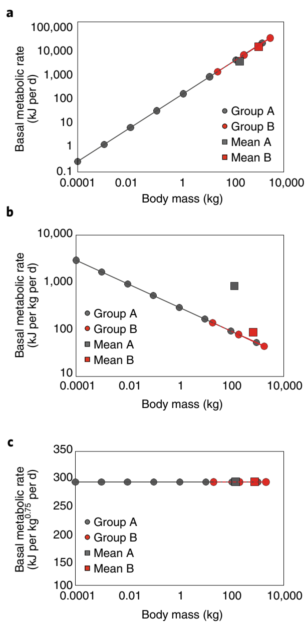

Fig. 1 | Three different methods of displaying the same model dataset of two groups of animals. The daily basal metabolic rate, calculated for each individual's body mass as 293 kJ per kg$^{0.75}$ per d, is shown for groups A and B (representing the wild and domesticated species in Milla, et al.[1]). **a–c**, Results are displayed as absolute metabolic rates (kJ per d) (**a**), mass-specific metabolic rates (kJ per kg per d) (**b**), and relative metabolic rates (kJ per kg$^{0.75}$ per d) (**c**). The squares indicate the average calculated from the individual data points of the datasets. Note that although both groups follow an identical pattern of metabolism with body mass, the calculated averages differ in **a** and **b**, suggesting a higher (**a**) or lower (**b**) level of metabolism for group B, whereas no difference in the levels of metabolism between the groups is evident in **c**.

The choice of the reference unit may be driven by the desire to make a certain rhetorical argument. The only unit that would, in theory, allow a reasonable comparison of the calculated average levels of metabolism is one that applies the correct 'body mass correction' based on the actual body mass scaling in the dataset; in the model example, that is metabolic body weight (Fig. 1c). ❐

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References

1. Milla, R. et al. *Nat. Ecol. Evol.* **2**, 1808–1817 (2018).
2. Kleiber, M. *Hilgardia* **6**, 315–353 (1932).
3. Clauss, M., Steuer, P., Müller, D. W., Codron, D. & Hummel, J. *PLoS One* **8**, e68714 (2013).

Competing interests

The author declares no competing interests.

Using allometries: a call for caution

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

~~*e.g.*~~
~~*"Larger animals have lower 'mass-specific' requirements – therefore they can use lower-quality food."*~~

no comparison to other scaling!

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

Using allometries: a call for caution

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

Do not trust one-scaling statements.

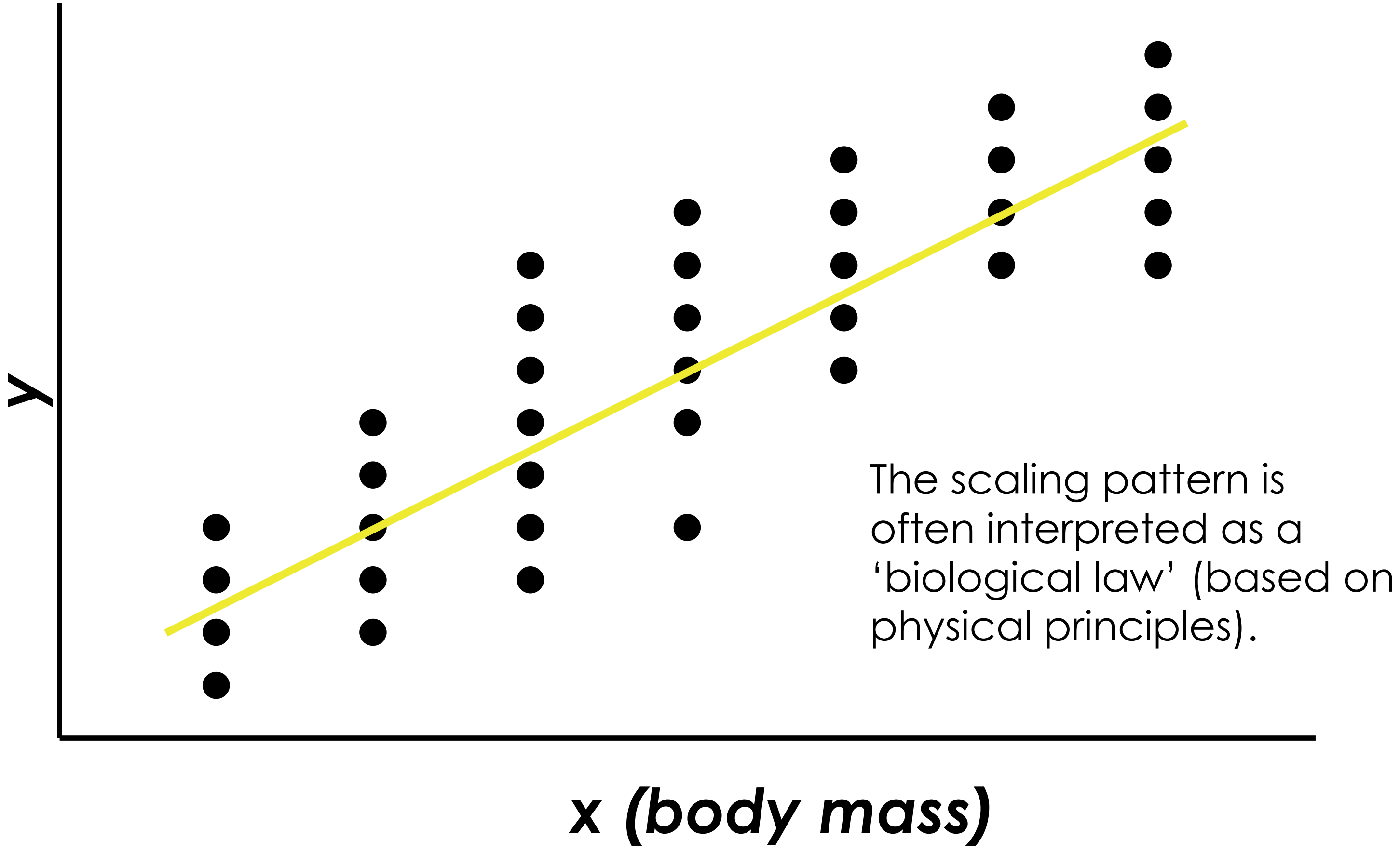
Using allometries: a call for caution

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

If x ~ $BM^{0.95}$ and y ~ $BM^{0.75}$, 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.

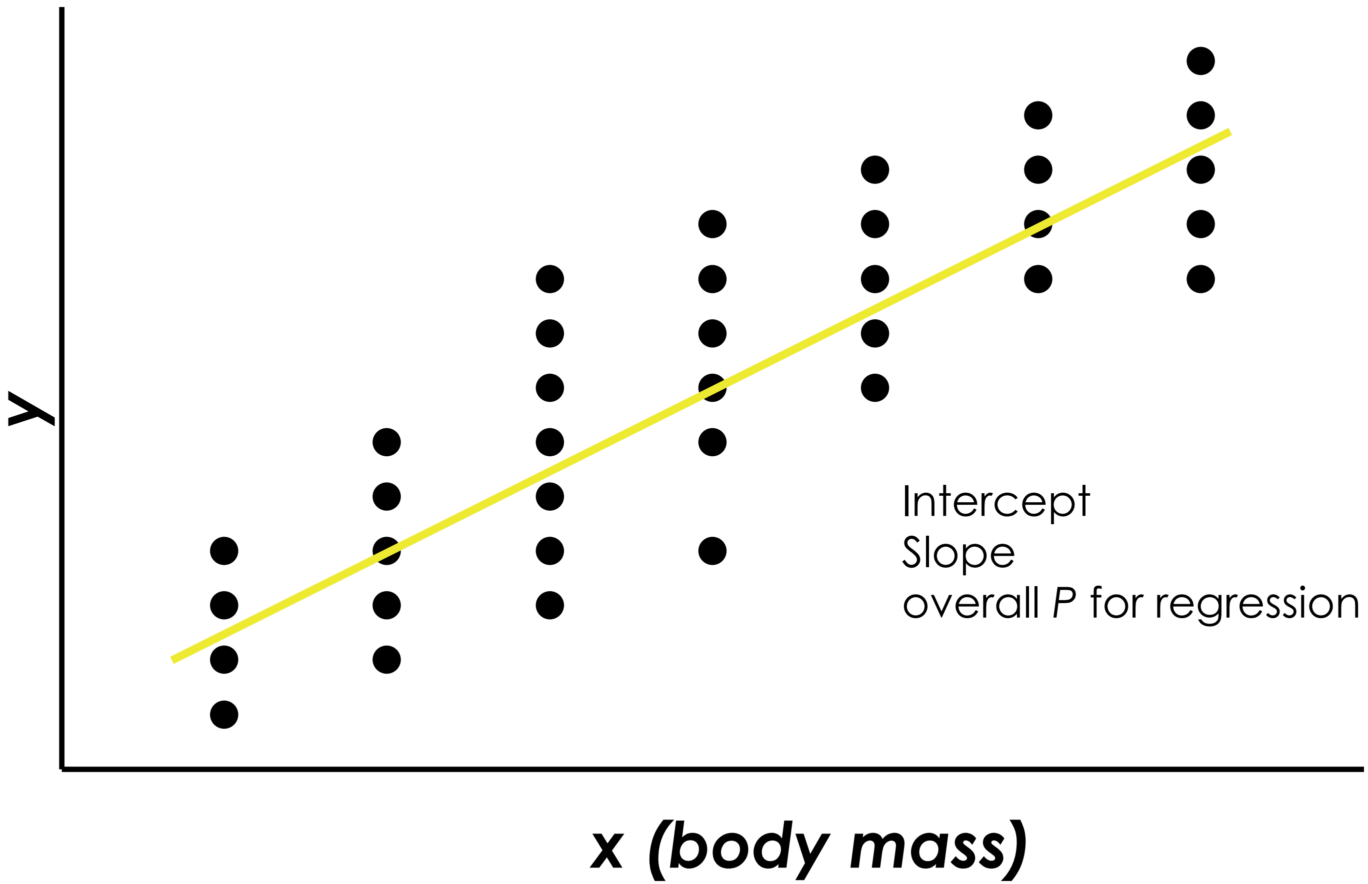
Interpreting allometries

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

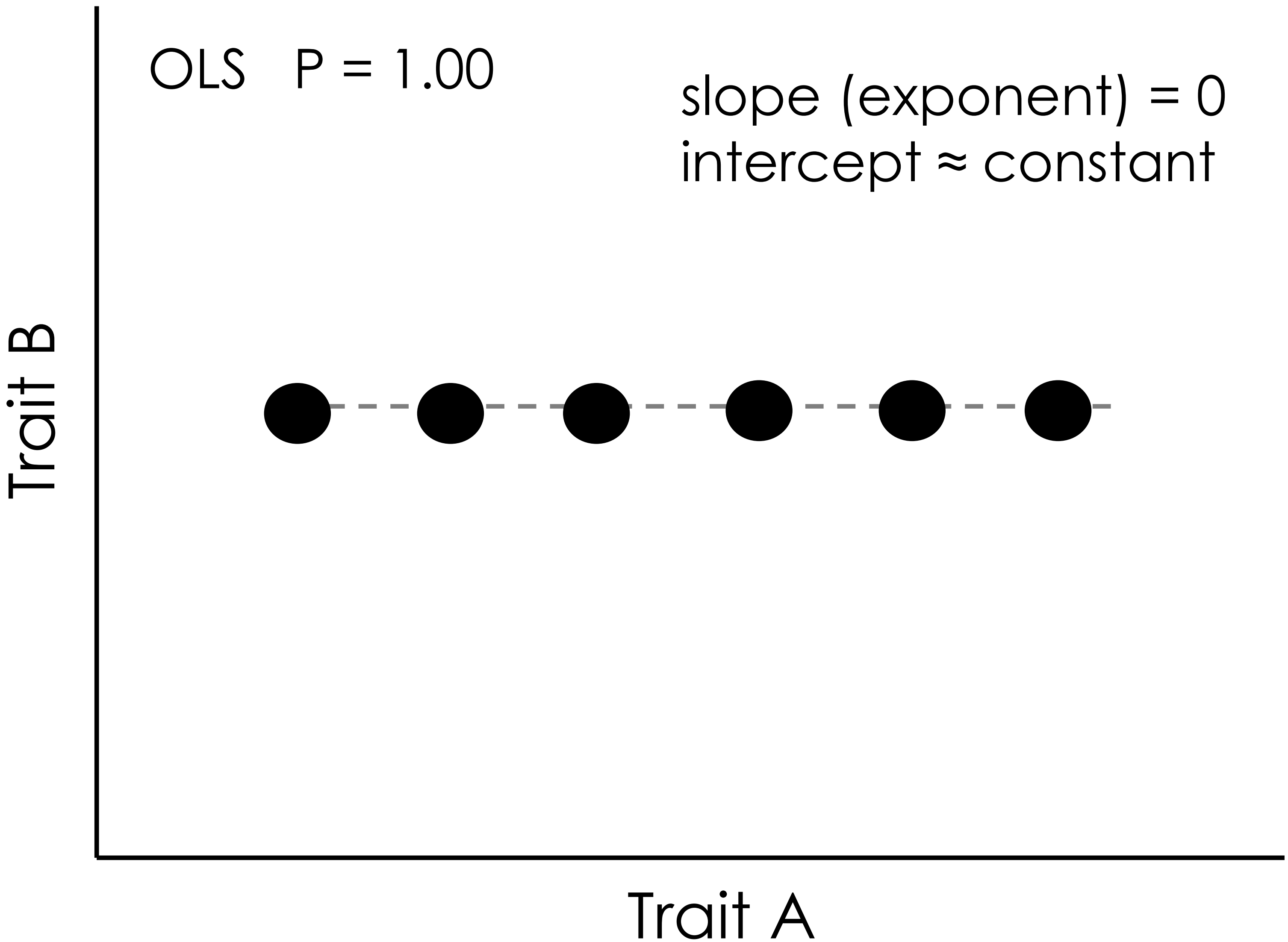


Testing for allometries

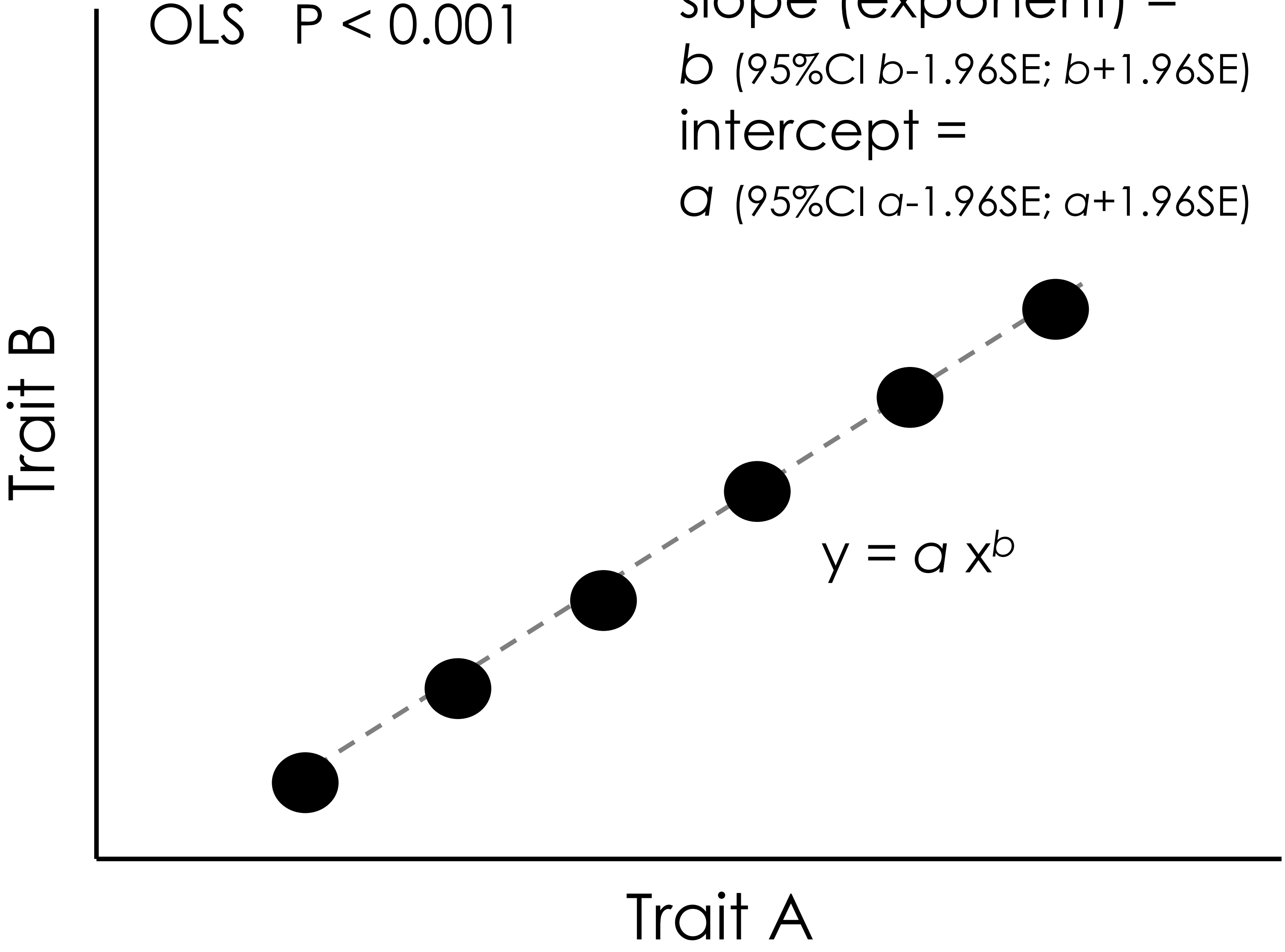
Morphological, physiological and life history variables scale with body mass.



Testing for allometries



Testing for allometries



slope (exponent) =

b (95%CI *b*-1.96SE; *b*+1.96SE)

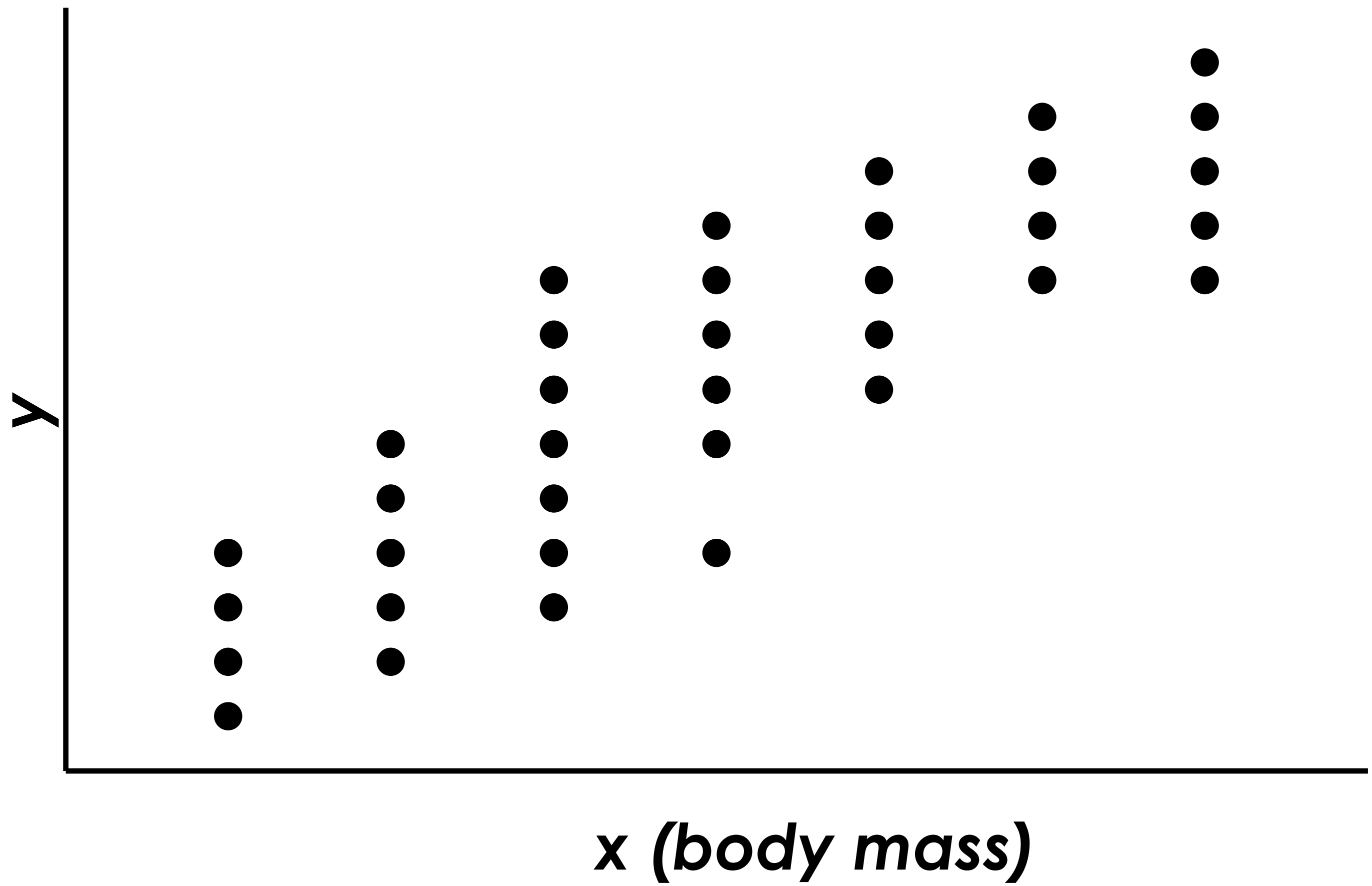
intercept =

a (95%CI *a*-1.96SE; *a*+1.96SE)

Phylogenetic statistics

Comparative statistics

Conventional regression analysis assumes independence of data points.
But this is violated by phylogenetic relationships.



Comparative statistics

Conventional regression analysis assumes independence of data points.
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.

Comparative statistics

Three (of many) important test statistics:

Intercept *a*: mainly significant if 95%CI does not include 0

Slope *b*: significant if 95%CI does not include 0; indicates non-linearity if 95%CI does not include 1

Pagel's lambdaλ: if 95%CI includes 0, then there is no phylogenetic structure in the dataset.
Does not decide whether the relationship is significant or not, but whether phylogenetic statistics need to be used or not.
Assumes Brownian motion; other measures of phylogenetic structure assuming other evolutionary scenarios exist.

