The art of allometry: extrapolating and comparing morphometric and physiological data

Marcus Clauss

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

Wildlife Digestive Physiology Course Vienna 2013

Research Unit 533
Sauropod Biology
DFG

better late than never

SAUROPOD NUTRITION SQUAD

Fundamental aim

Herbivore diversity and niche differentiation

Fundamental aim:

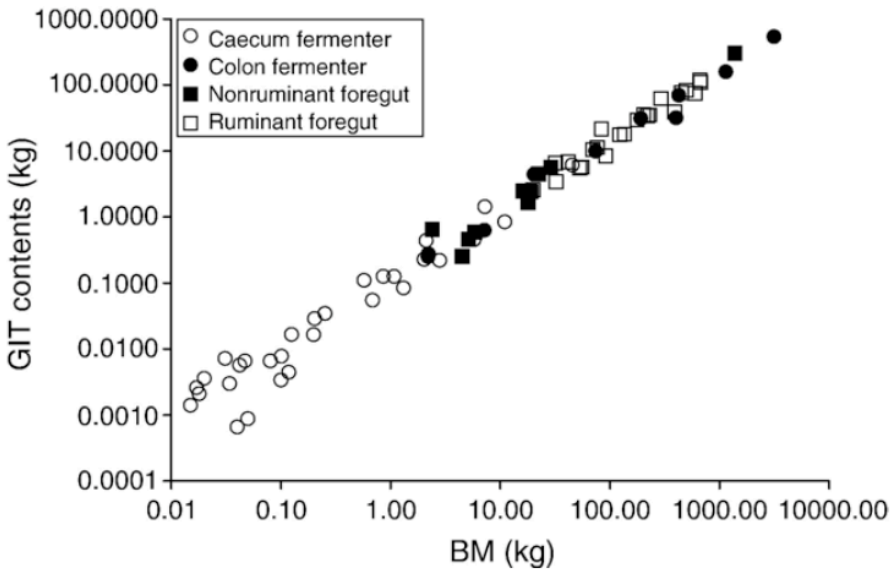
to use physiological / biological characteristics to explain diversity and differentiation

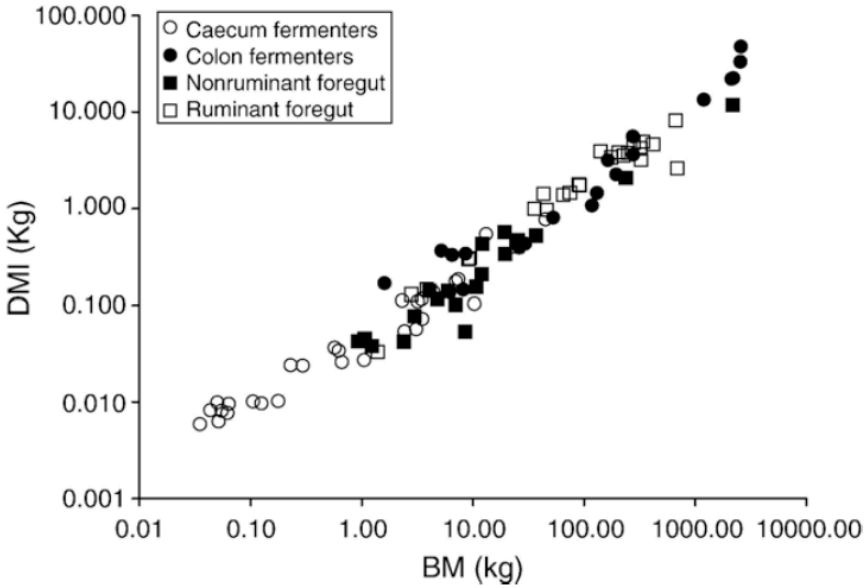
to reduce these characteristics to simple rules