Comparative statistics - errors

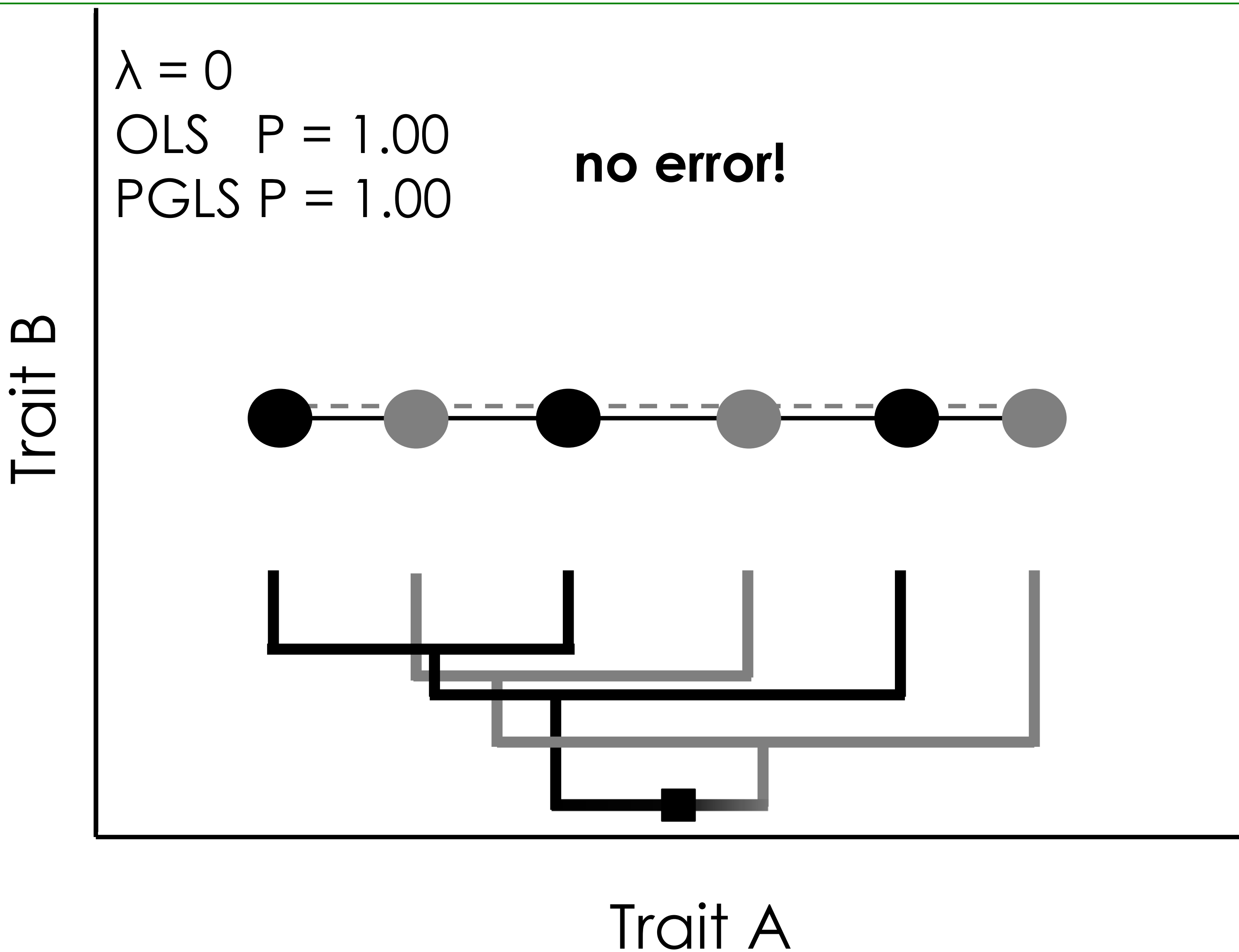
Type I error: you find a relationship where there is none (but it is caused by the phylogenetic structure of the data)

Type II error: you overlook a relationship where there is one (evident when you account for the phylogenetic structure of the data)

Just an error: you estimate a different parameter (e.g., allometric slope) depending on whether you account for phylogeny or not

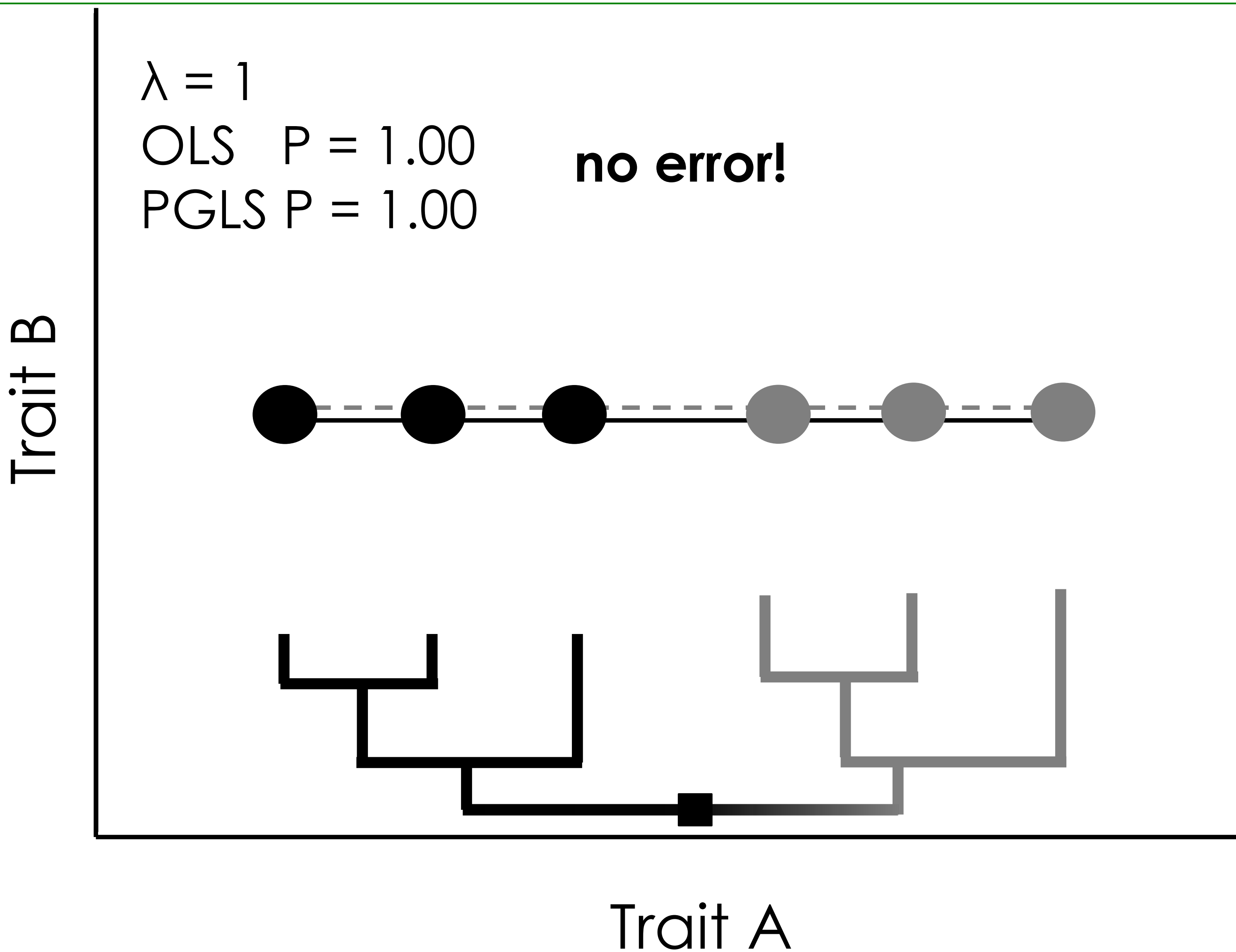
Pagel's lambda(λ) examples

Accounting for phylogeny



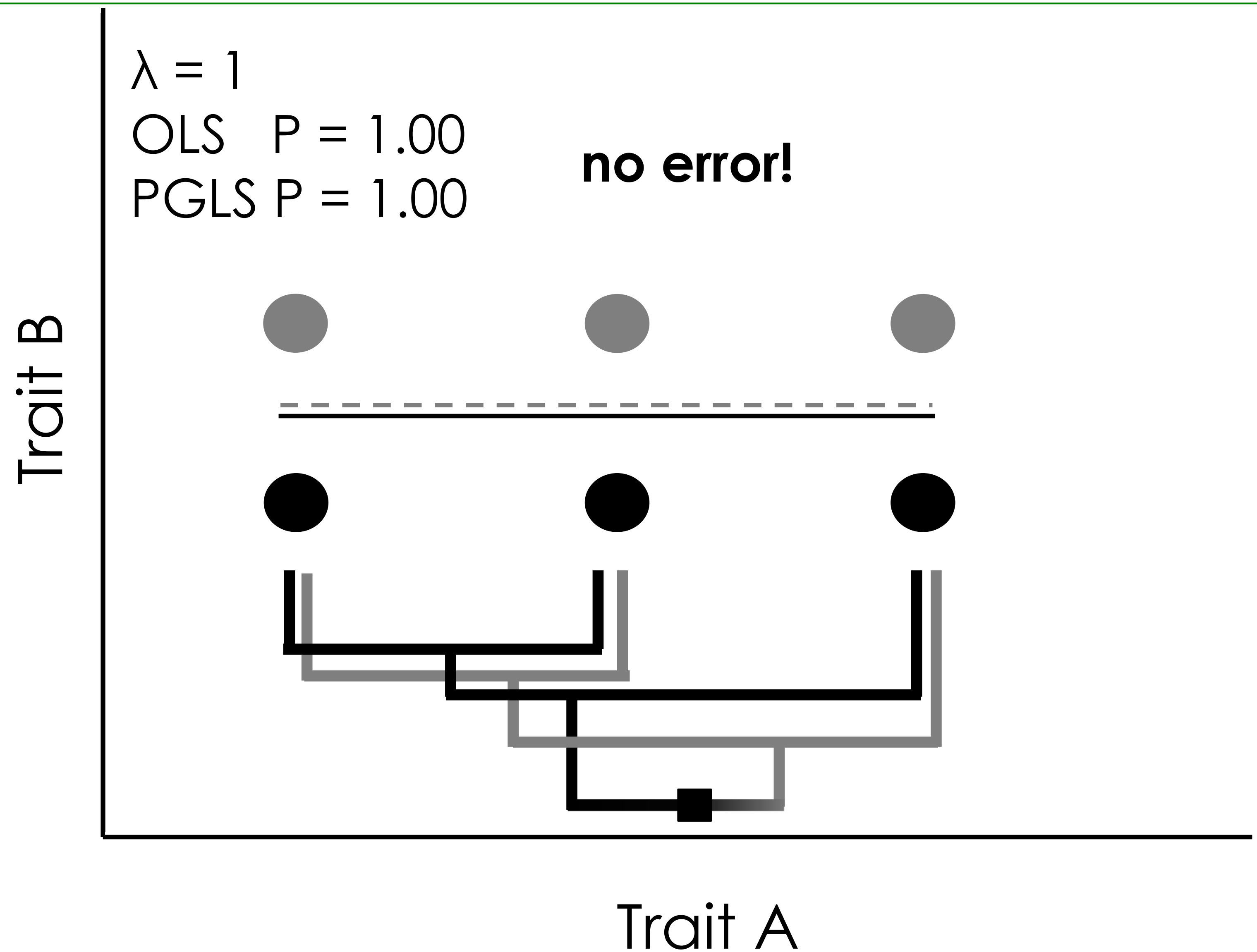
from Dittmann et al. (2015)

Accounting for phylogeny



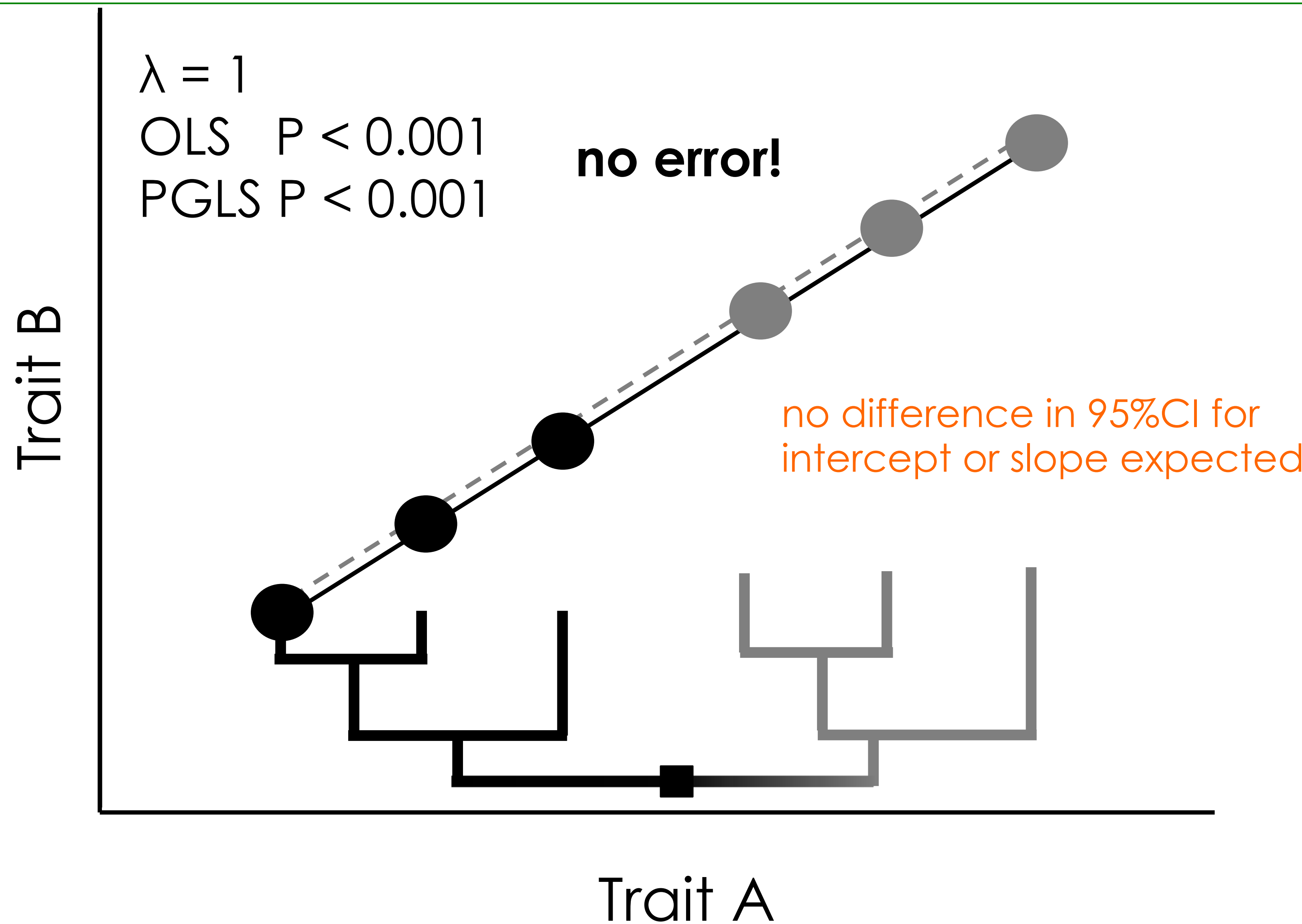
from Dittmann et al. (2015)

Accounting for phylogeny



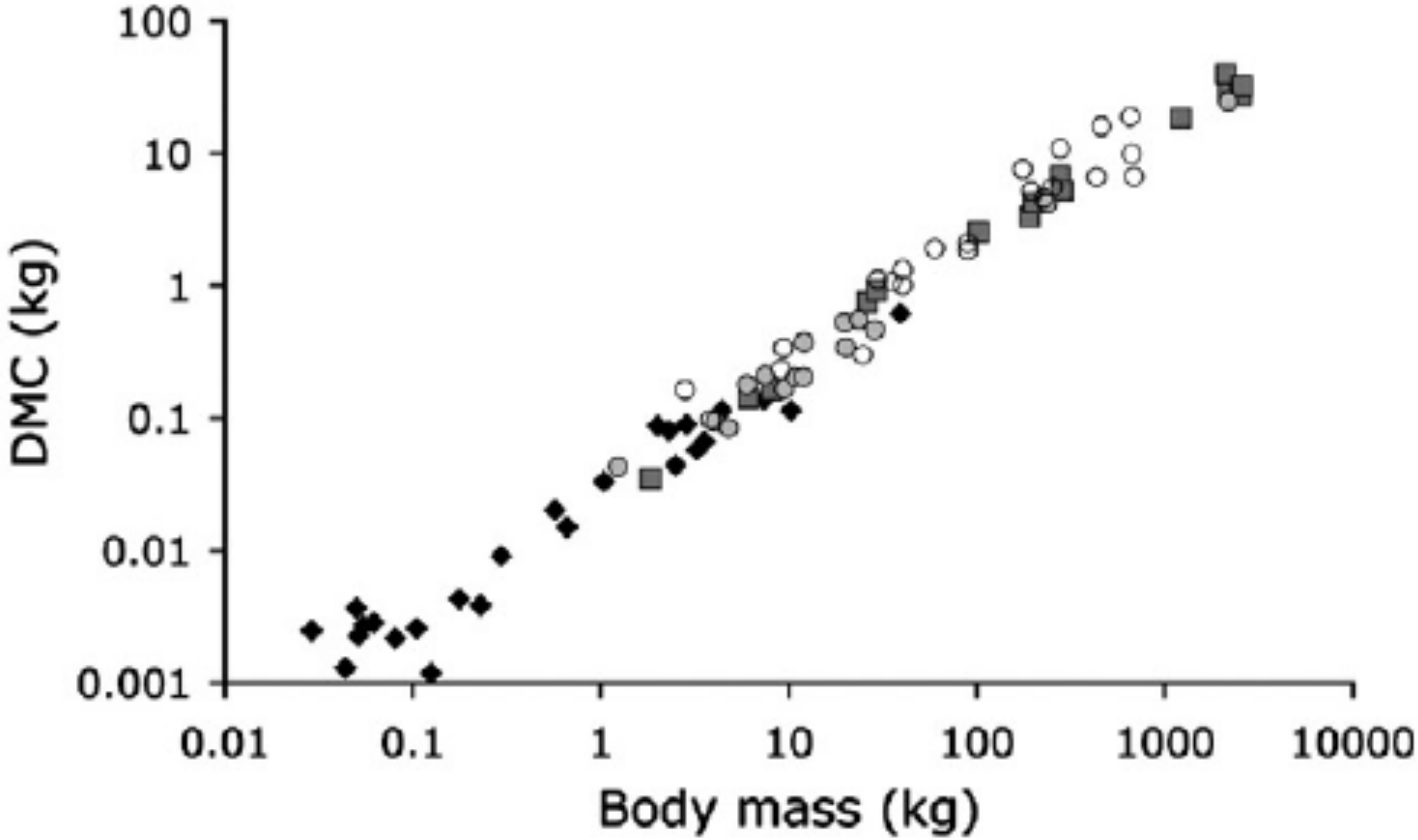
from Dittmann et al. (2015)

Accounting for phylogeny



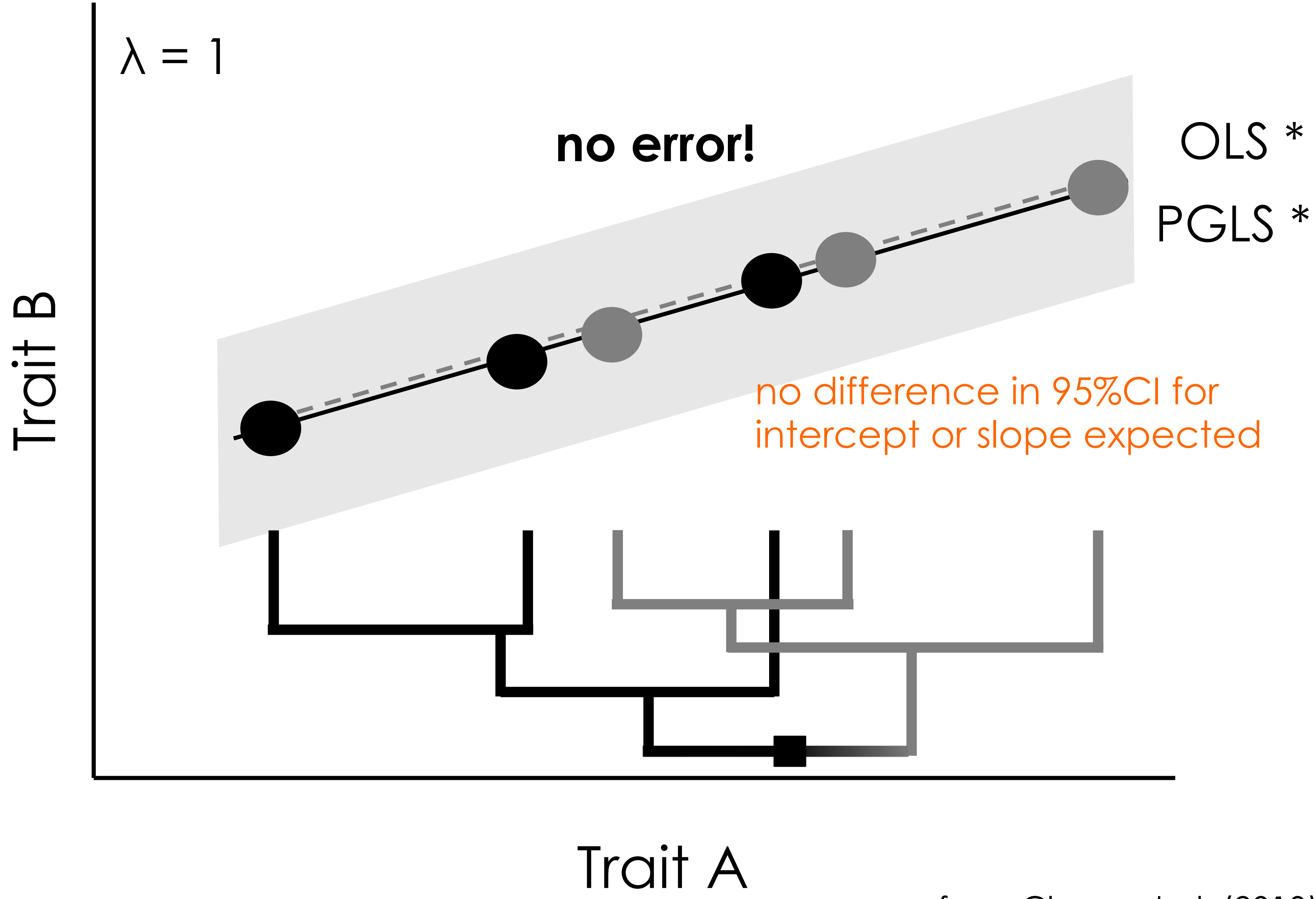
from Dittmann et al. (2015)

Example I: gut contents



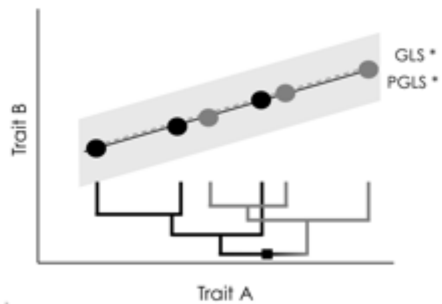
from Müller et al. (2013) CBP A

Accounting for phylogeny



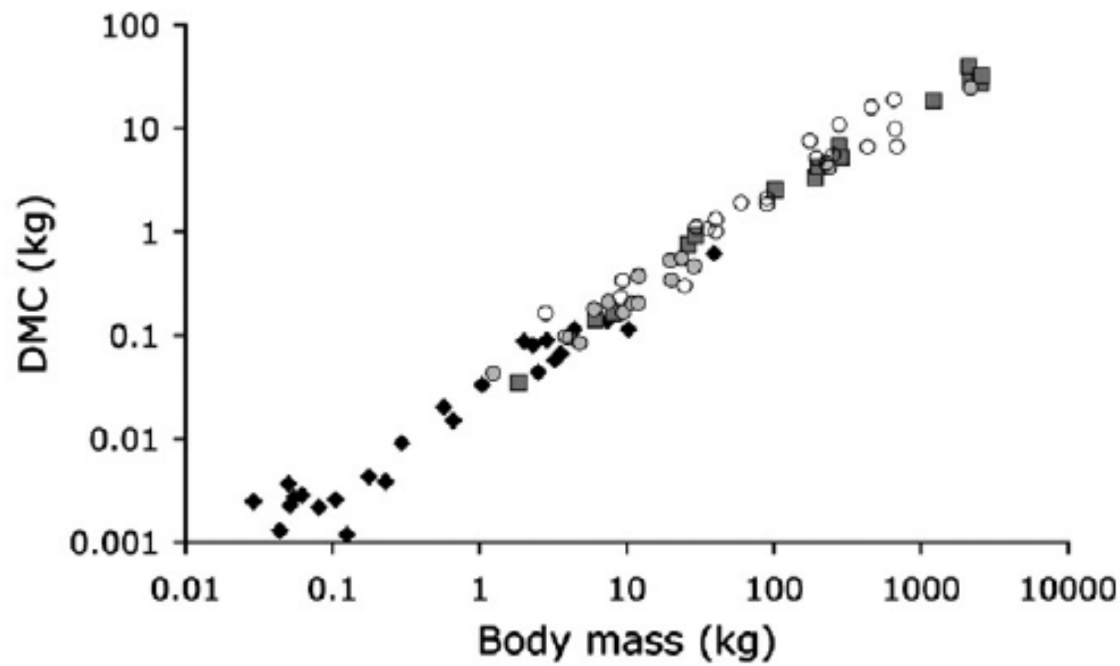
from Clauss et al. (2013)

Example I: gut contents



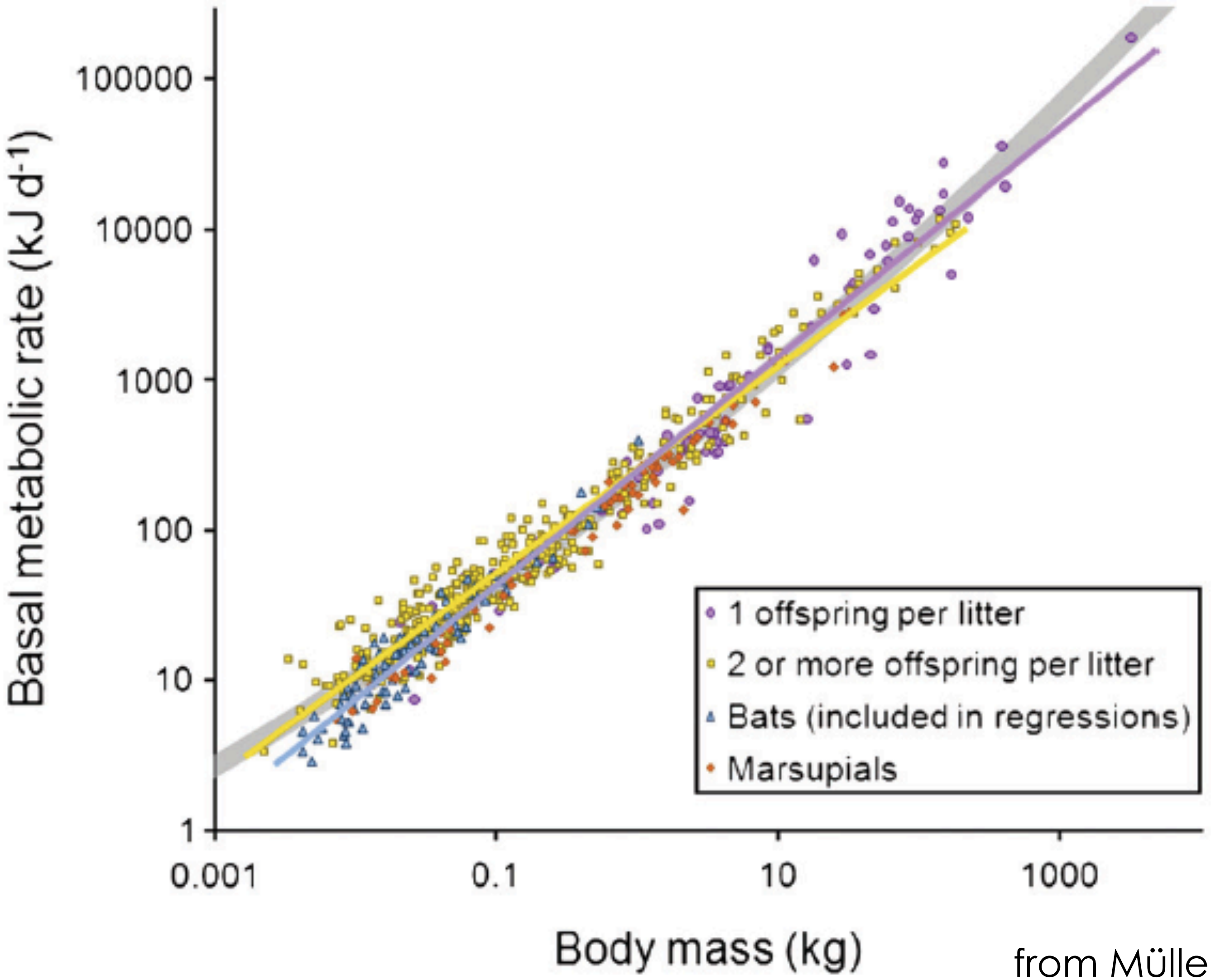
OLS: 0.03 (0.025-0.032) $BM^{0.93\ (0.90-0.96)}$

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



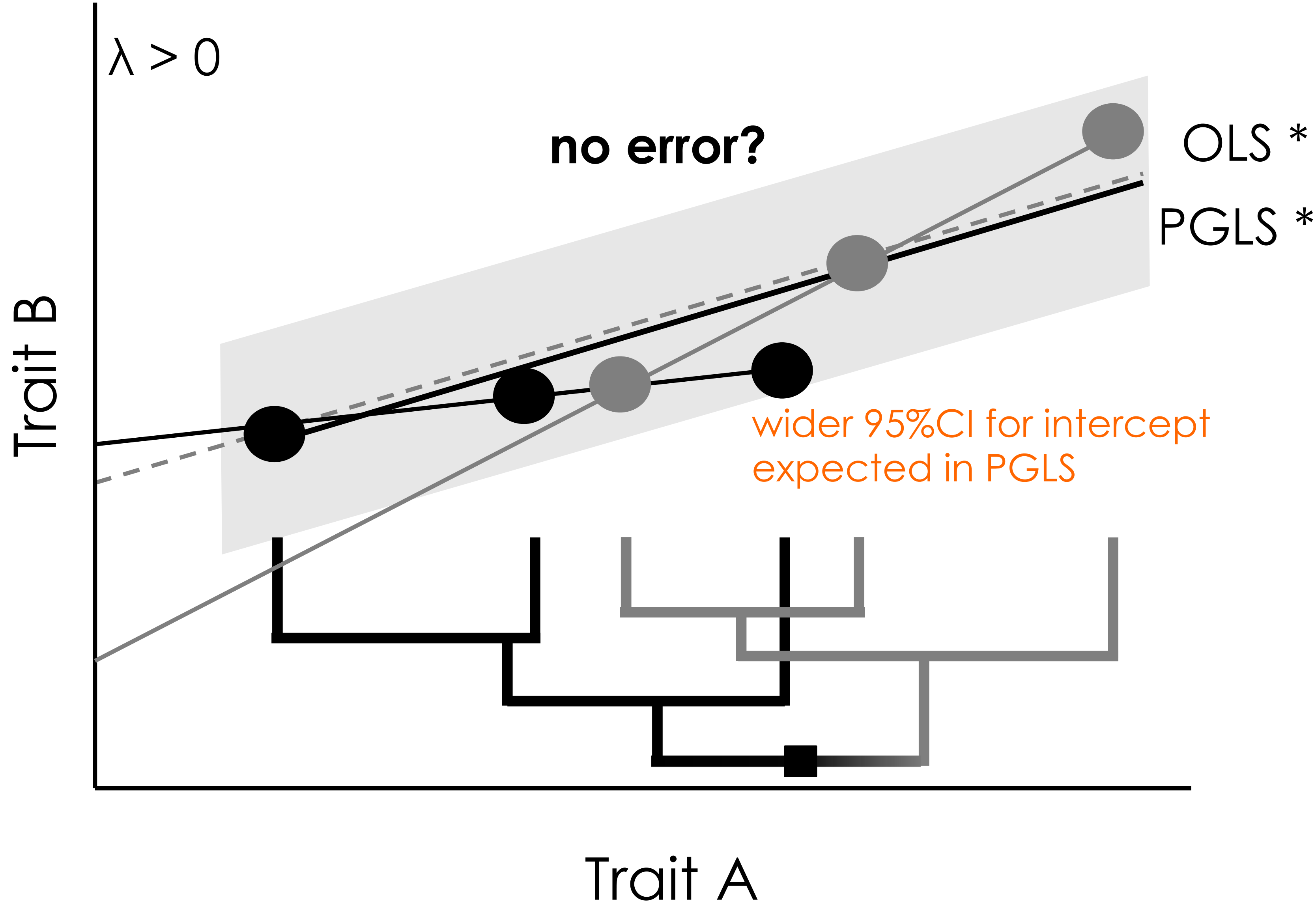
from Müller et al. (2013)

Example II: basal metabolic rate



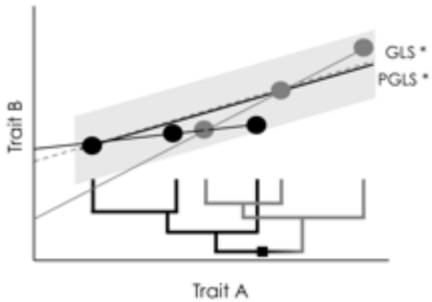
from Müller et al. (2012)

Accounting for phylogeny



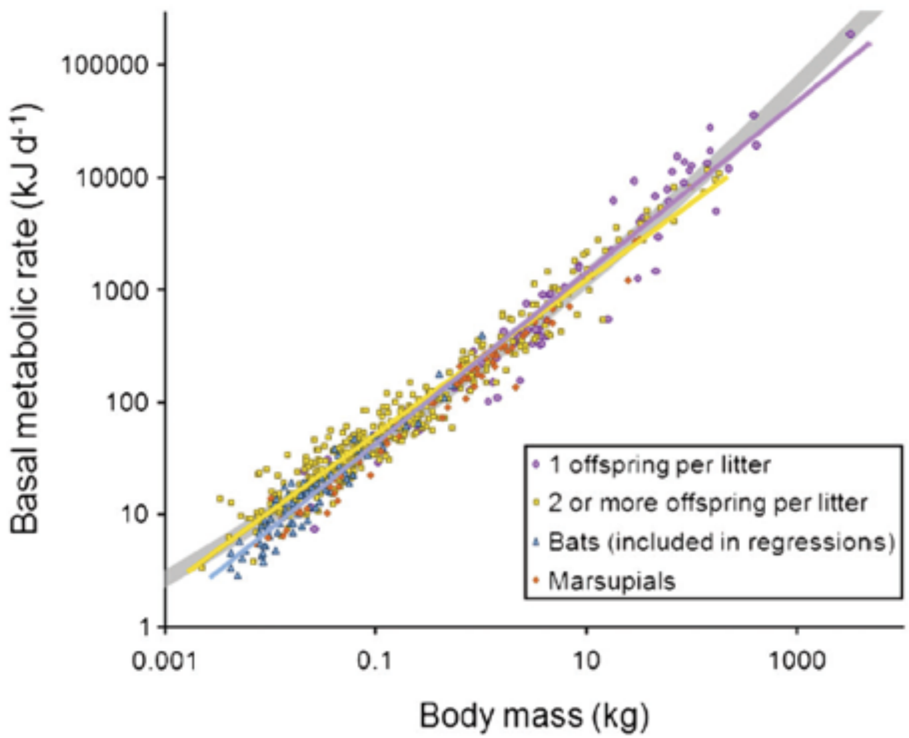
from Clauss et al. (2013)

Example II: basal metabolic rate



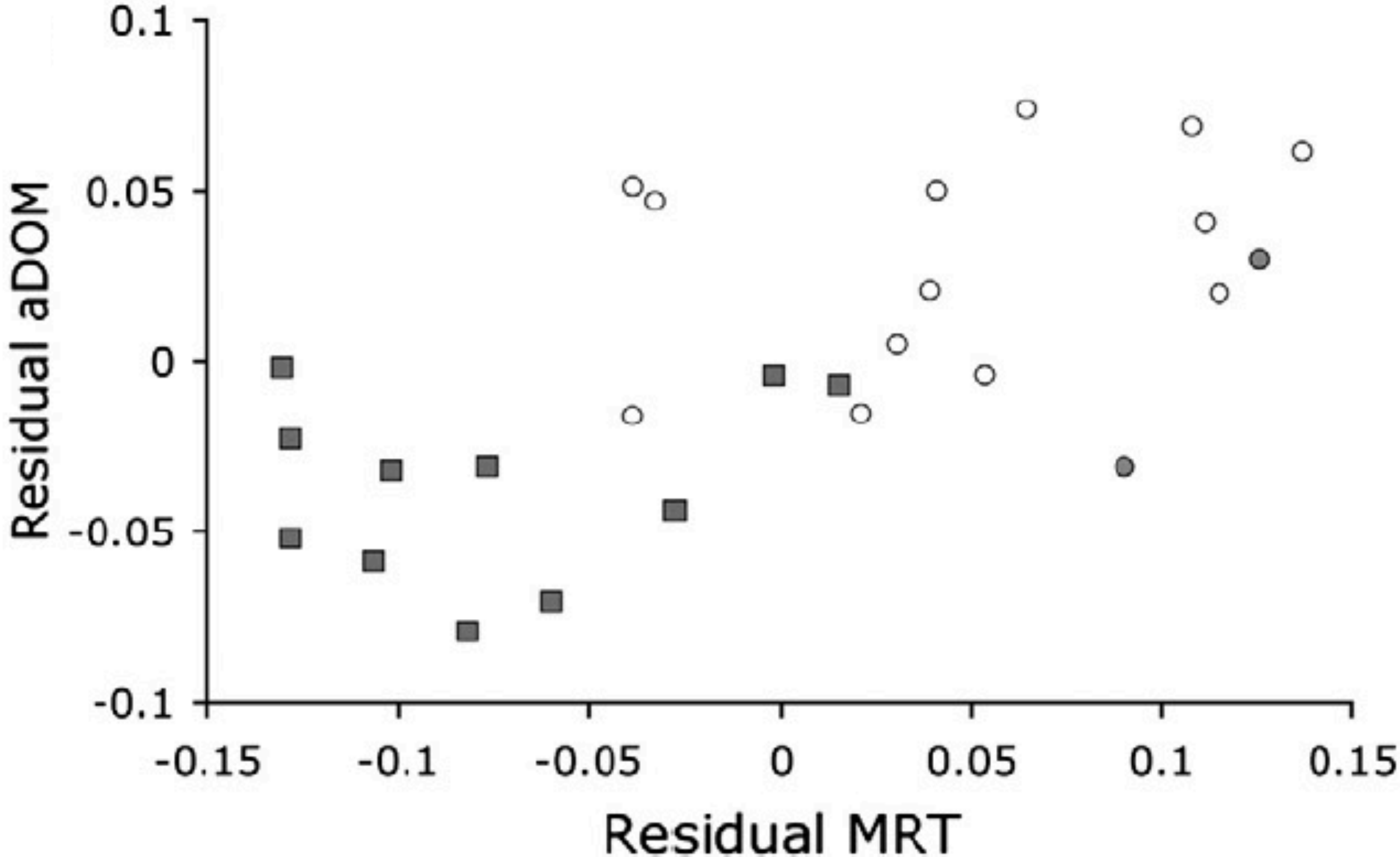
OLS: 2.38 (2.37-2.40) $BM^{0.72\ (0.71-0.73)}$

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



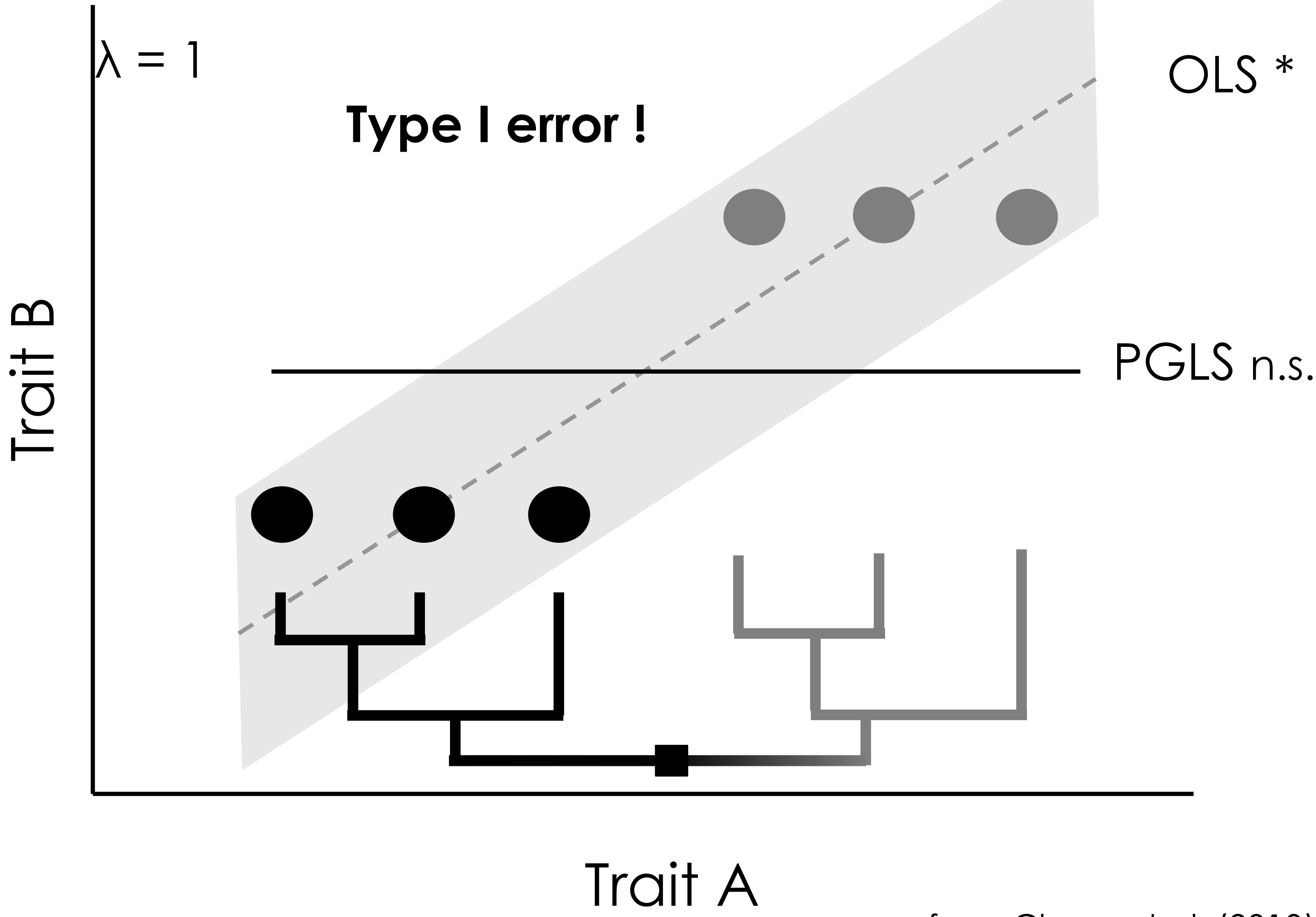
from Müller et al. (2012)

Example III: retention/digestibility



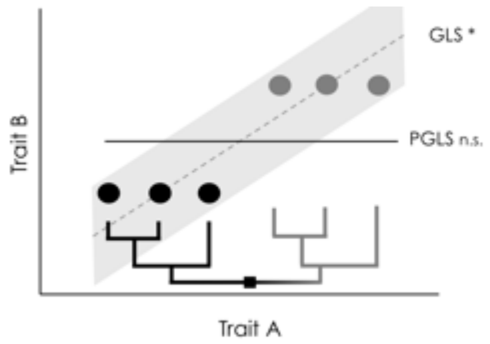
from Müller et al. (2013)

Accounting for phylogeny



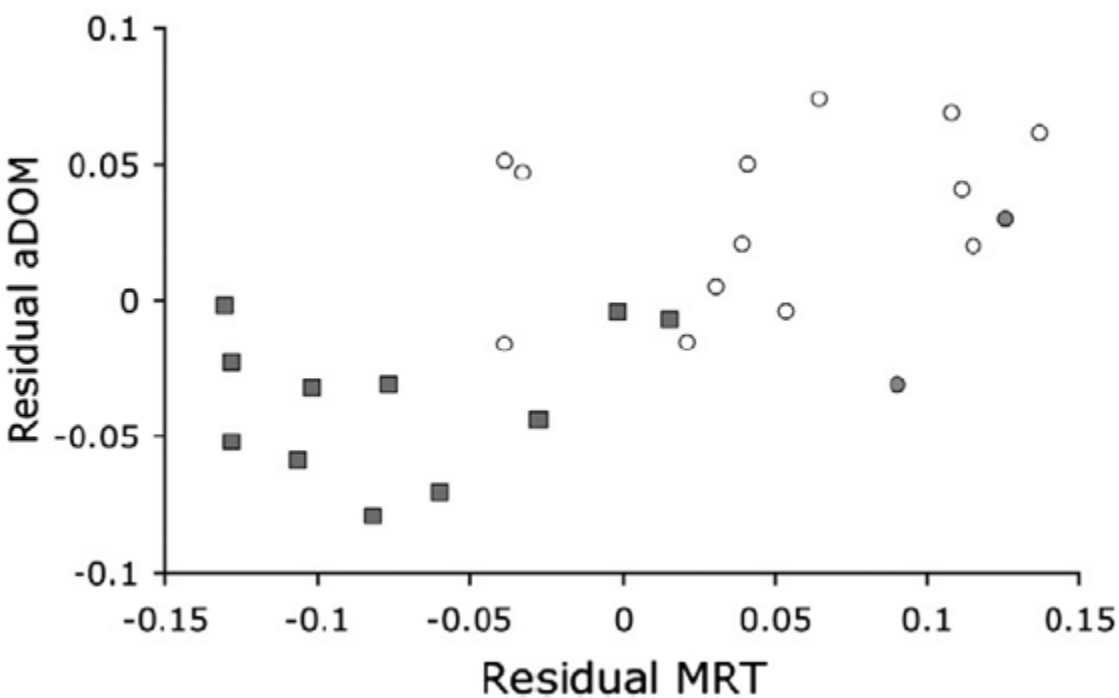
from Clauss et al. (2013)

Example IIIa: retention/digestibility



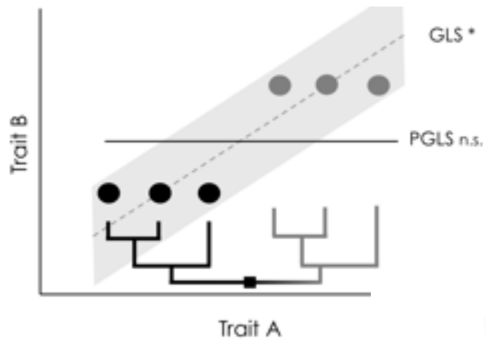
OLS: significant

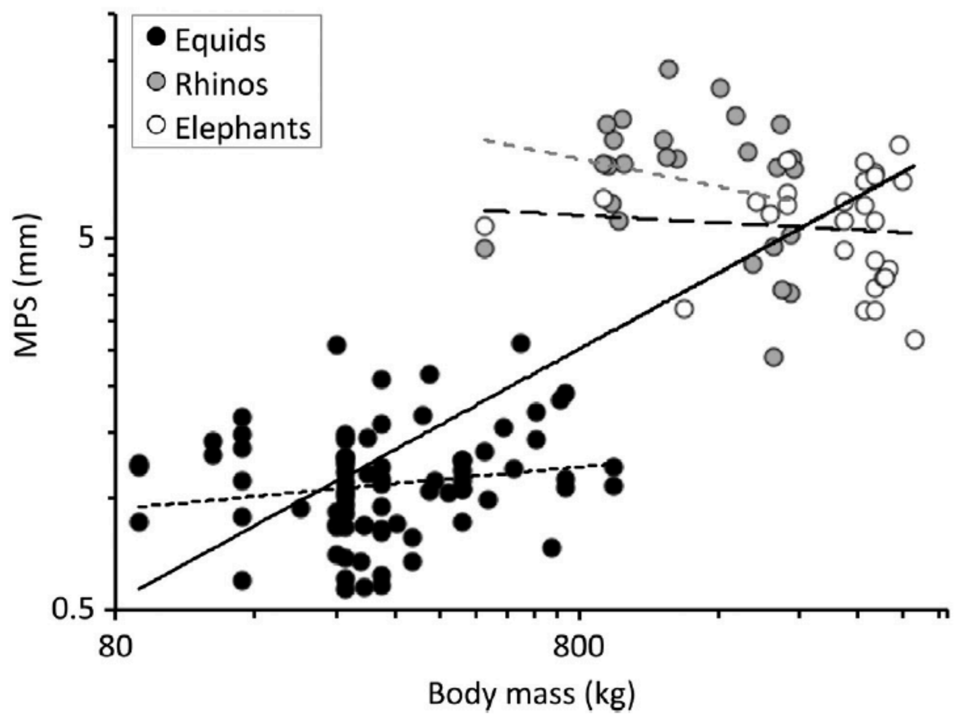
PGLS: not significant



from Müller et al. (2013)