the ‘most simple rule’: body size-related allometries

Rules

- Varying complexity and ease of measurement

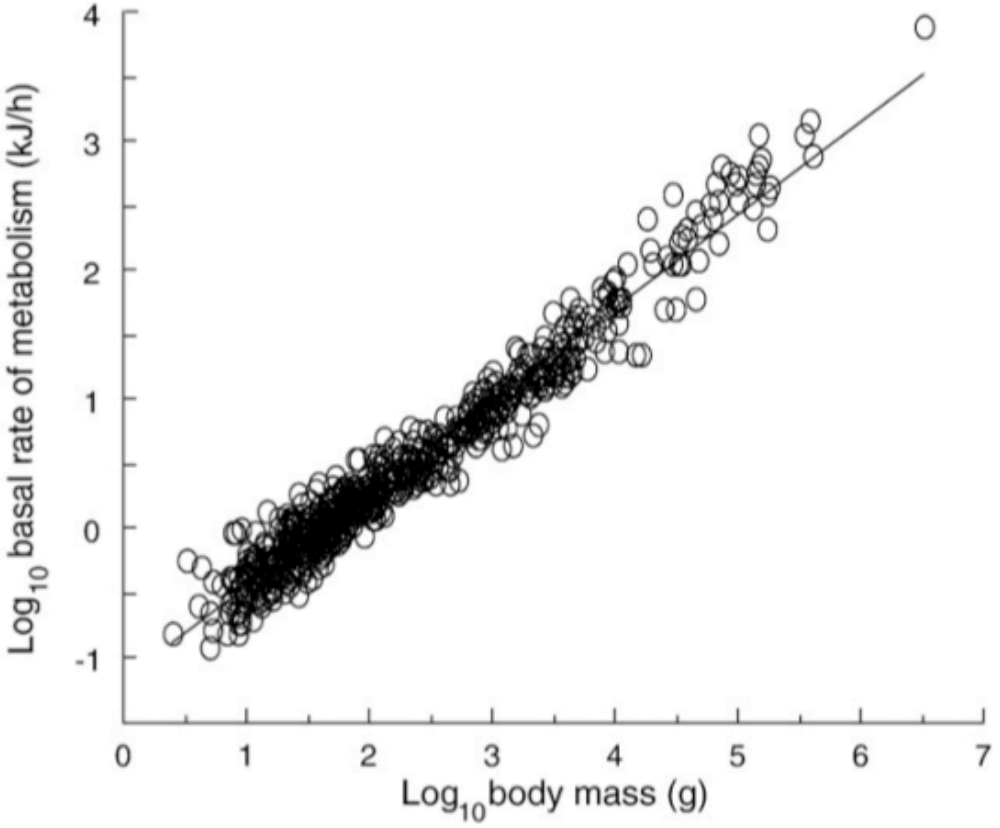




from Clauss et al. (2007)

Rules

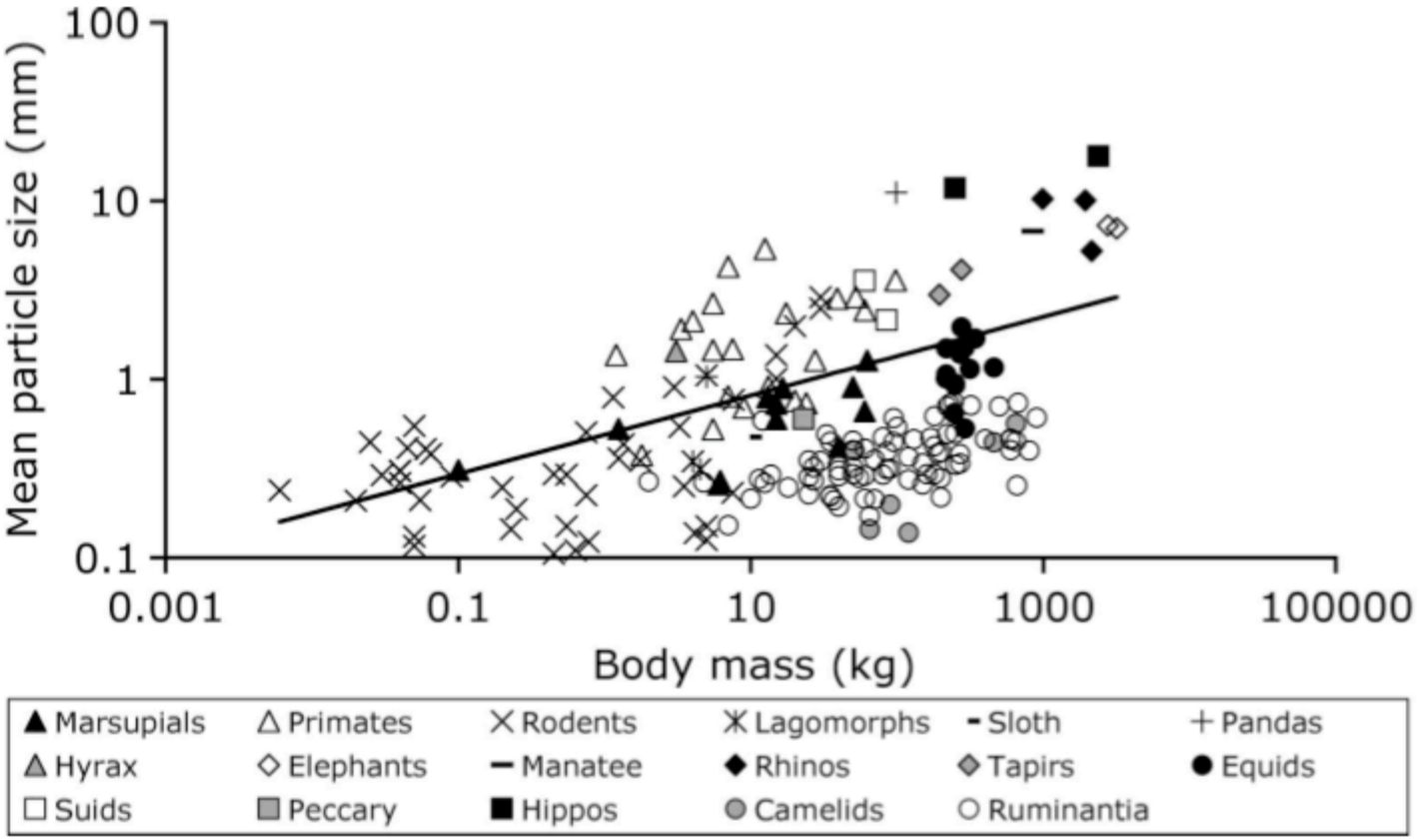
- Varying complexity and ease of measurement