Example IIIb: fecal particle size





from Clauss et al. (2015)

Ecology Letters, (2014) **17**: 1553–1559 doi: 10.1111/ele.12375

Geometric factors influencing the diet of vertebrate predators in marine and terrestrial environments

Chris Carbone,[1]* Daryl Codron,[2,3]
Conrad Scofield,[1] Marcus Clauss[3]
and Jon Bielby[1]

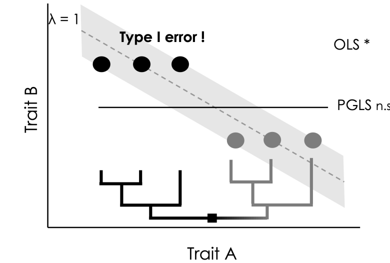
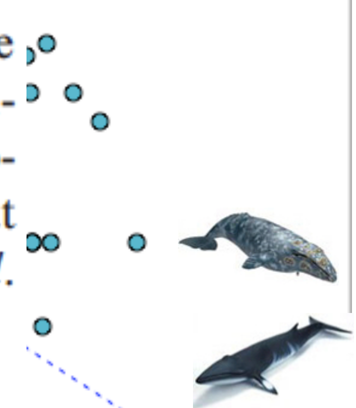
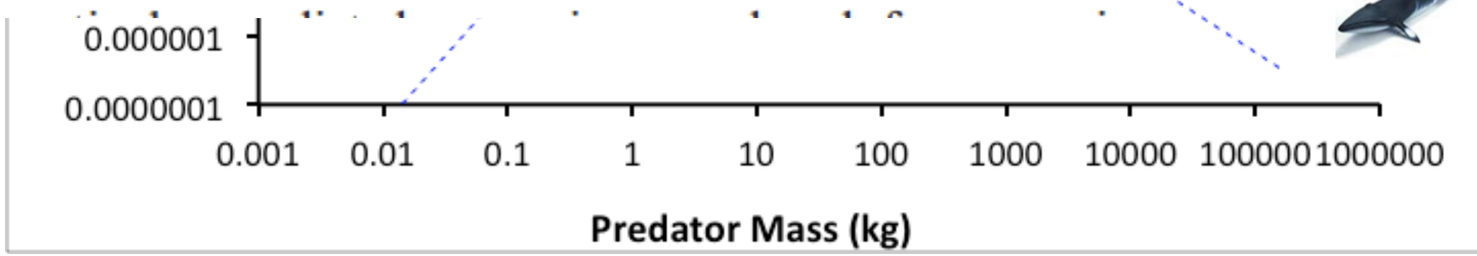


Table 2 Result of comparative analyses of how minimum prey size varies as a function of predator size

Taxonomic group/biome	*n*	Body mass (kg, mode, range) Predator	Prey	Stat	λ*	a (95% CI)	*t*	*P*	b (95% CI)	*t*	*P*
Terrestrial mammals	270	0.112 (0.002–371)	0.0001 (0.000001–189)	OLS	(0)	0.007 (0.004; 0.010)	−22.456	0.000	1.05 (0.90; 1.20)	13.709	0.000
				PGLS§	0.929‡	0.0003 (0.00001; 0.013)	−4.276	0.000	0.82 (0.60; 1.03)	7.381	0.000
				PGLS¶	1.0†	0.0001 (0.00001; 0.001)	−7.923	0.000	0.36 (0.15; 0.57)	3.293	0.001
Marine Mammals	126	23000 (4–154160)	0.100 (0.00003–12)	OLS	(0)	0.546 (0.215; 1.386)	−1.274	0.205	−0.30 (−0.45; −0.15)	−3.975	0.000
				PGLS¶	0.978†	0.013 (0.001; 0.232)	−2.940	0.004	0.16 (−0.13; 0.44)	1.054	0.294

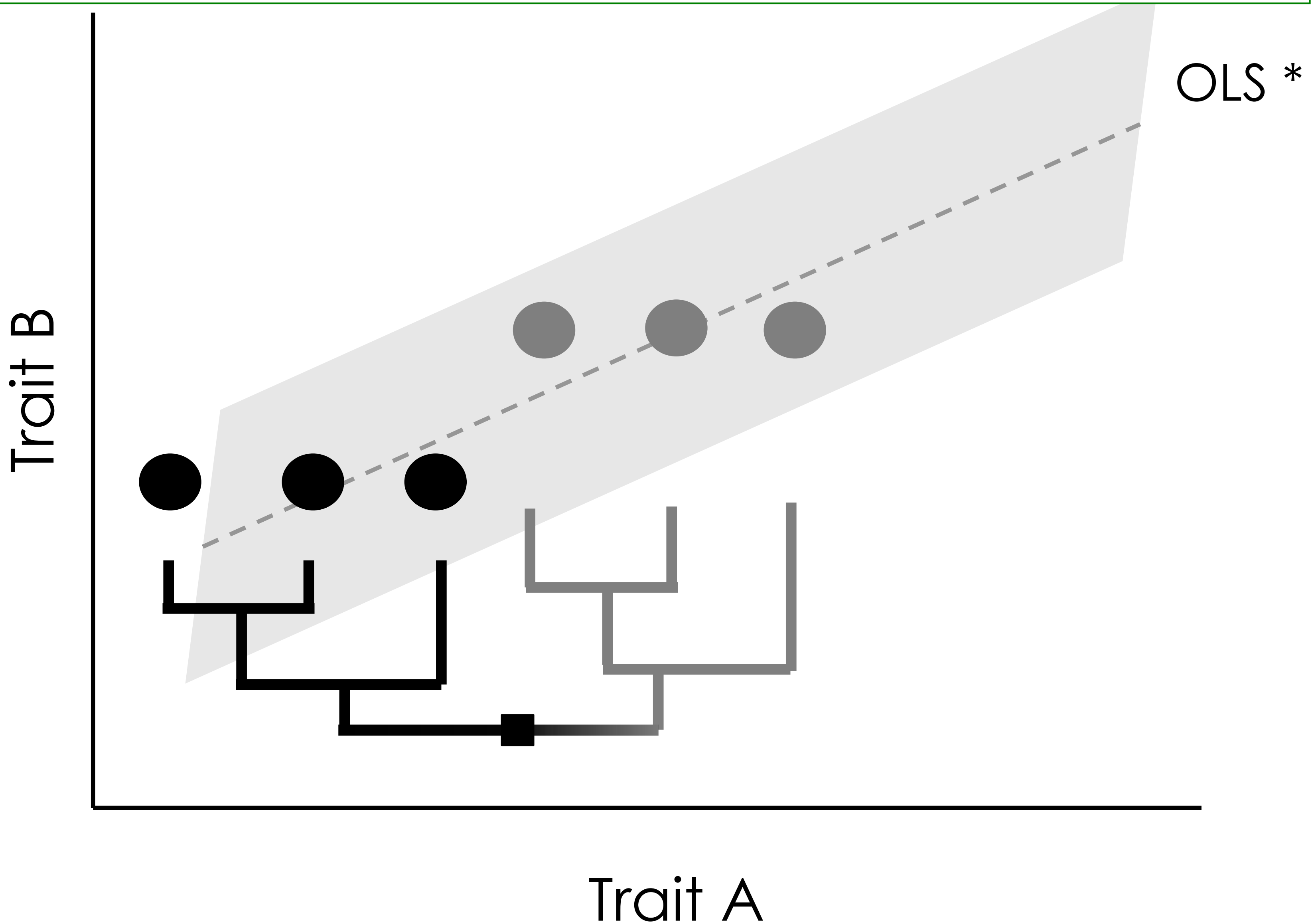
... the difference between the OLS and PGLS results within the marine mammals indicates that there are not multiple taxonomic subgroups in which the relationship can be observed, but that small-prey (filter) feeding evolved only once (Slater *et al.* 2010).





from Carbone et al. (2014)

Accounting for phylogeny



from Clauss et al. (2013)

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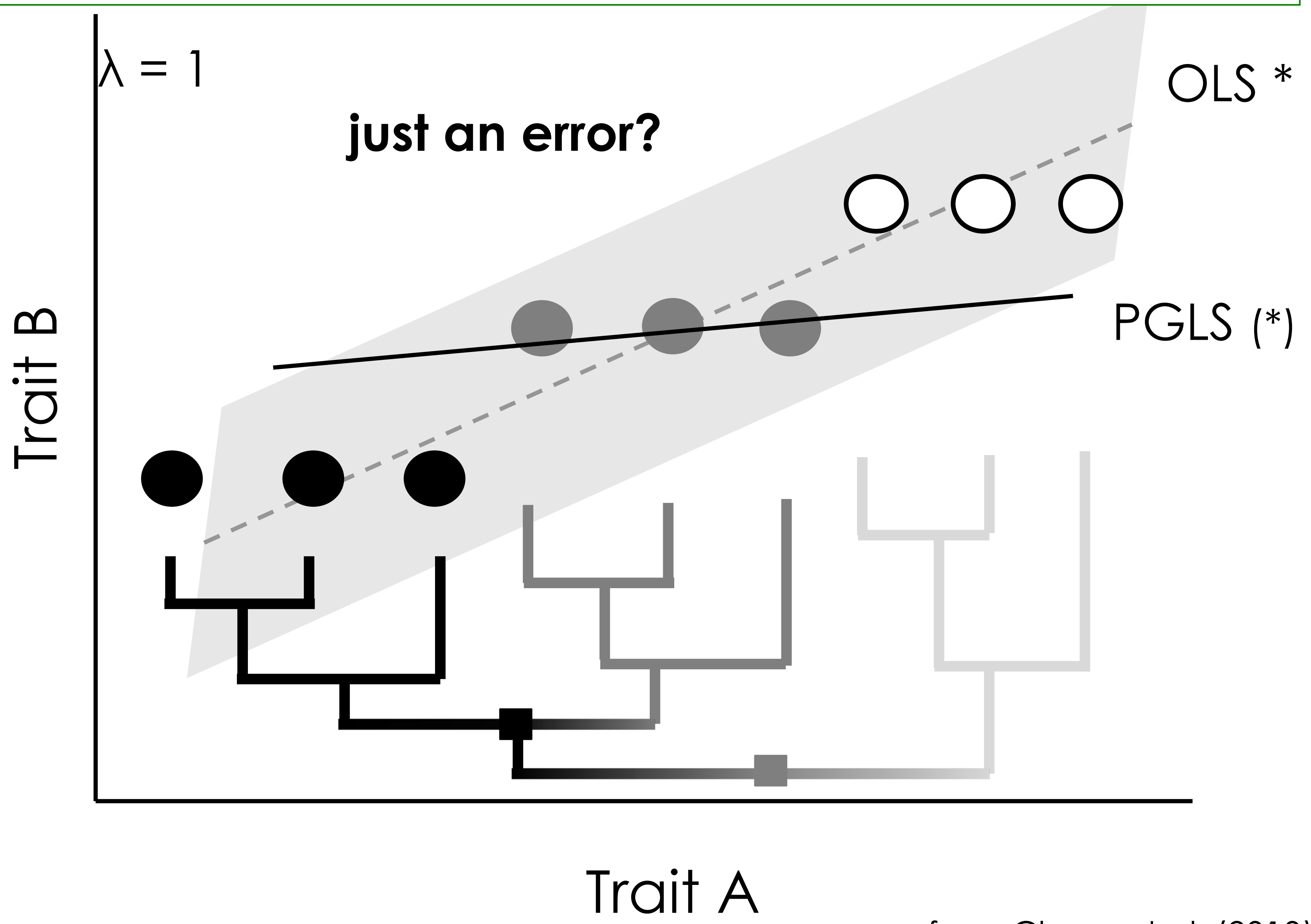
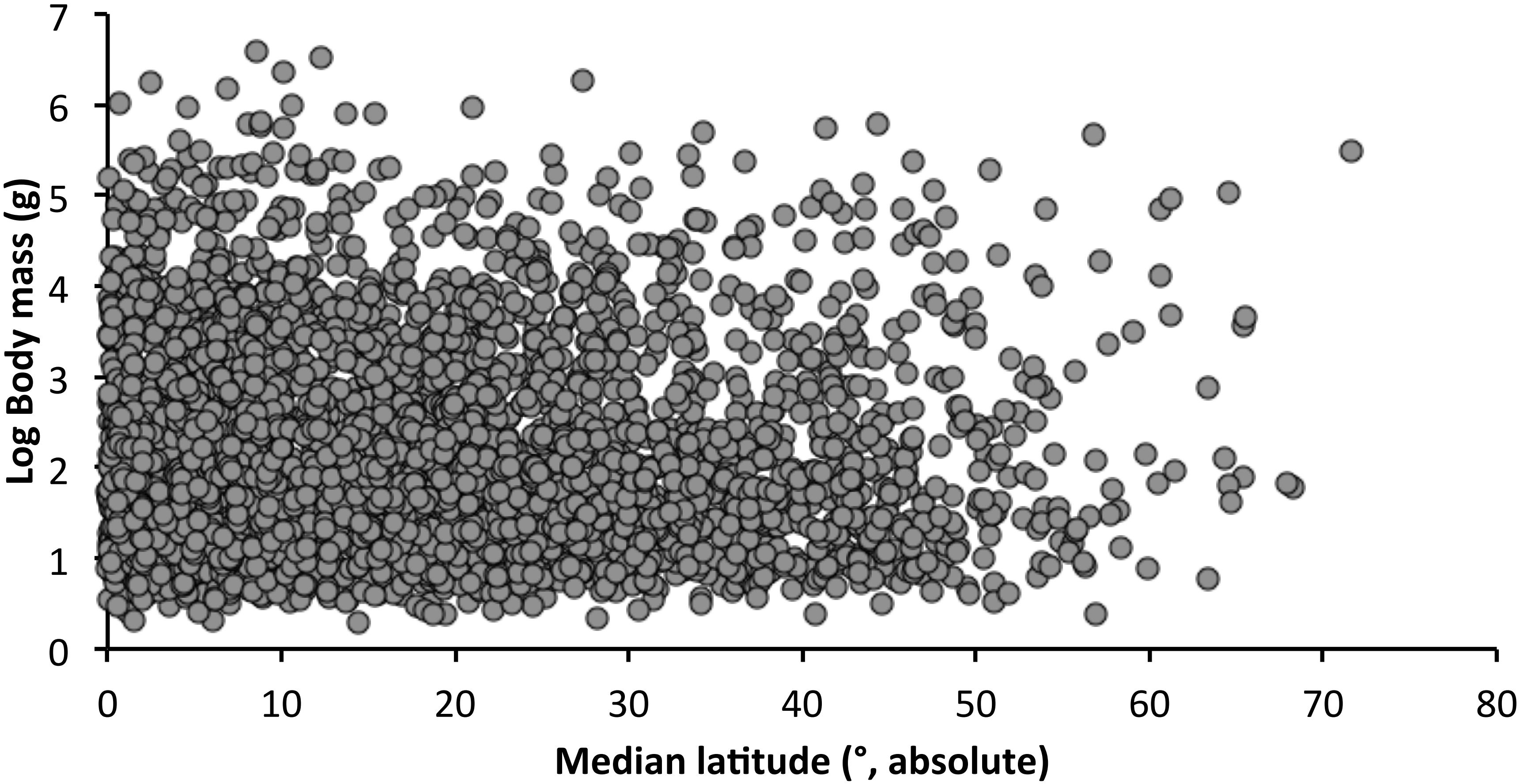


from Clauss et al. (2013)

Example IV: Bergmann's rule



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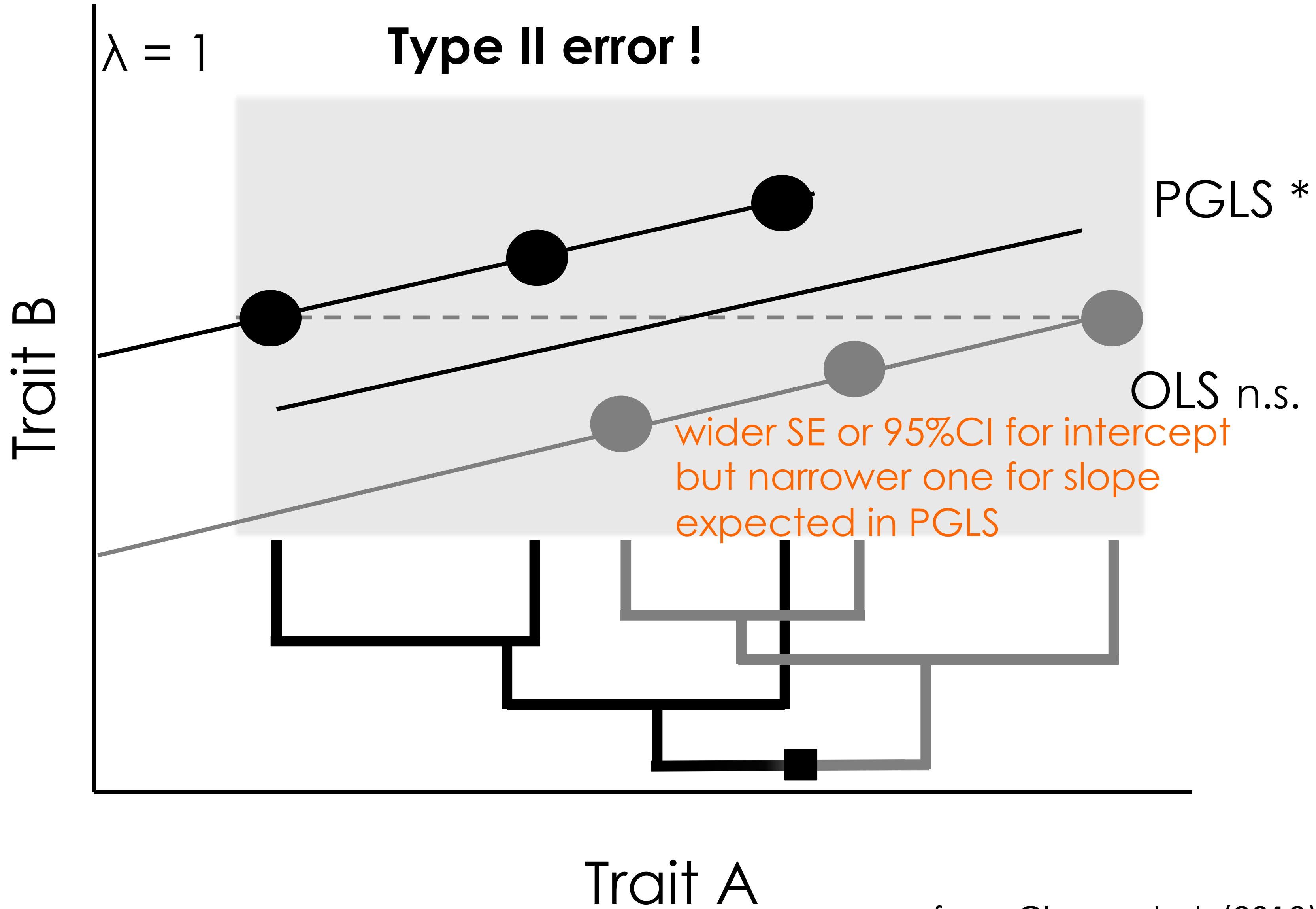

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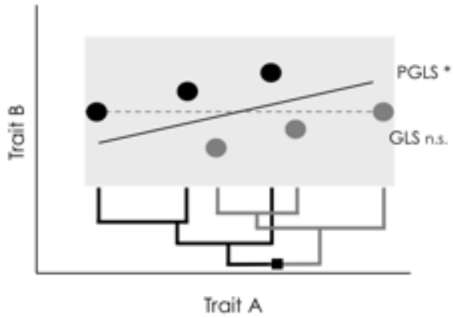
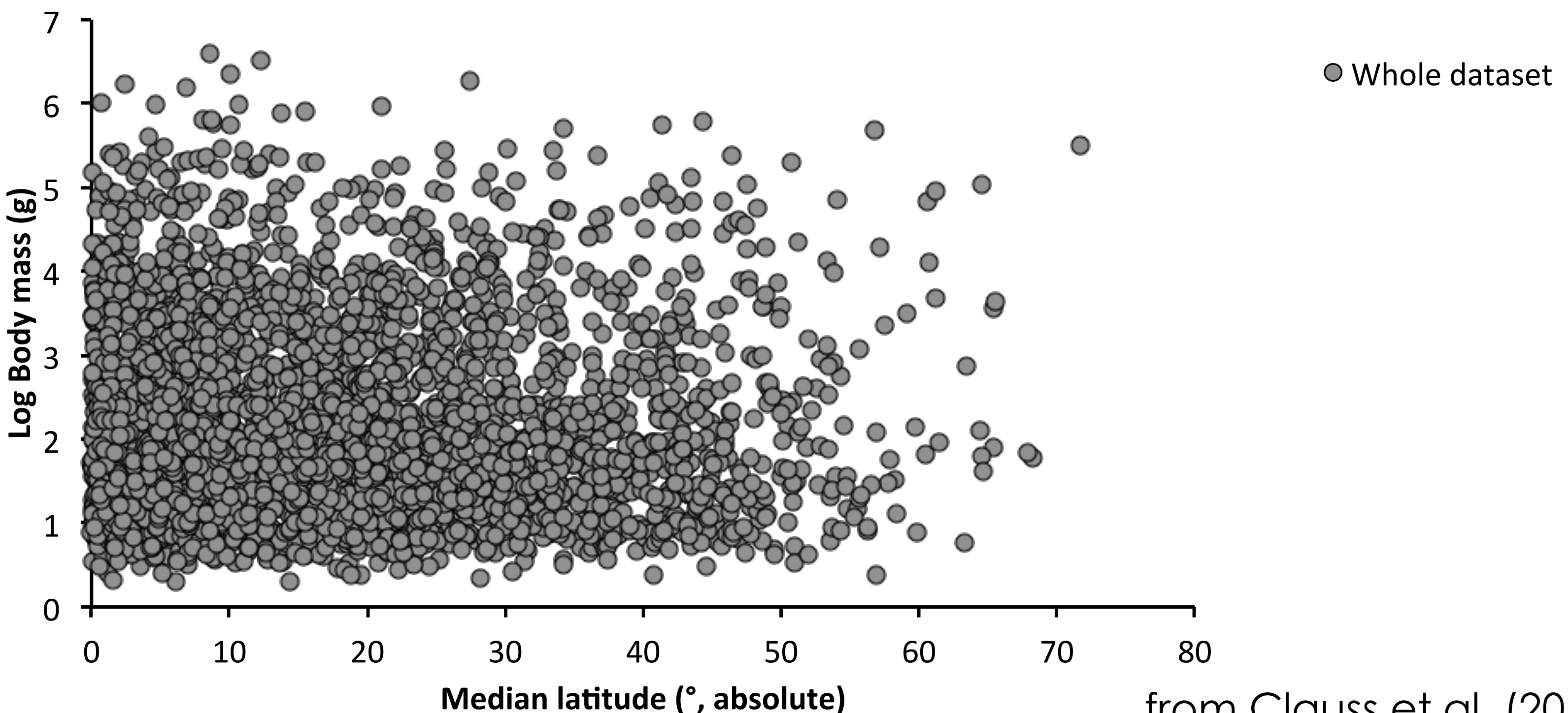


OLS: 2.19 (±0.03) - 0.0012 (±0.0013) Lat.

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



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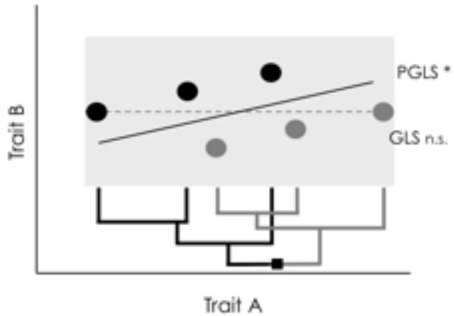

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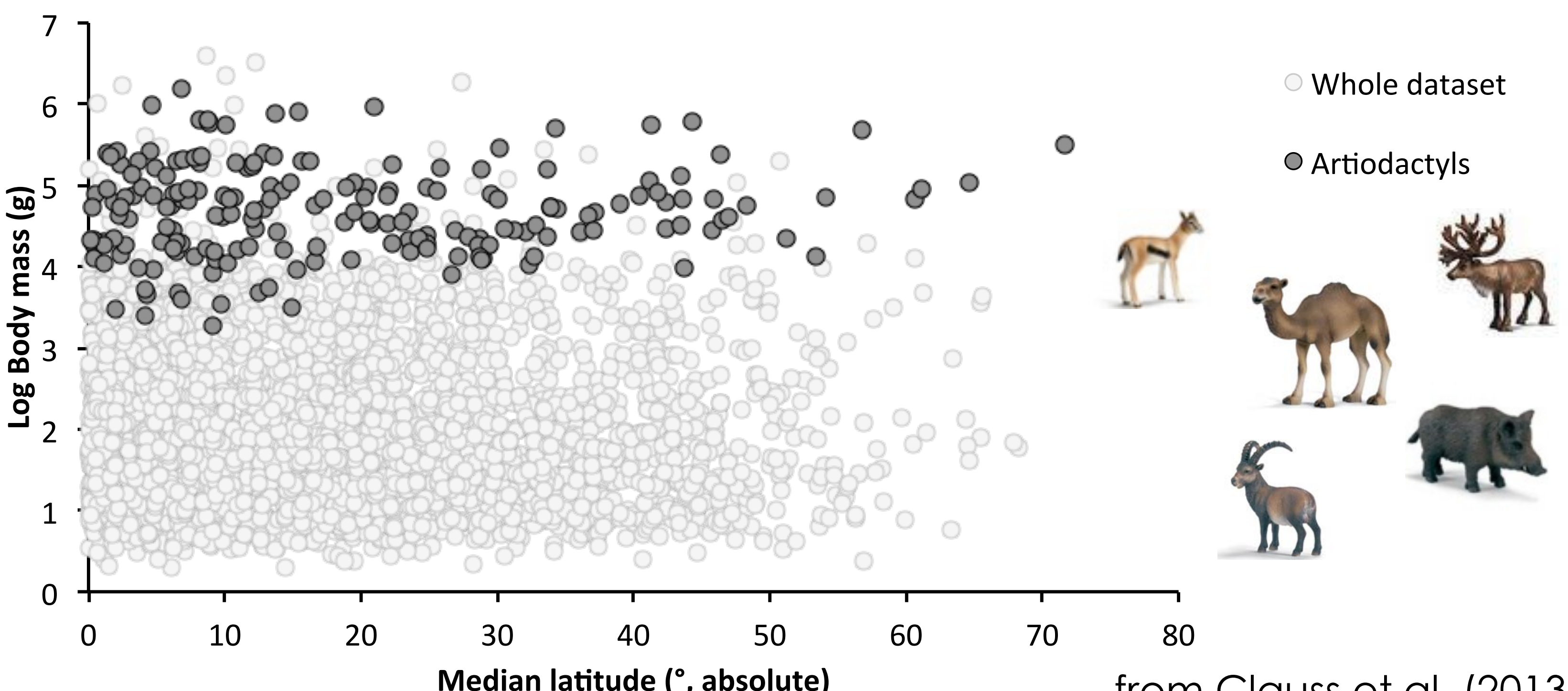

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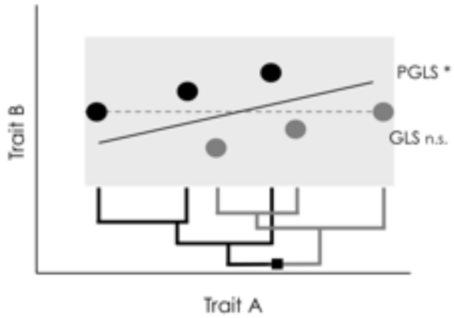

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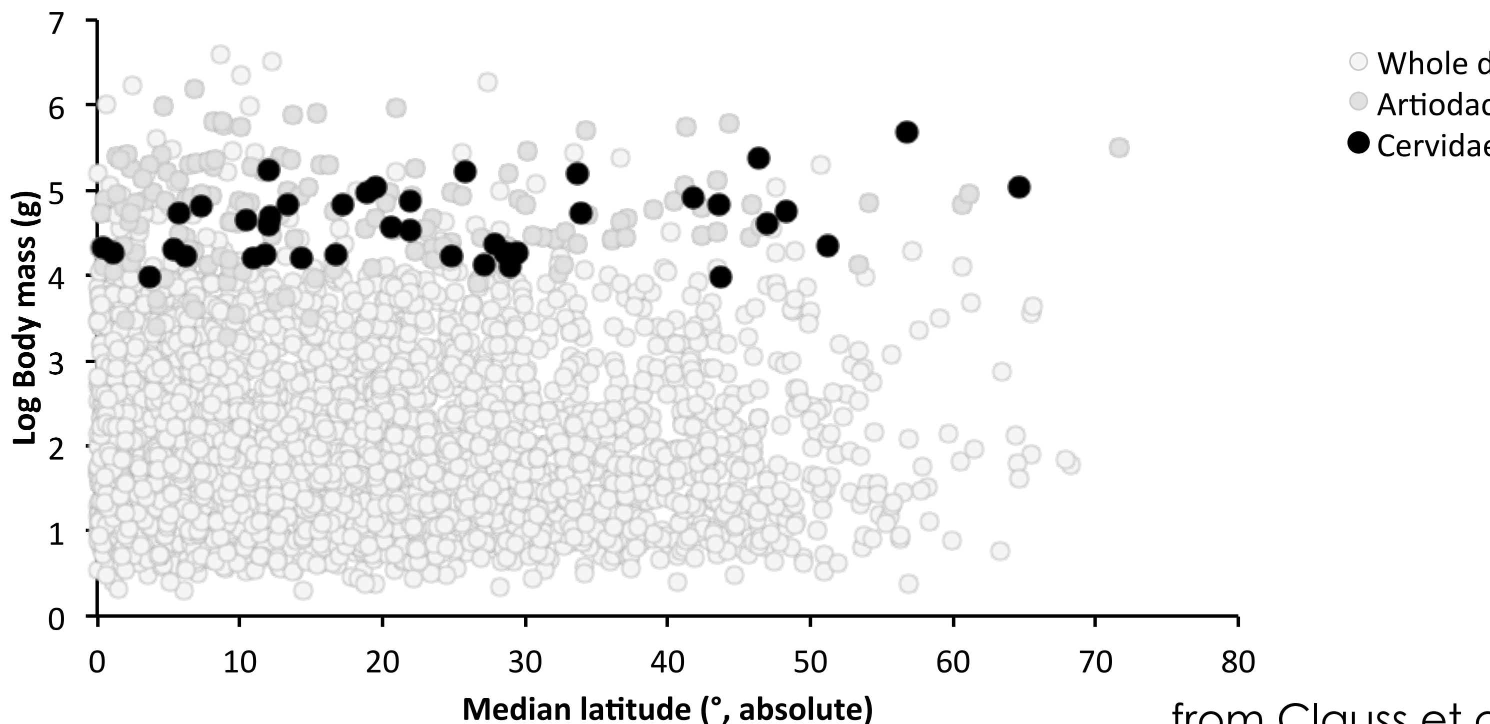

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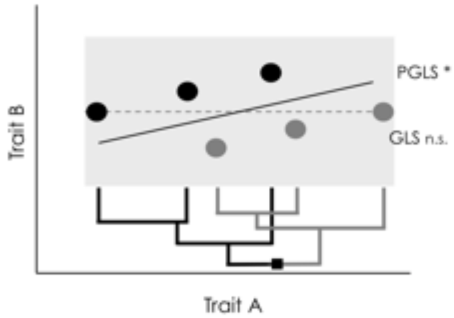

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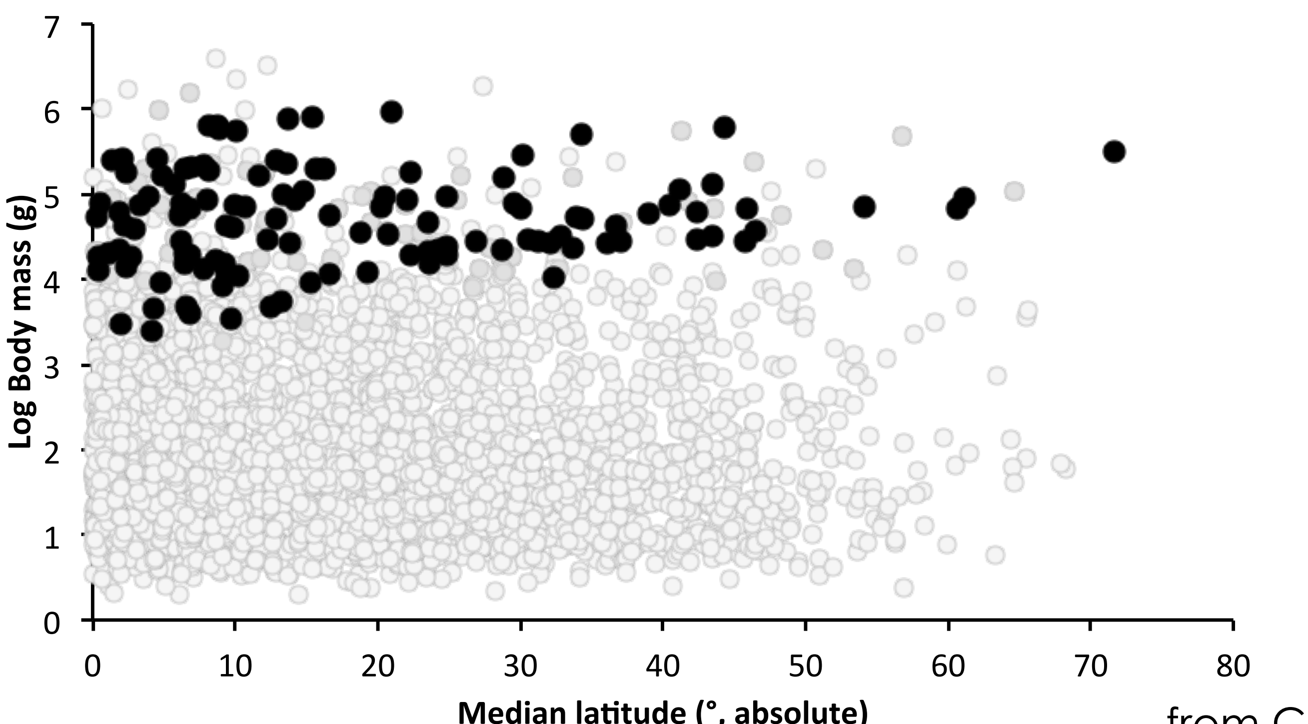

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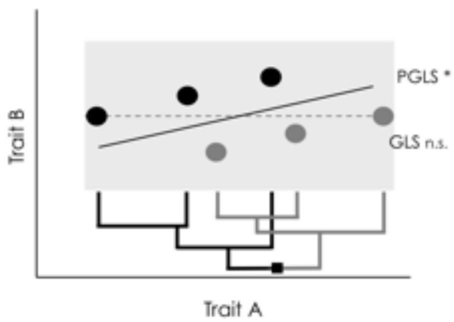

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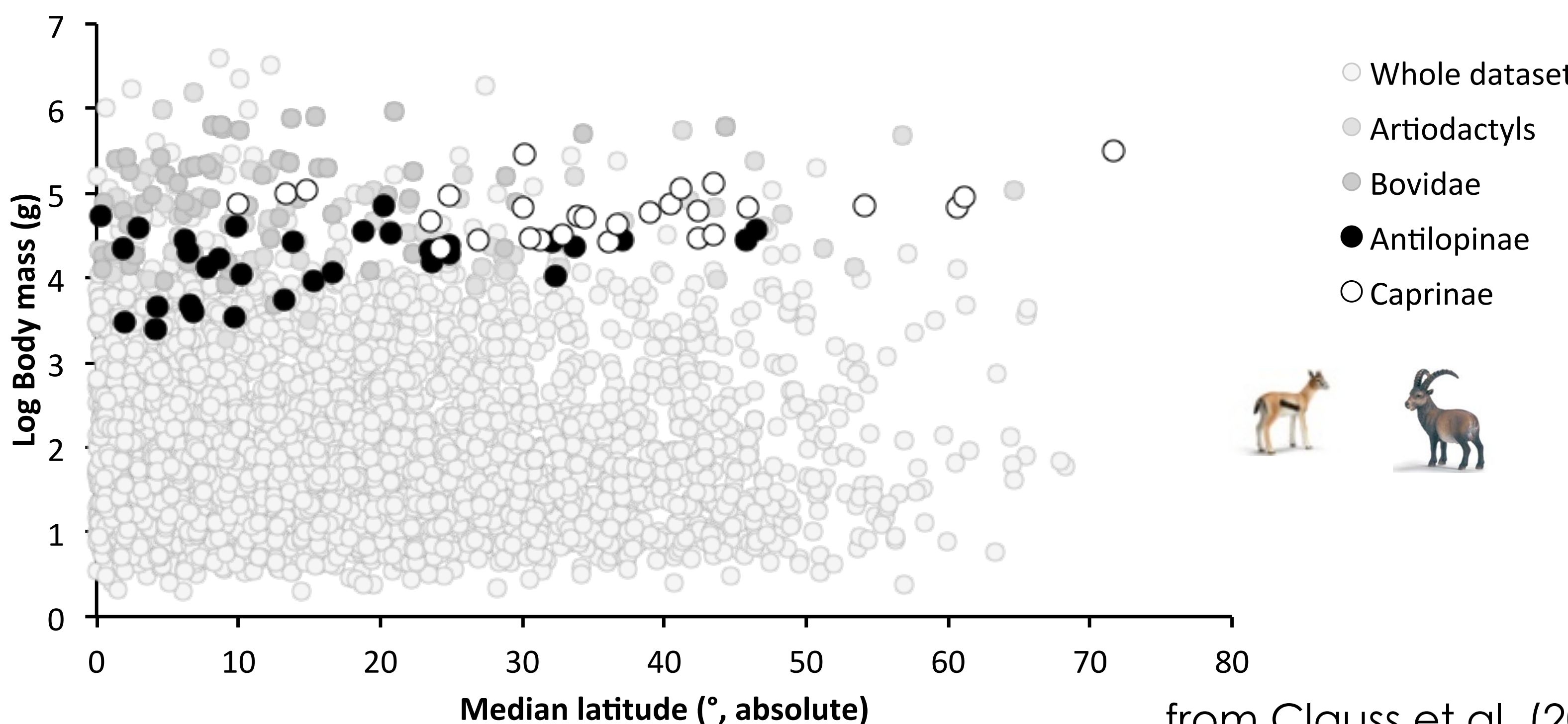
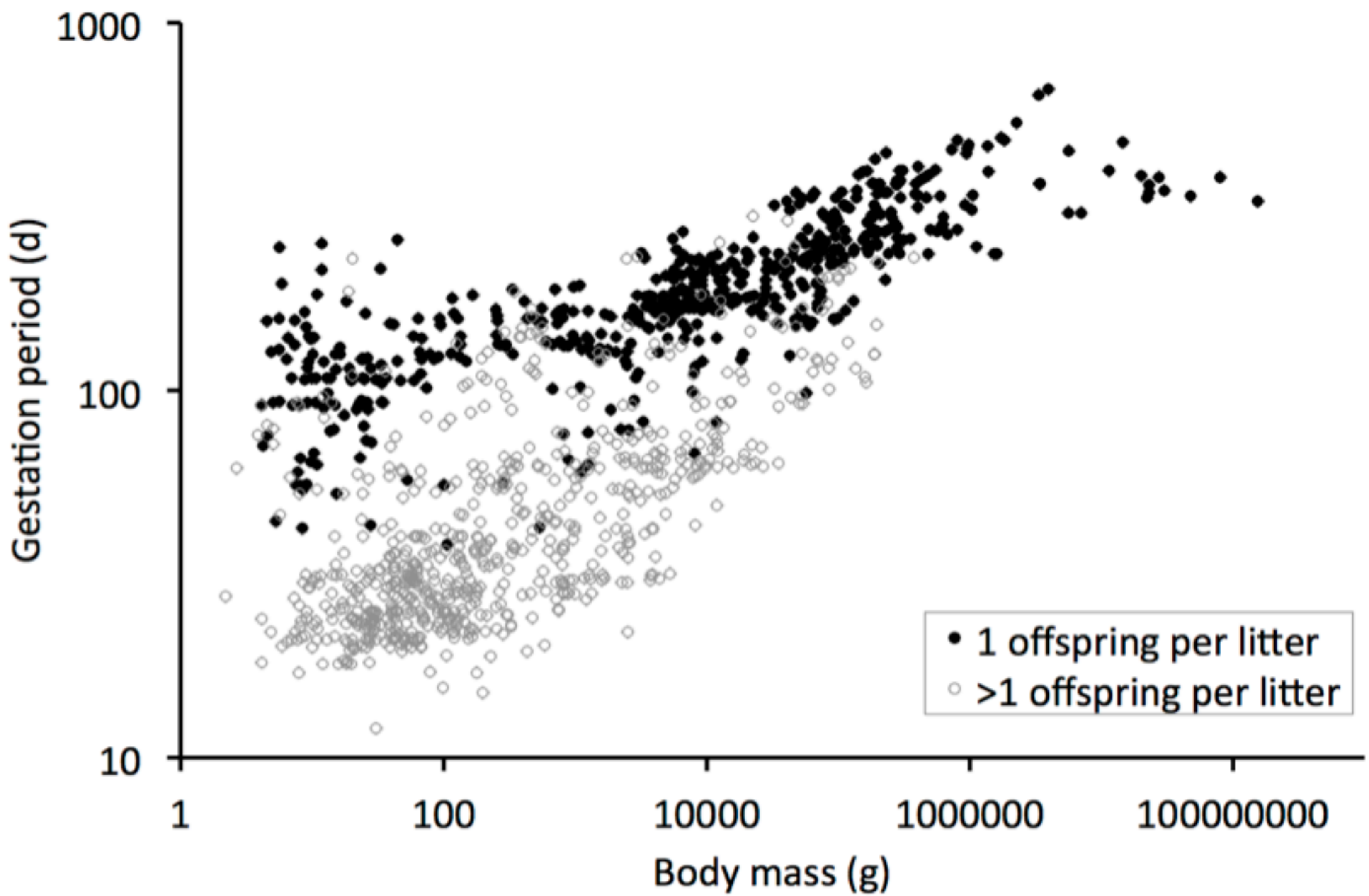


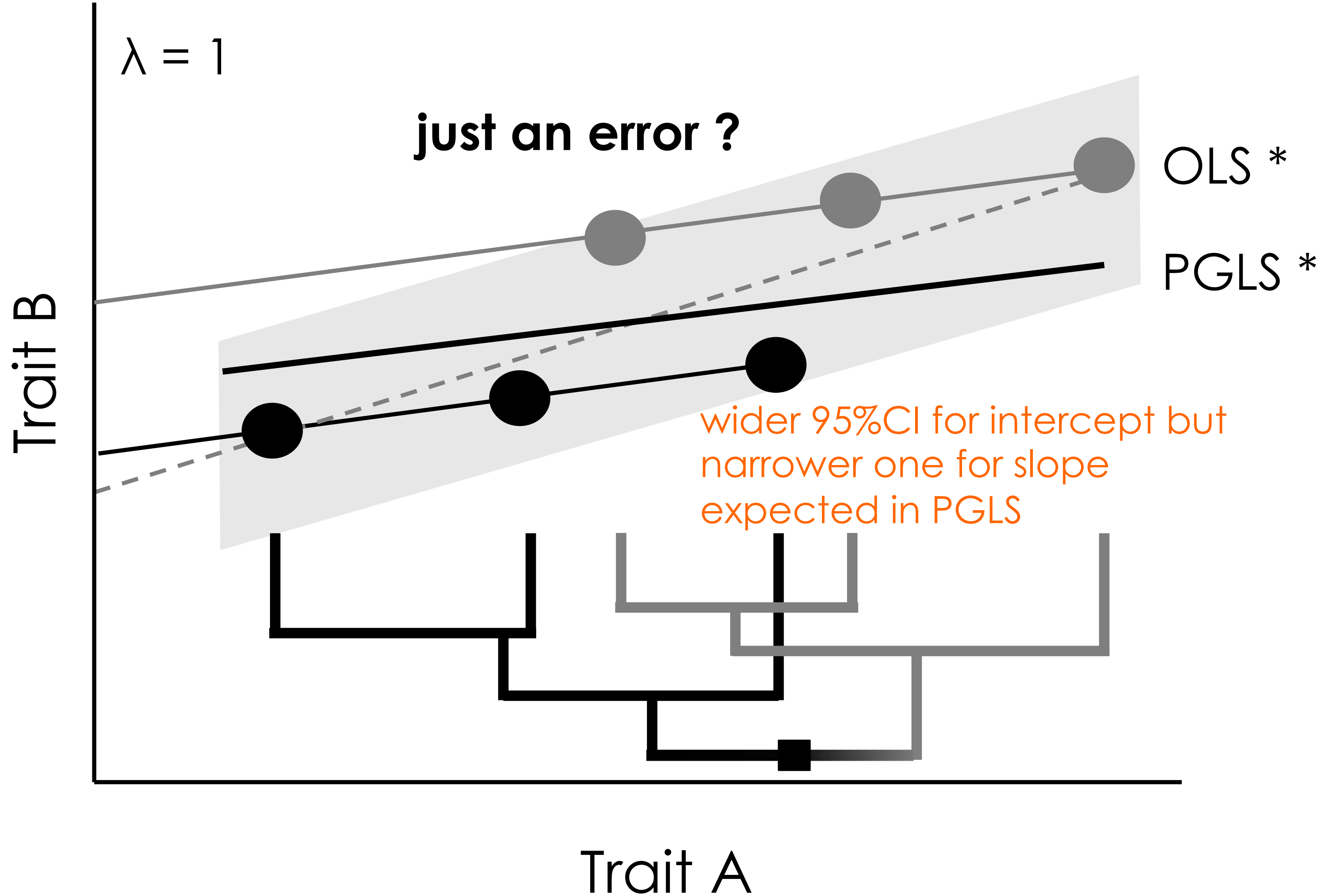
from Clauss et al. (2013)

Example V: Gestation time



from Clauss et al. (2014)

Accounting for phylogeny



from Clauss et al. (2013)

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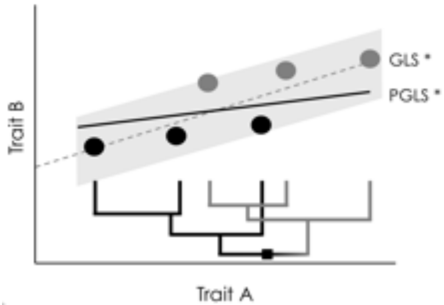
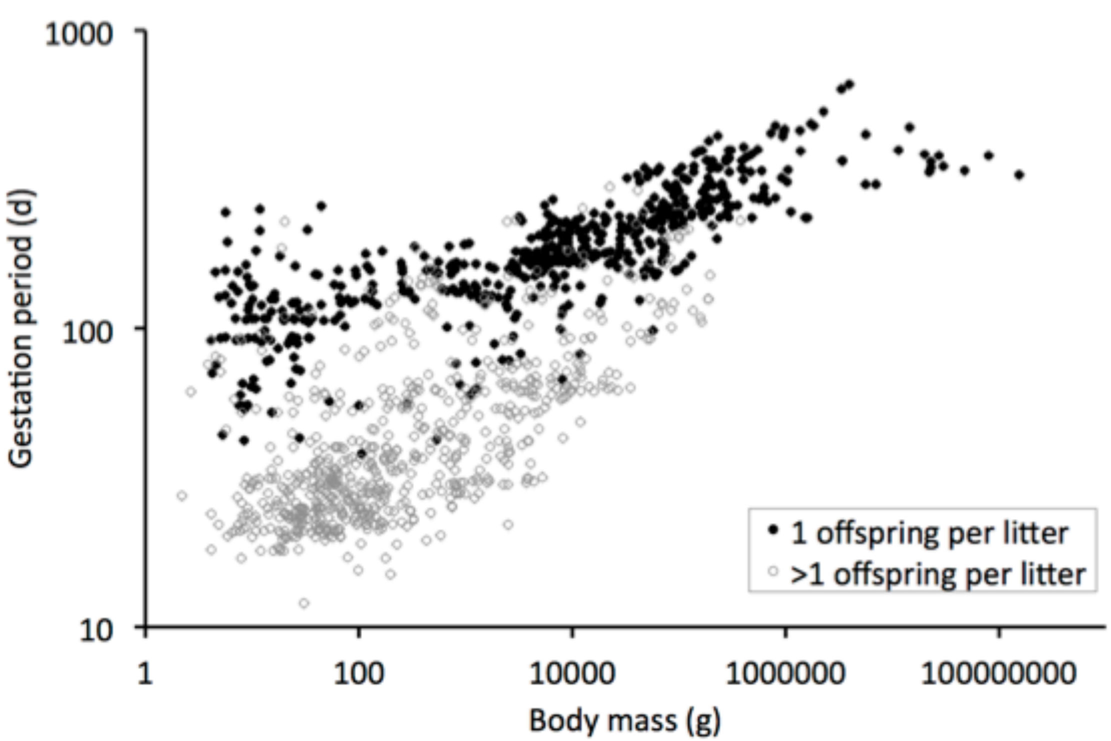


OLS: 21.5 (19.9-23.3) $BM^{0.19\ (0.18-0.20)}$

PGLS: 52.4 (41.3-66.3) $BM^{0.09\ (0.08-0.10)}$



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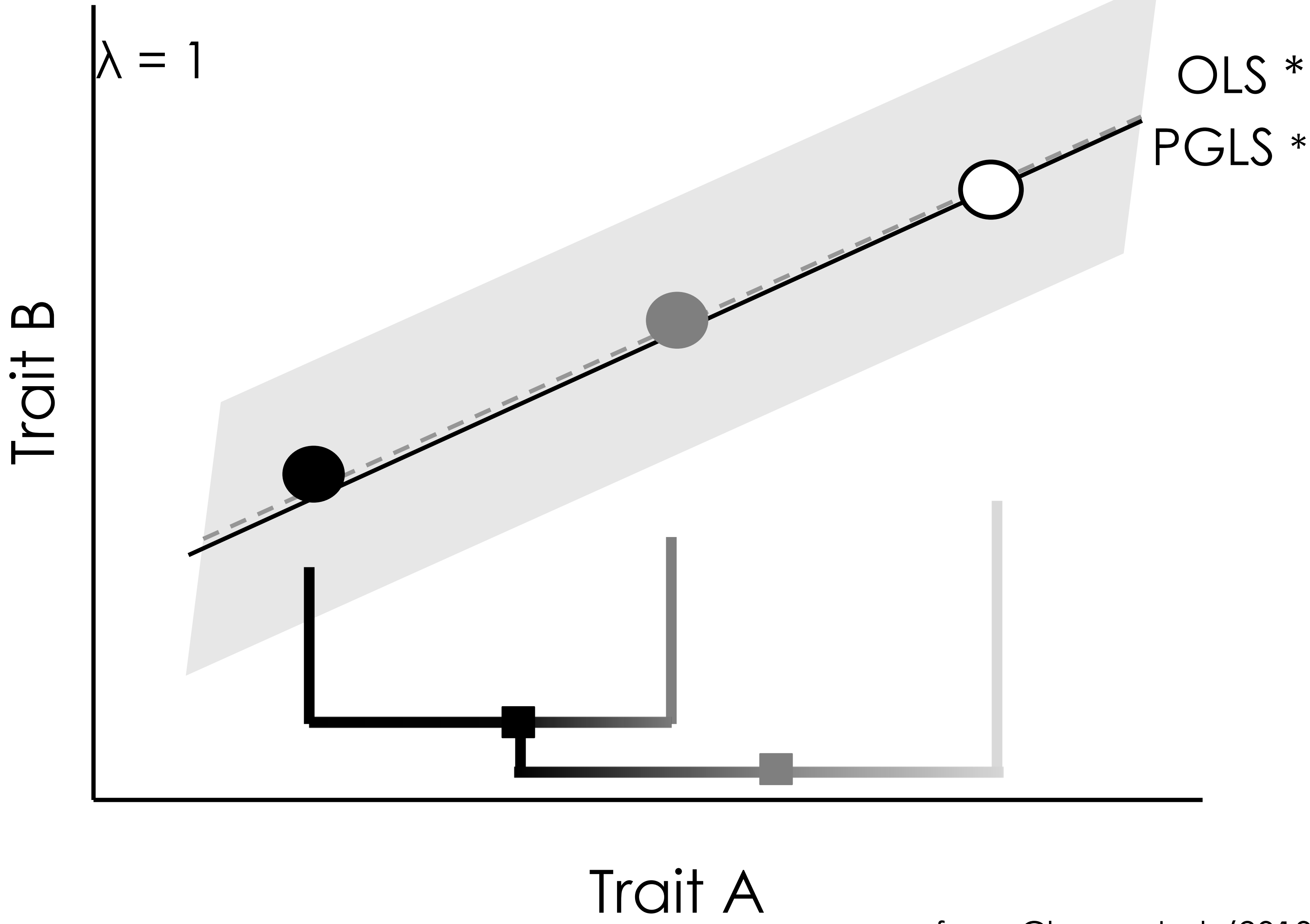
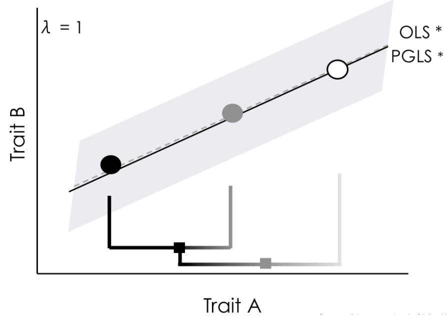


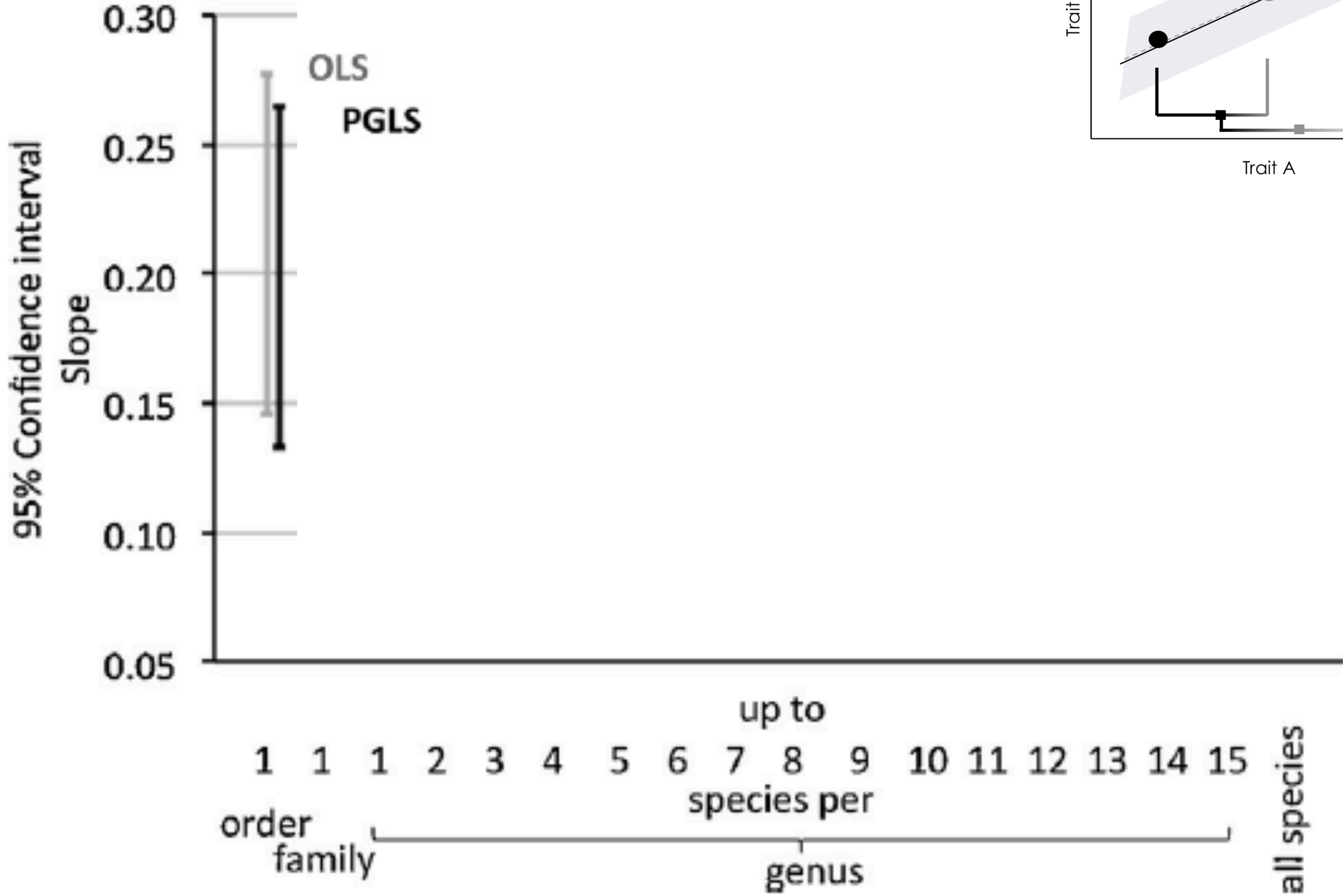
from Clauss et al. (2013)

Low scaling of a life history variable: Analysing eutherian gestation periods with and without phylogeny-informed statistics

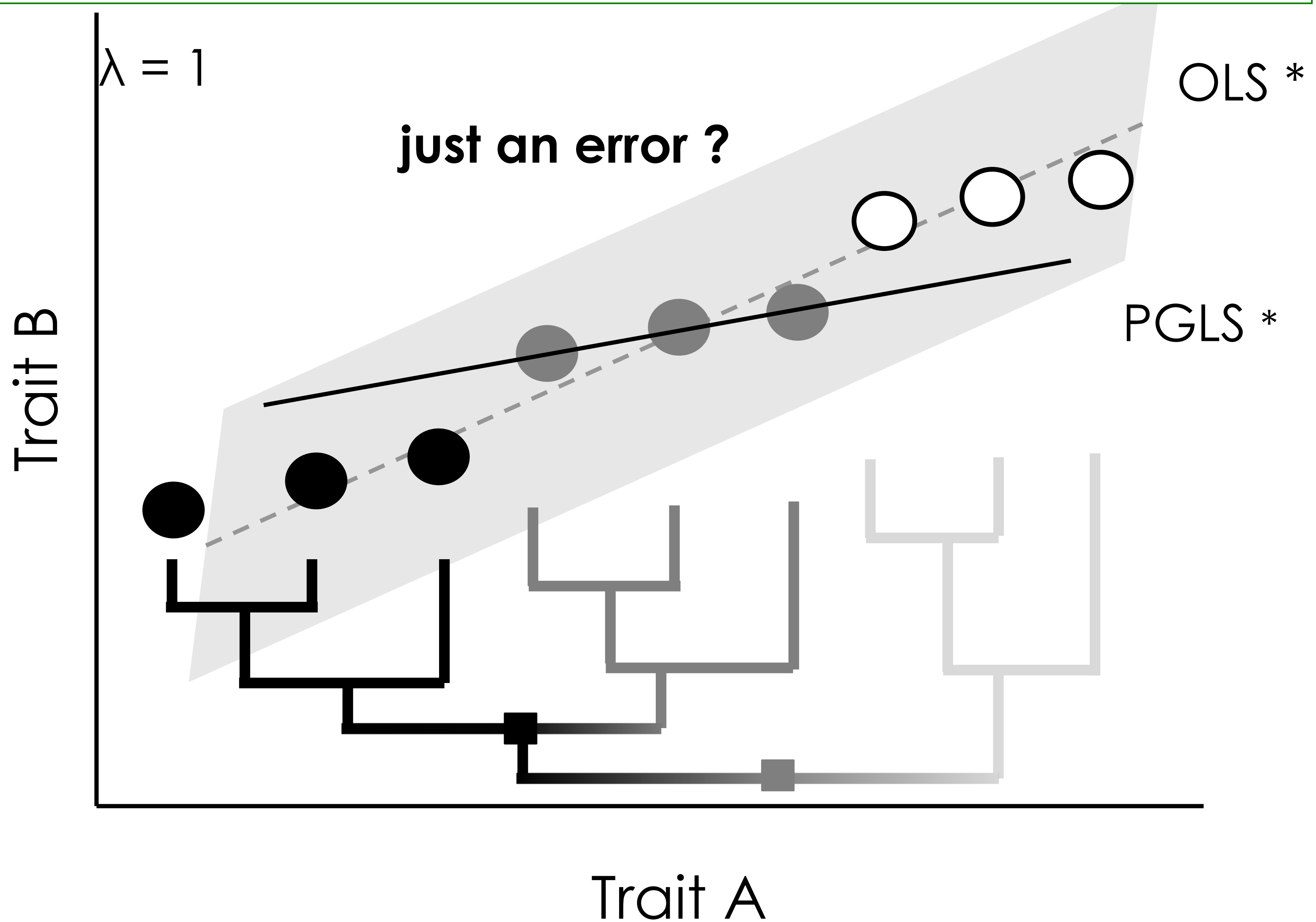
Marcus Clauss[a,*], Marie T. Dittmann[b], Dennis W.H. Müller[a,c], Philipp Zerbe[a,d], Daryl Codron[a,e]

Mammalian Biology 79 (2014) 9–16





Accounting for phylogeny



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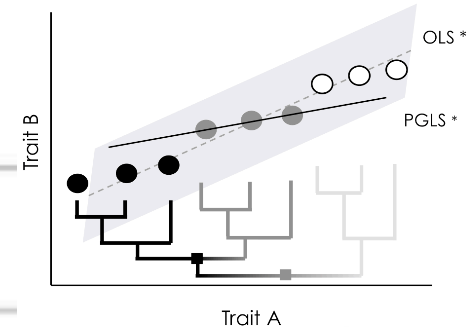
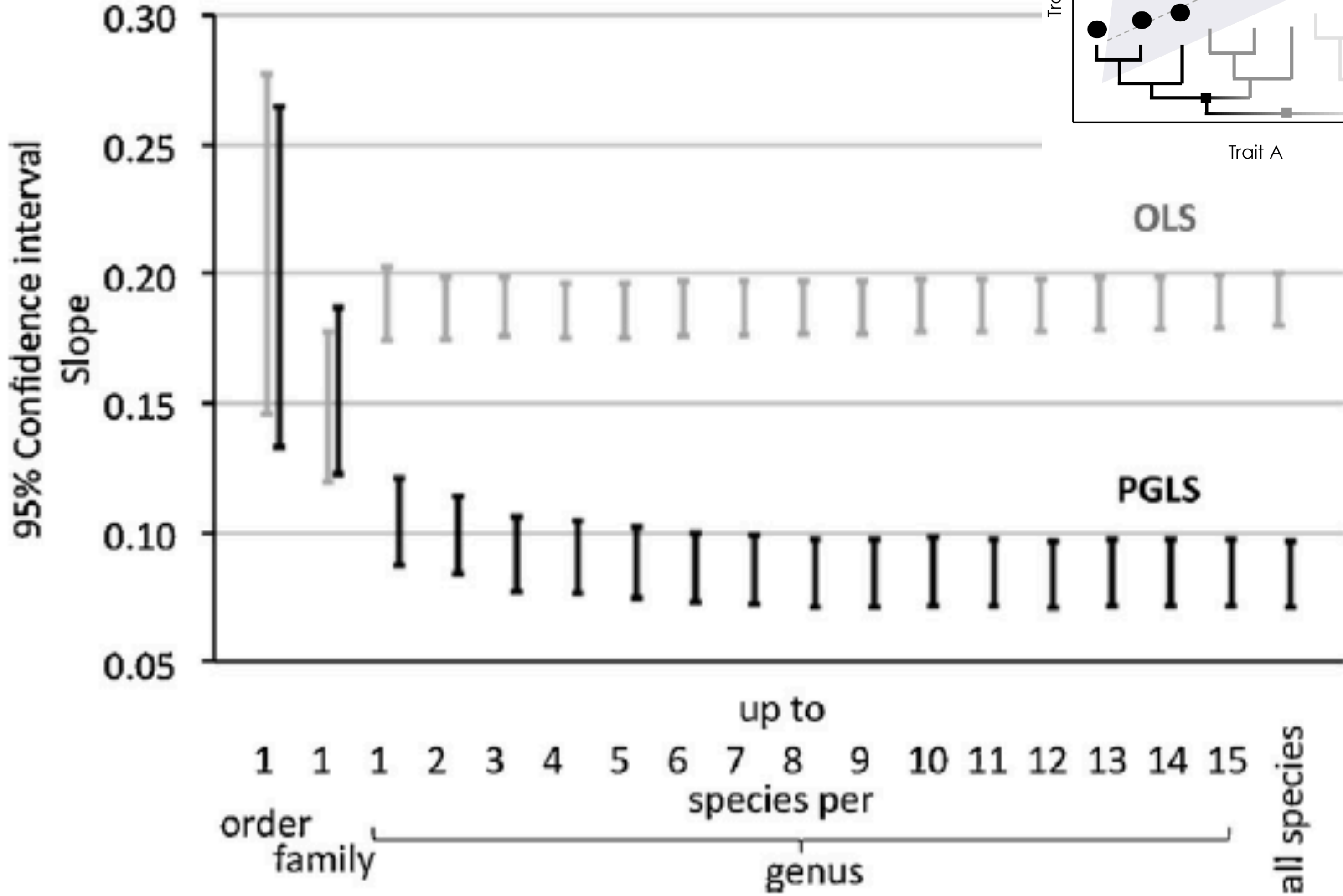




A deadly sin ? – ***No !***

REVIEW

The seven deadly sins of comparative analysis

R. P. FRECKLETON

J. EVOL. BIOL. **22** (2009) 1367–1375

~~**Reporting both PI and PC analyses**~~

~~Frequently, both across-species and phylogenetically corrected analyses of the same data are reported simultaneously. This is despite the fact that the two forms of analysis make very different assumptions about the distribution of the data.~~

A comparison of OLS and PGLS results is an important tool for understanding the structure of the data! (irrespective of which is the 'correct' one) ***because the two make very different assumptions about the data***

Just test it !

DOI: 10.1002/ece3.5214

Ecology and Evolution Open Access WILEY

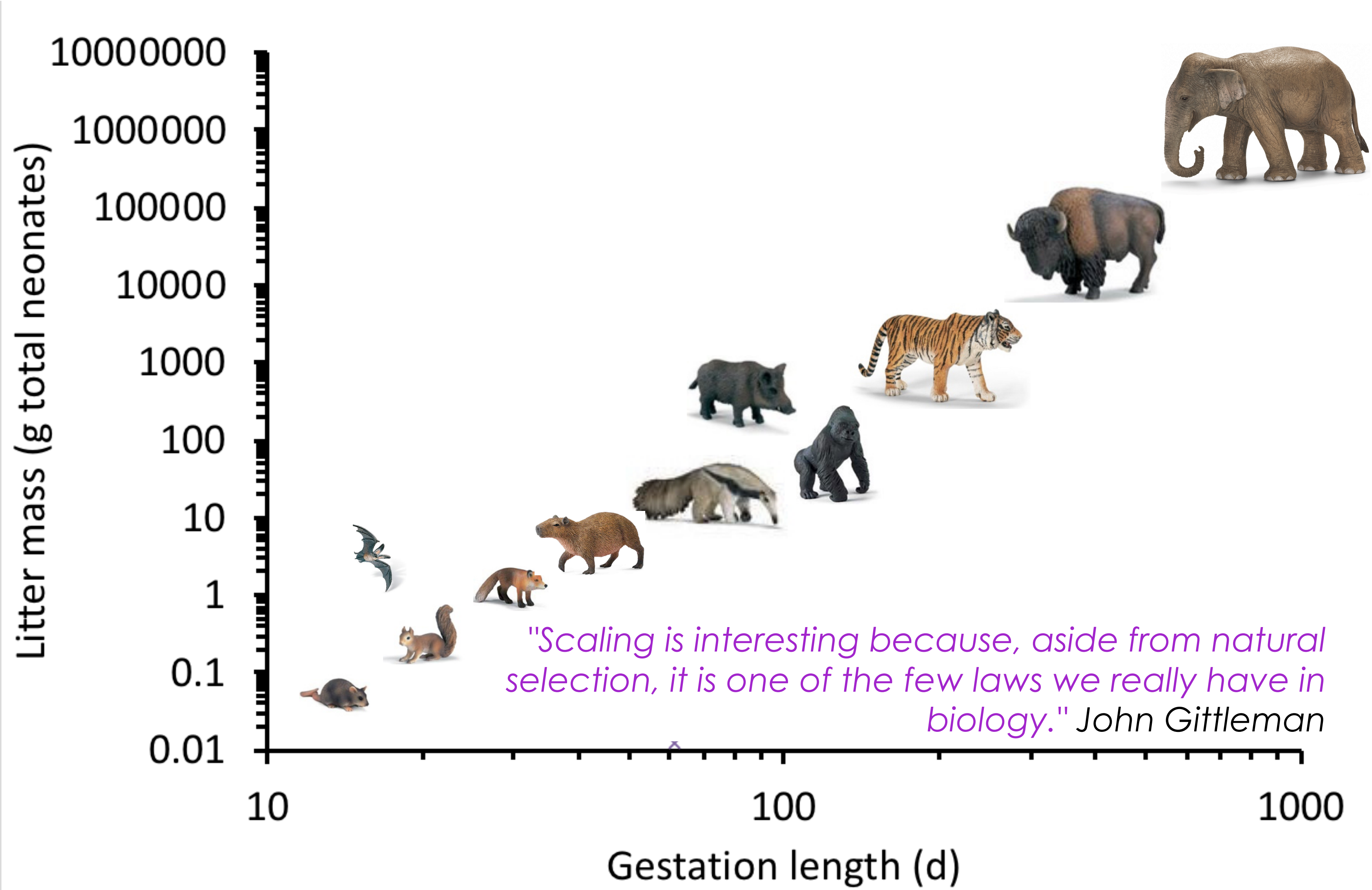
EDITORIAL

Phylogenetic signal in tooth wear? A question that can be answered—By testing

Directionality in Evolution:

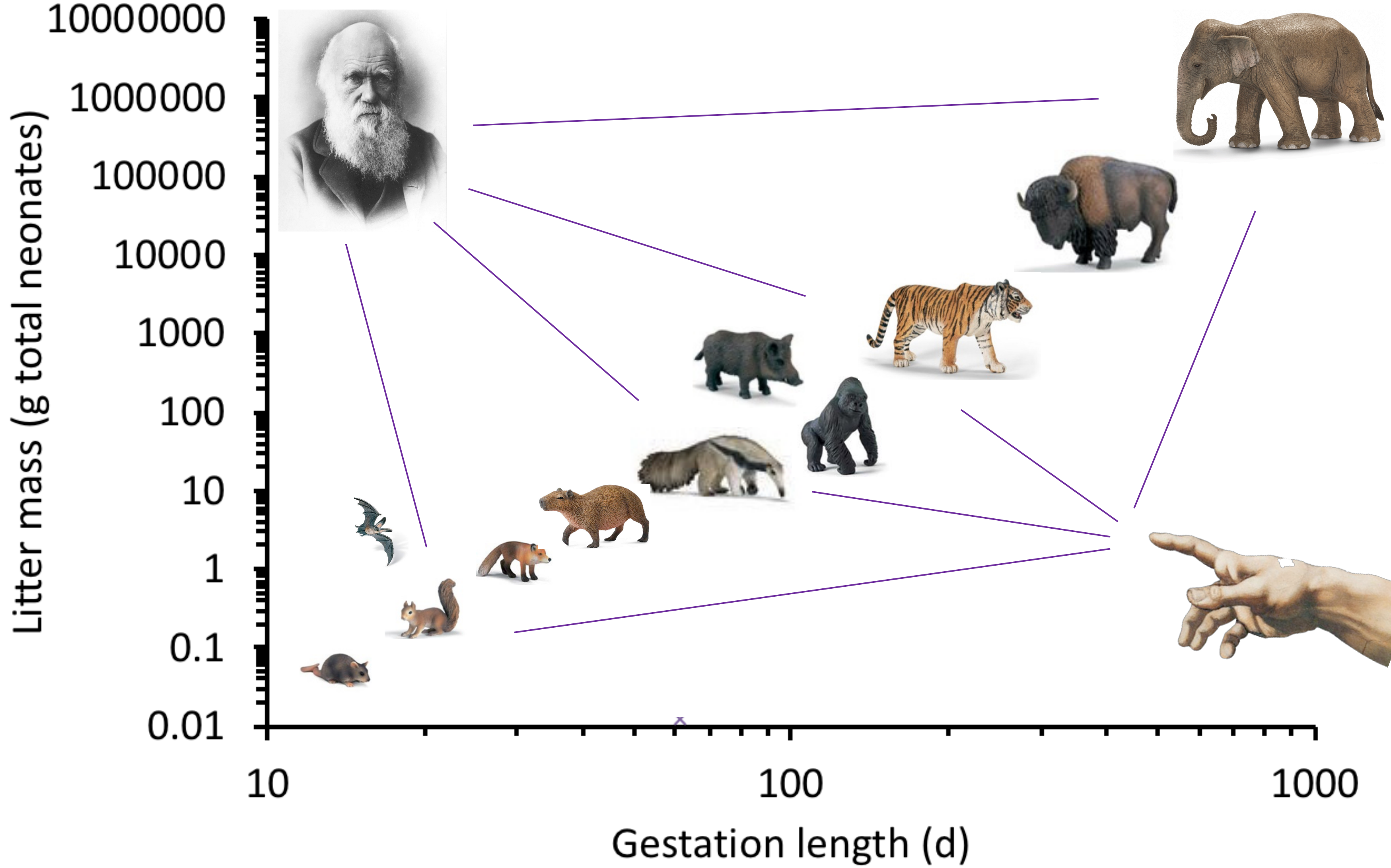
Allometries as snapshots in evolutionary time

Biology: fixed laws ?

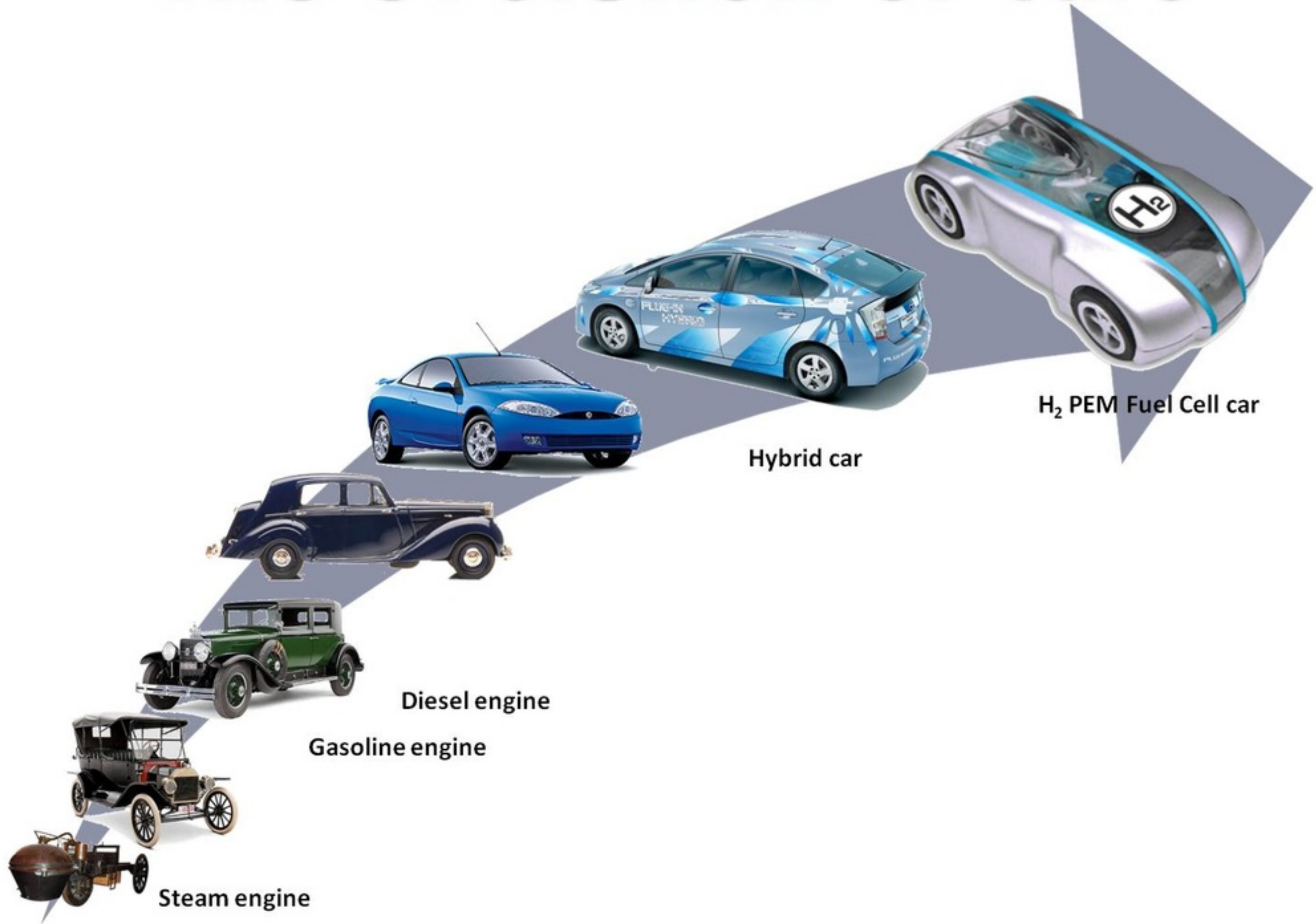


"Scaling is interesting because, aside from natural selection, it is one of the few laws we really have in biology." John Gittleman

Biology: fixed laws ?



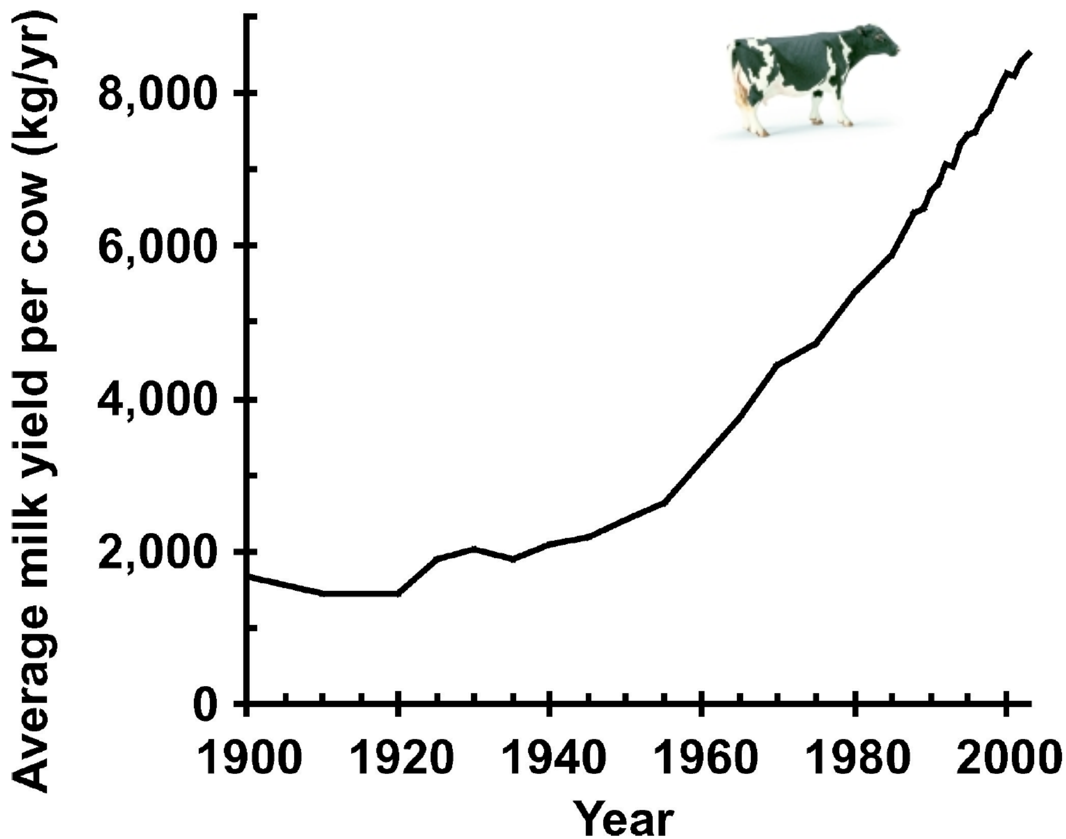
The evolution of cars

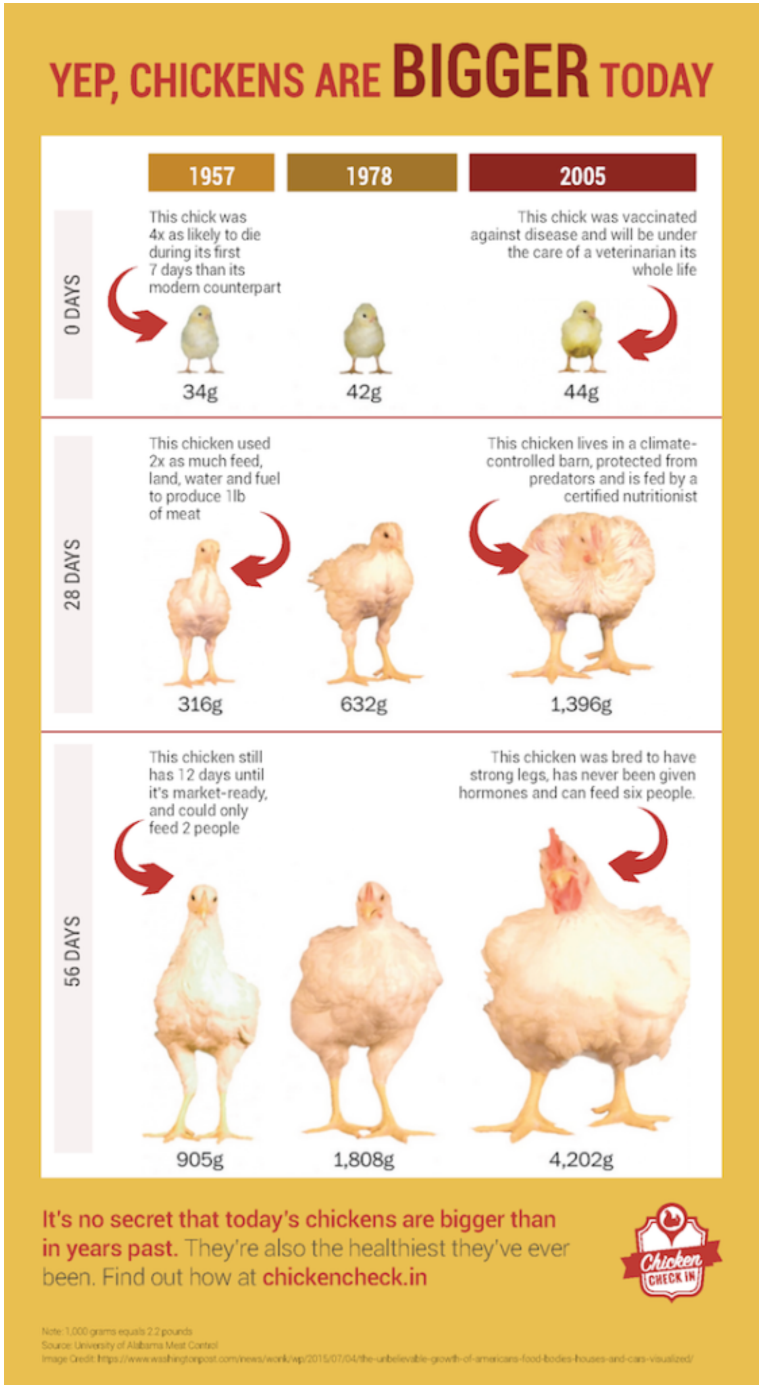


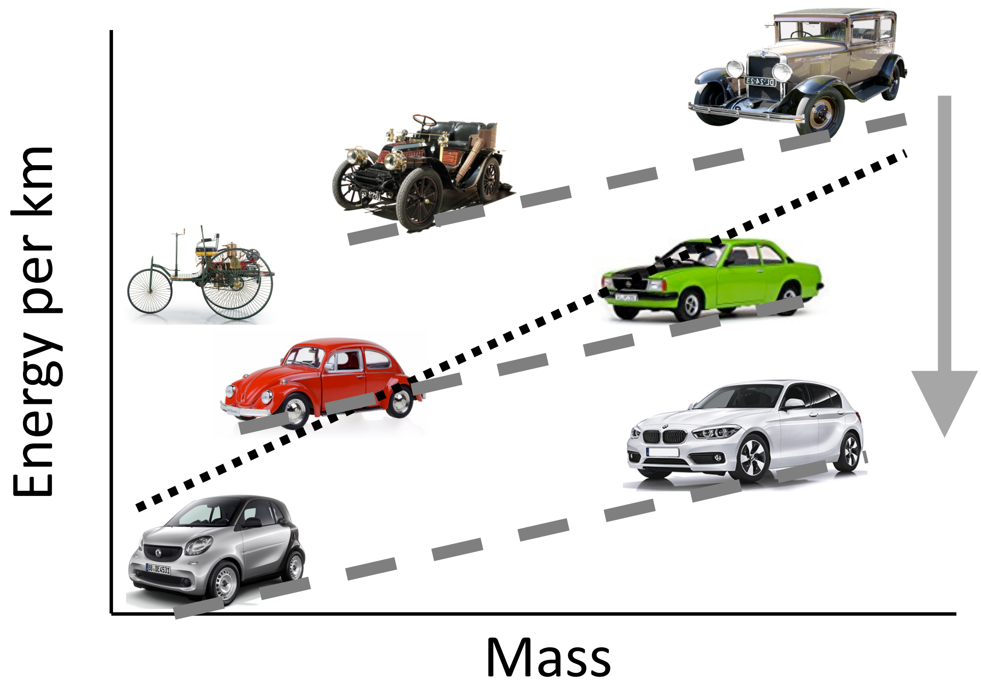
J. Dairy Sci. 89:1280–1291

Major Advances in Nutrition: Relevance to the Sustainability of the Dairy Industry

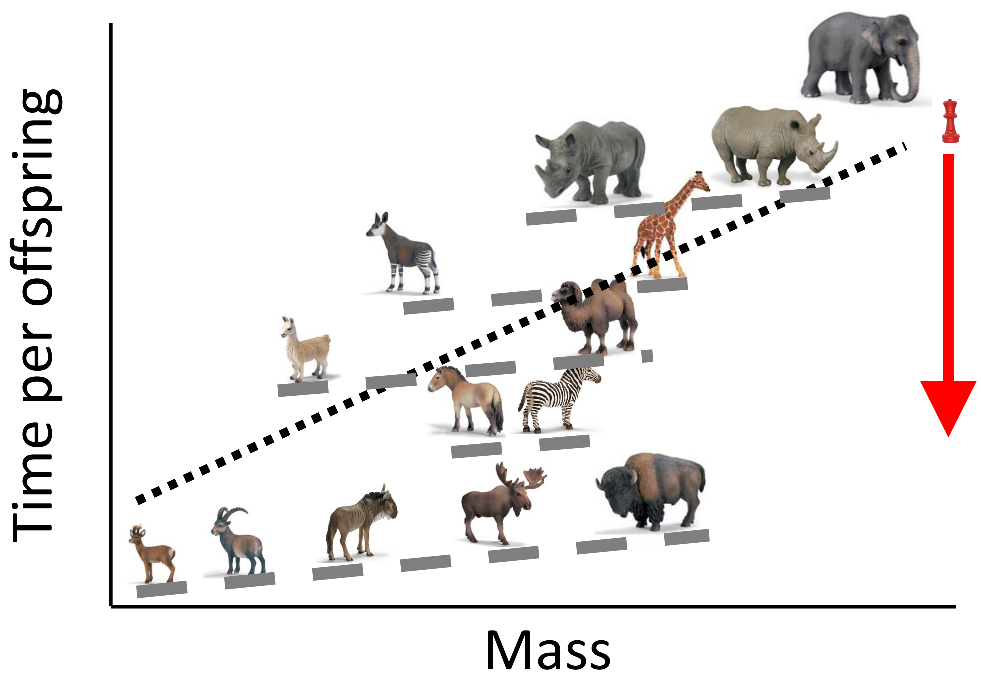
M. J. VandeHaar*[1] and N. St-Pierre†




YEP, CHICKENS ARE BIGGER TODAY
1957
1978
2005
0 DAYS
This chick was 4x as likely to die during its first 7 days than its modern counterpart
This chick was vaccinated against disease and will be under the care of a veterinarian its whole life
34g
42g
44g
28 DAYS
This chicken used 2x as much feed, land, water and fuel to produce 1lb of meat
This chicken lives in a climate-controlled barn, protected from predators and is fed by a certified nutritionist
316g
632g
1,396g
56 DAYS
This chicken still has 12 days until it's market-ready, and could only feed 2 people
This chicken was bred to have strong legs, has never been given hormones and can feed six people.
905g
1,808g
4,202g
It's no secret that today's chickens are bigger than in years past. They're also the healthiest they've ever been. Find out how at chickencheck.in
Chicken CHECK IN
Note: 1,000 grams equals 2.2 pounds
Source: University of Alabama Meat Control
Image Credit: https://www.washingtonpost.com/news/wonk/wp/2015/07/04/the-unbelievable-growth-of-americans-food-bodies-houses-and-cars-visualized/



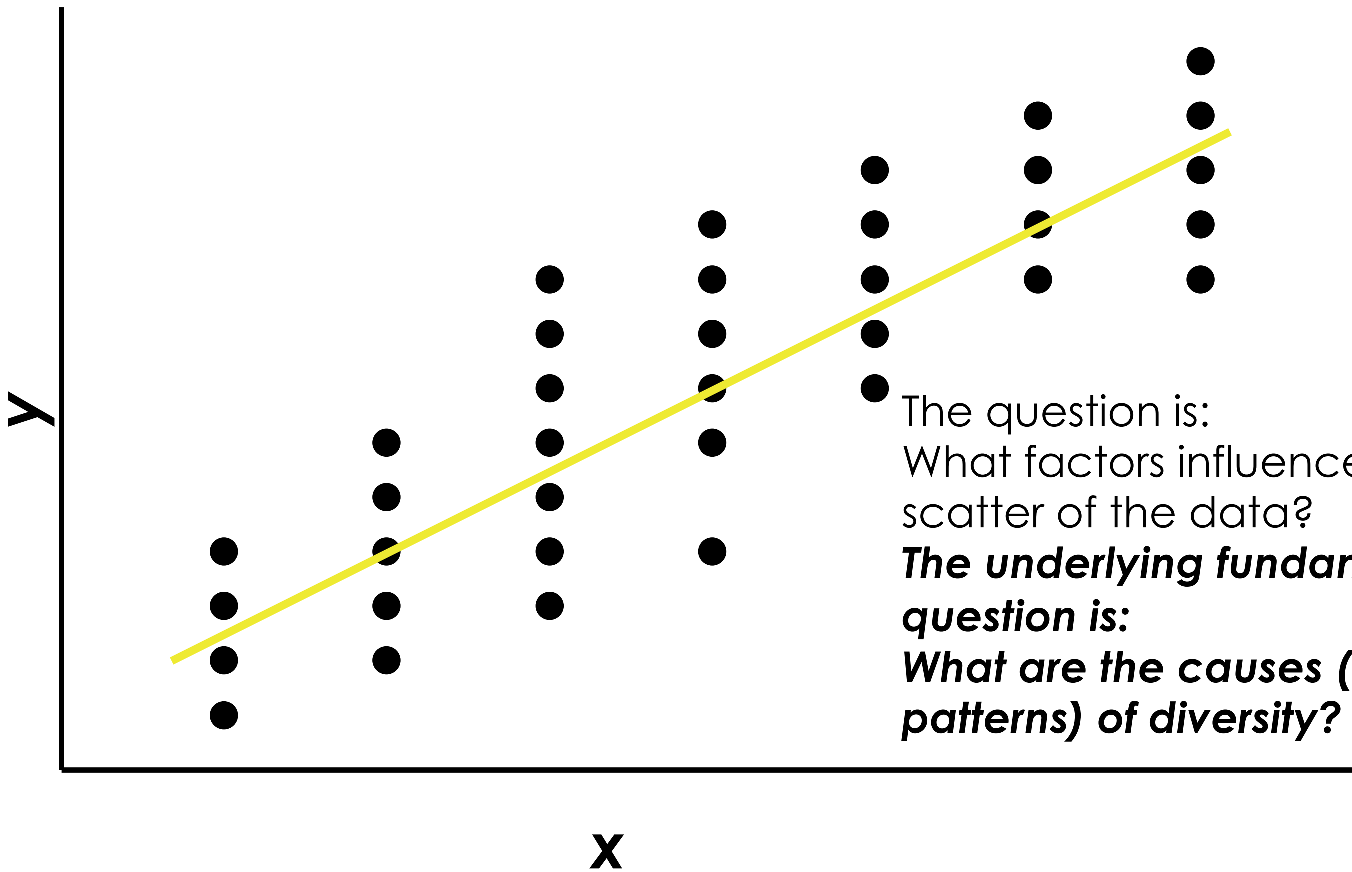
You would not consider the overall pattern a fixed law, but consider it with respect to technical progress.



Why would you consider this a pattern due to fixed life history tradeoff laws, and not rather a ***snapshot*** *in a process of optimization?*

Interpreting scaling

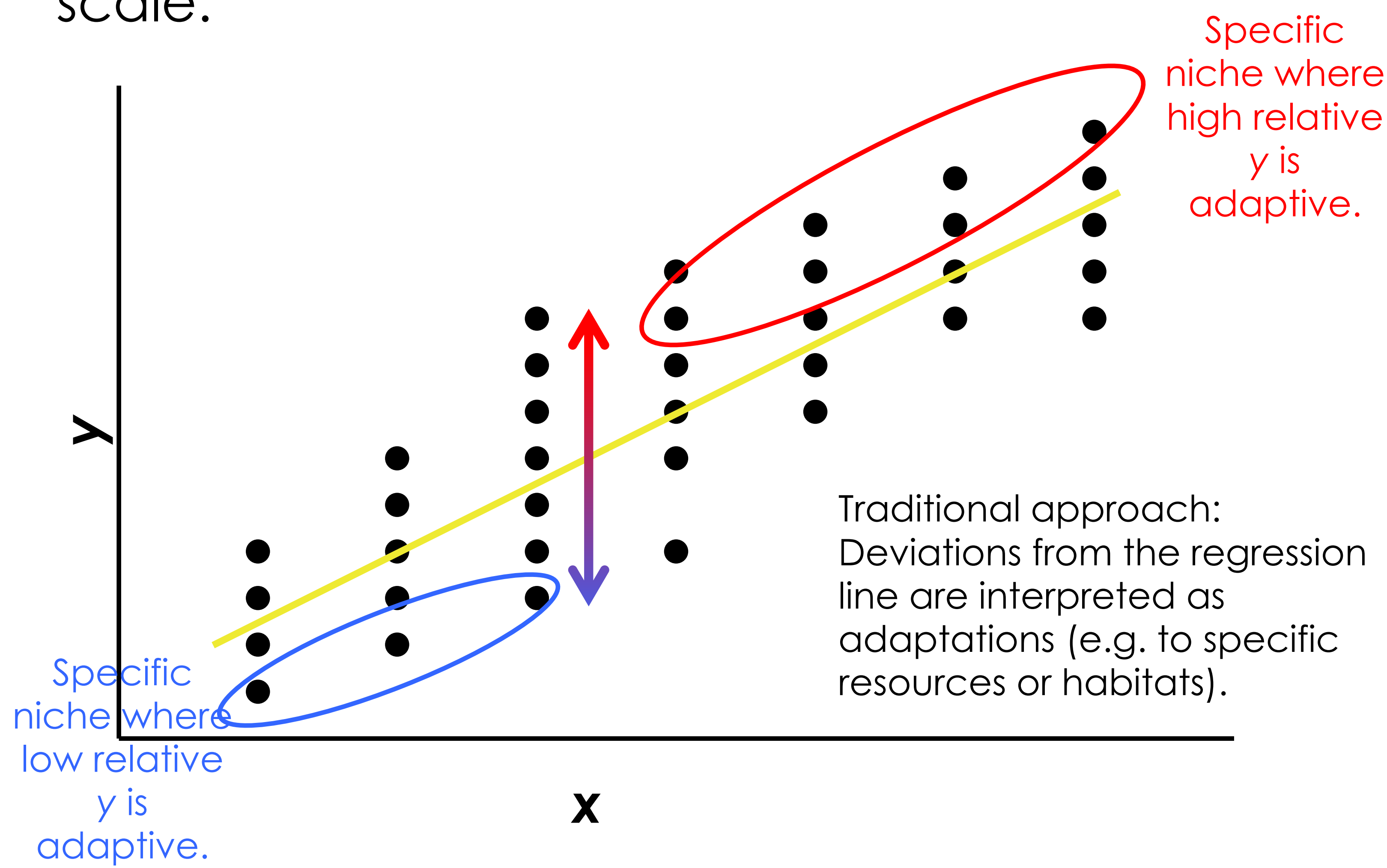
Morphological, physiological and life history variables scale.



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

Interpreting scaling

Morphological, physiological and life history variables scale.

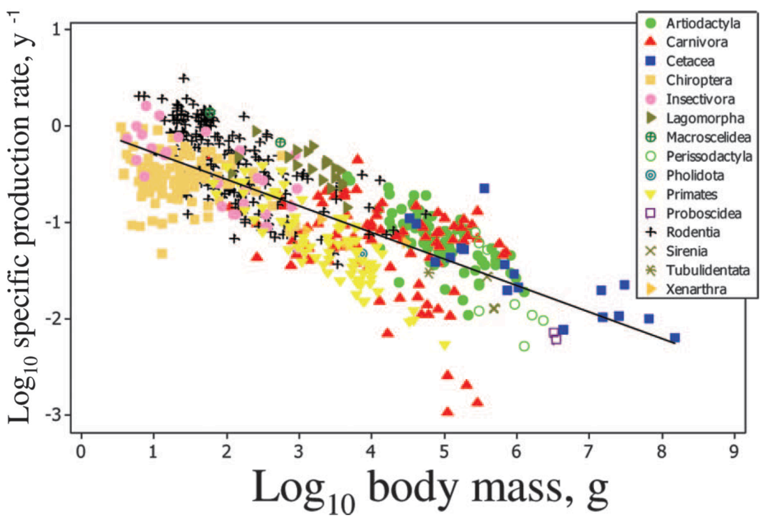


Traditional approach: Deviations from the regression line are interpreted as adaptations (e.g. to specific resources or habitats).

Effects of body size and lifestyle on evolution of mammal life histories

Richard M. Sibly*†‡ and James H. Brown‡§¶

PNAS | November 6, 2007 | vol. 104 | no. 45 | 17707–17712



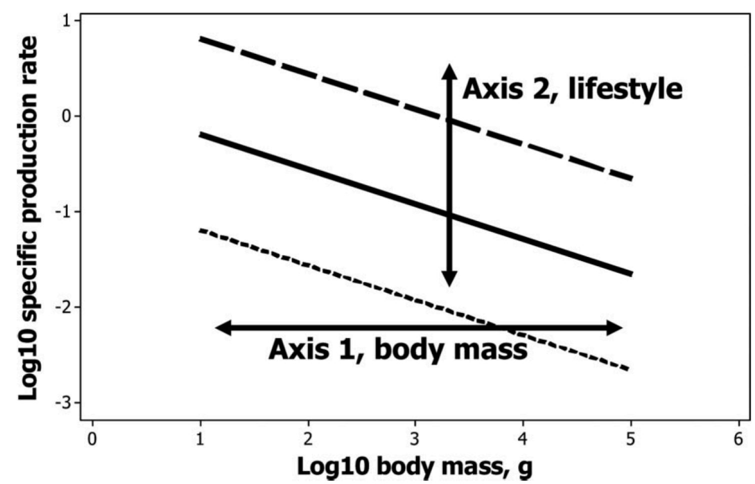
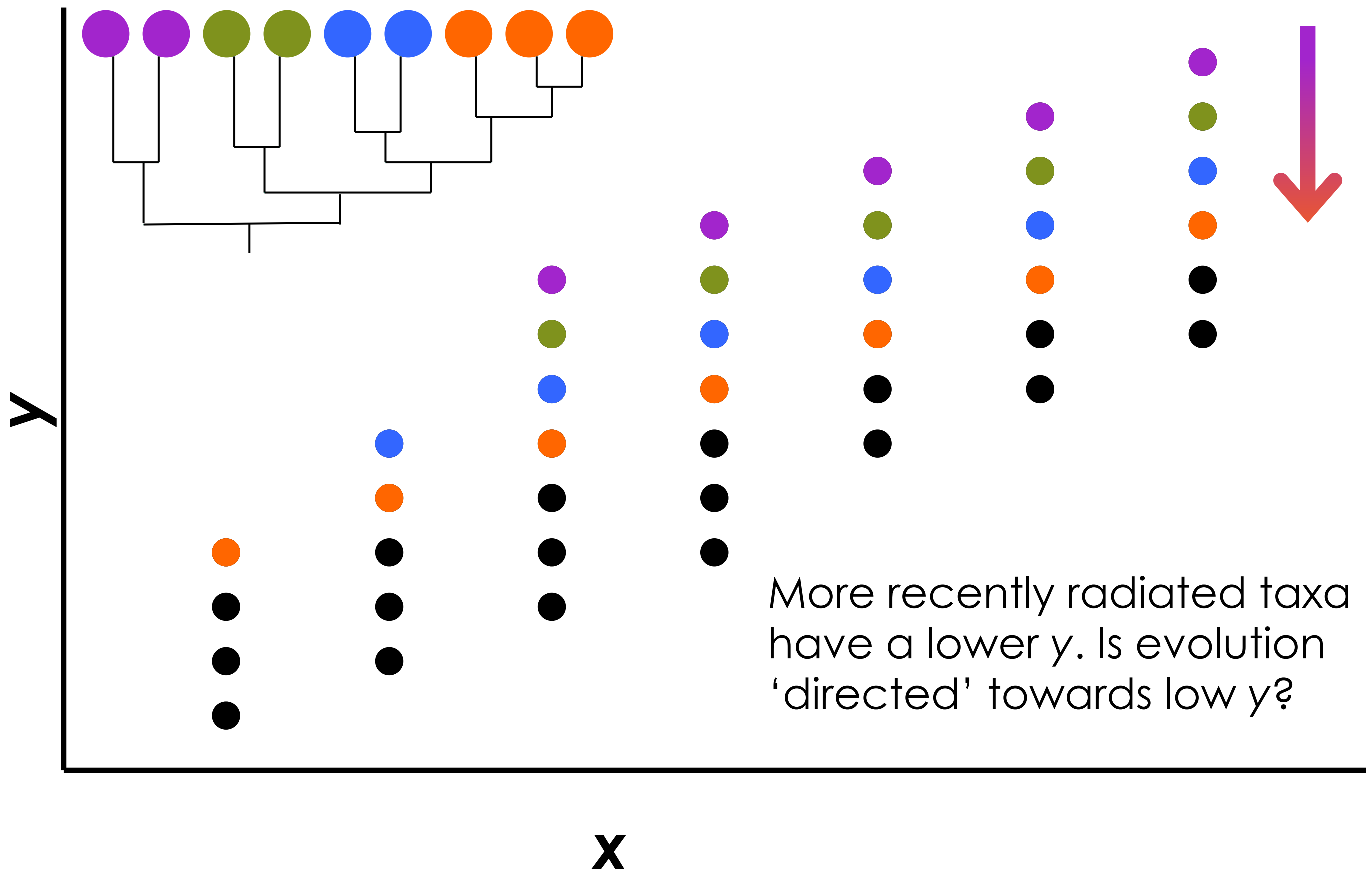


Fig. 4. The two major axes of the slow–fast life-history continuum, body mass, and lifestyle. To the well known axis of allometric variation due to body size, we have added a second orthogonal axis based on ecological lifestyle. Here the solid line represents an unspecialized ancestral condition, the dashed line depicts a more productive ''live fast die young'' lifestyle, and the dotted line shows a lifestyle with a lower death rate, slower life history, and consequently lower production.

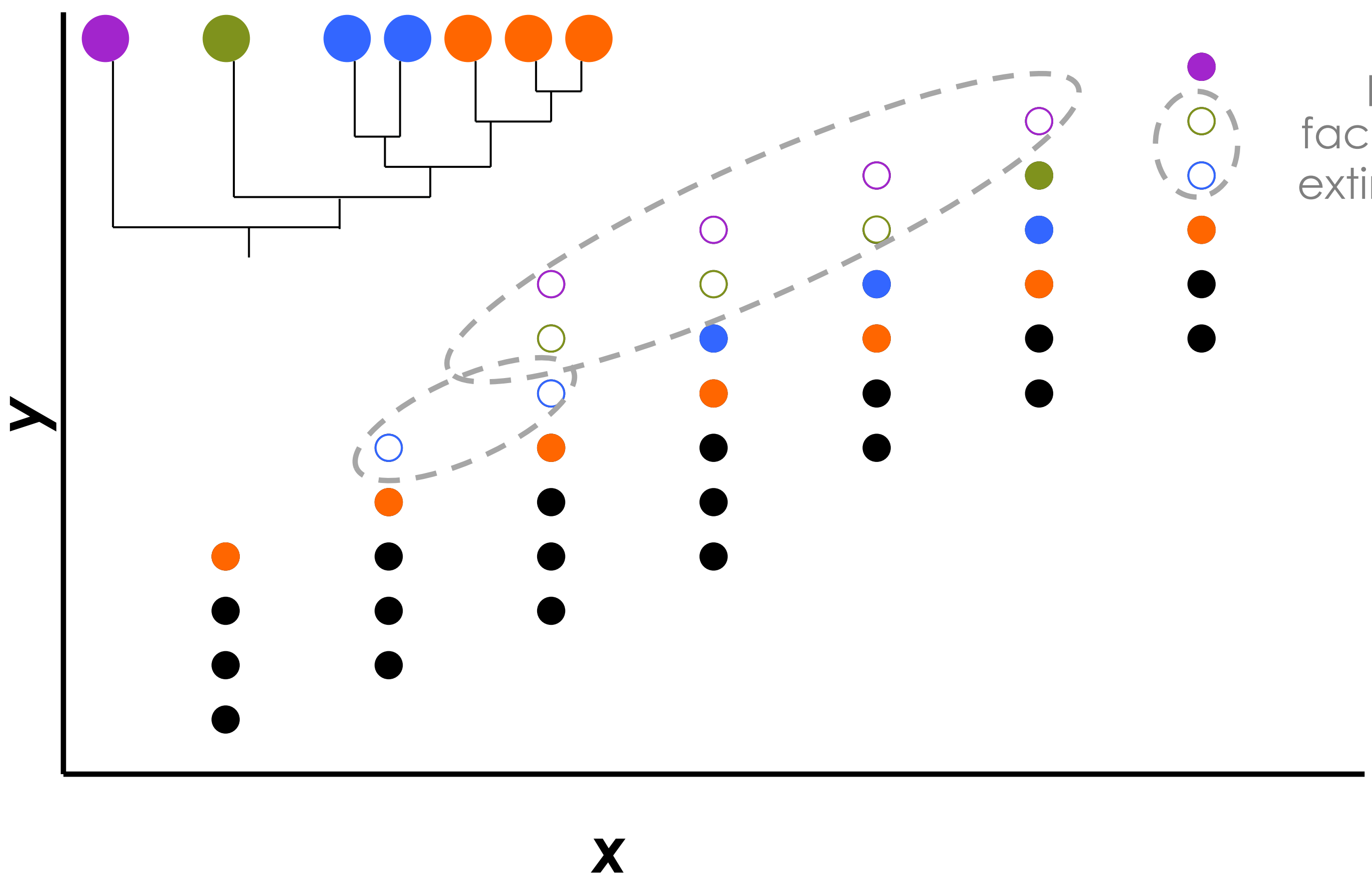
Interpreting scaling

Is there a systematic phylogenetic structure in the dataset?



Interpreting scaling

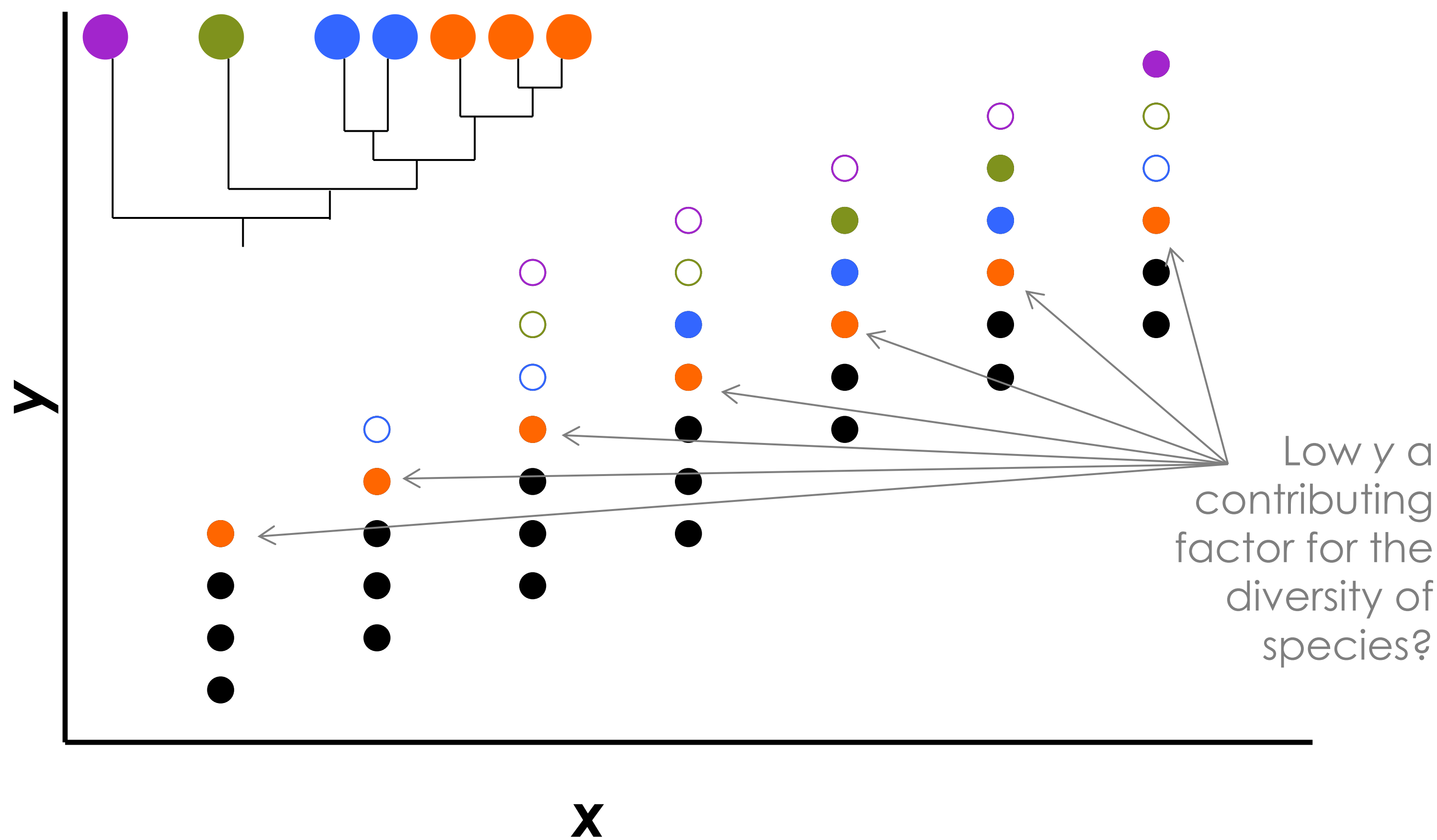
Is there a systematic phylogenetic structure in the dataset?



High y a potential factor in the extinction of species?

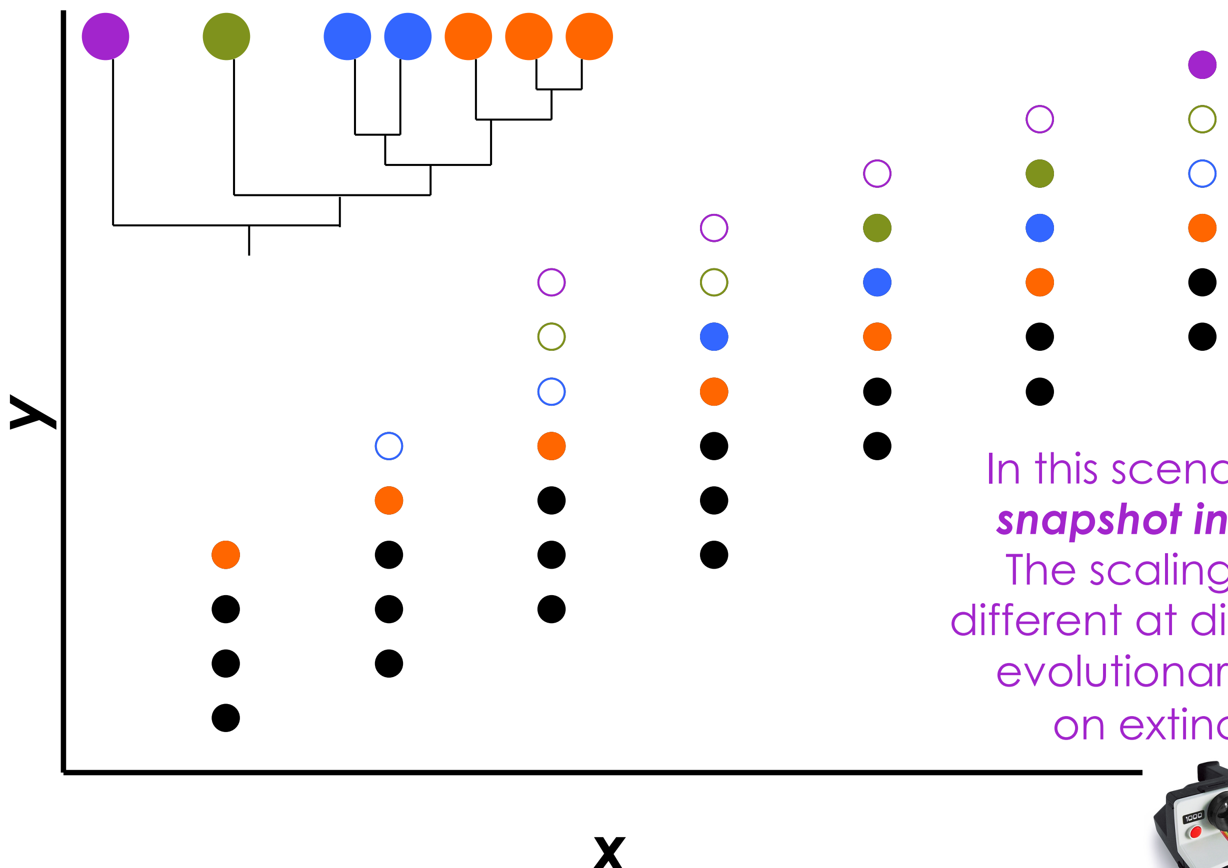
Interpreting scaling

Is there a systematic phylogenetic structure in the dataset?



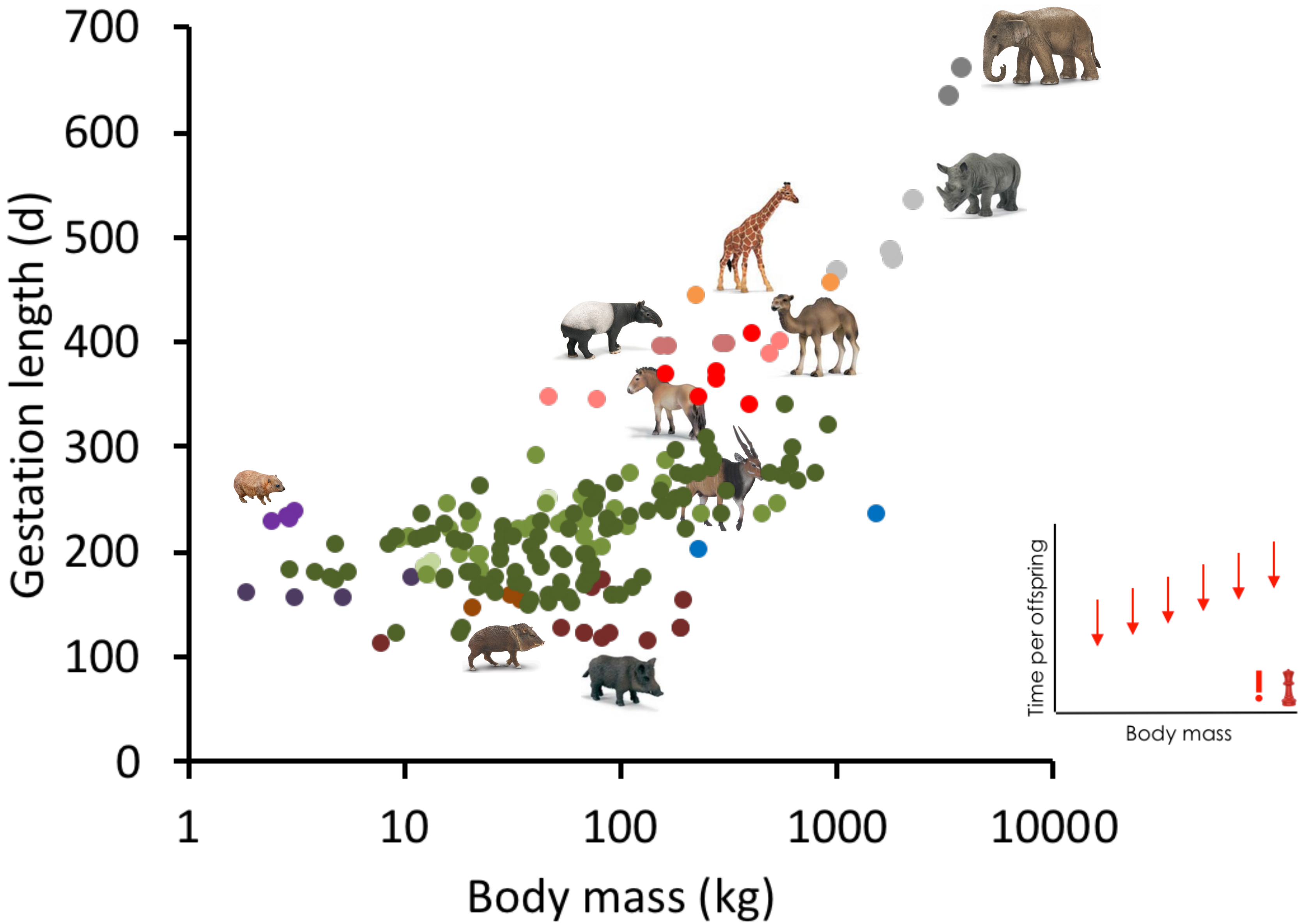
Interpreting scaling: snapshots

Is there a systematic phylogenetic structure in the dataset?



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

A clear picture for gestation length



(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).

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

The difference cannot be due to body size!

Rather than understanding tradeoffs along the fast-slow continuum as fixed physical laws, they can be considered as representing the efficiency of the organisms from which the data was taken – and that efficiency may evolve.