from McNab (2008)

Rules

- Varying complexity and ease of measurement



from Fritz et al. (2009)

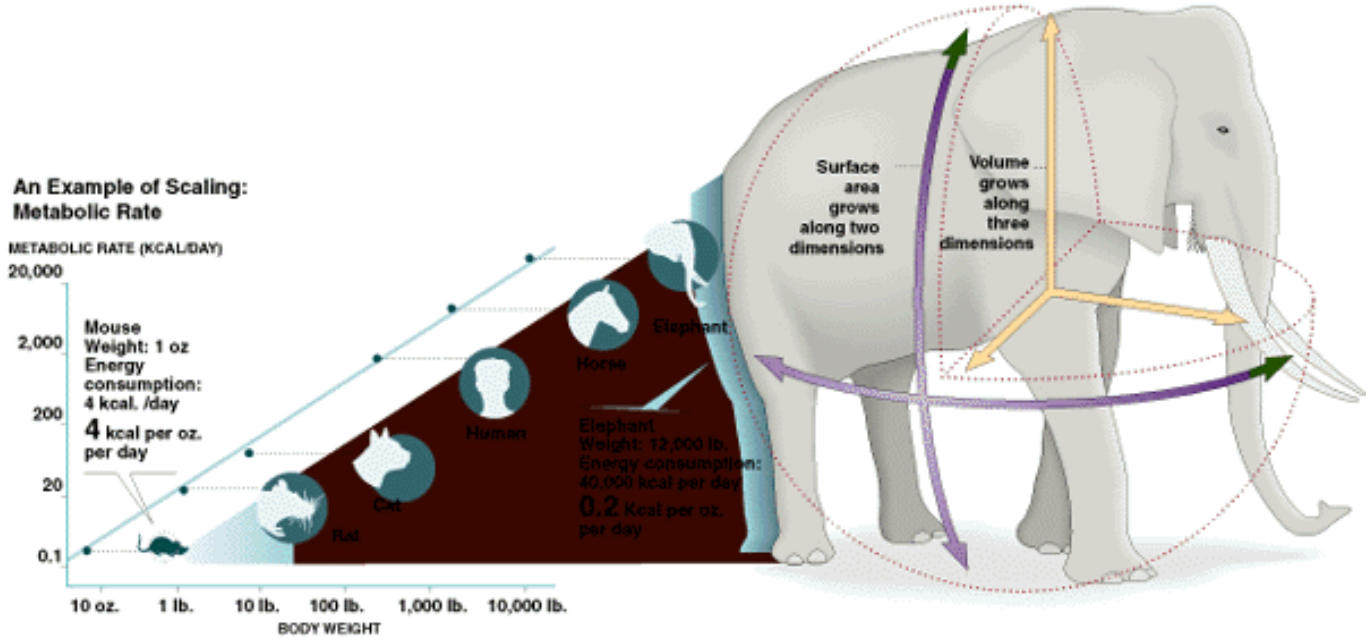
Allometry basics

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.

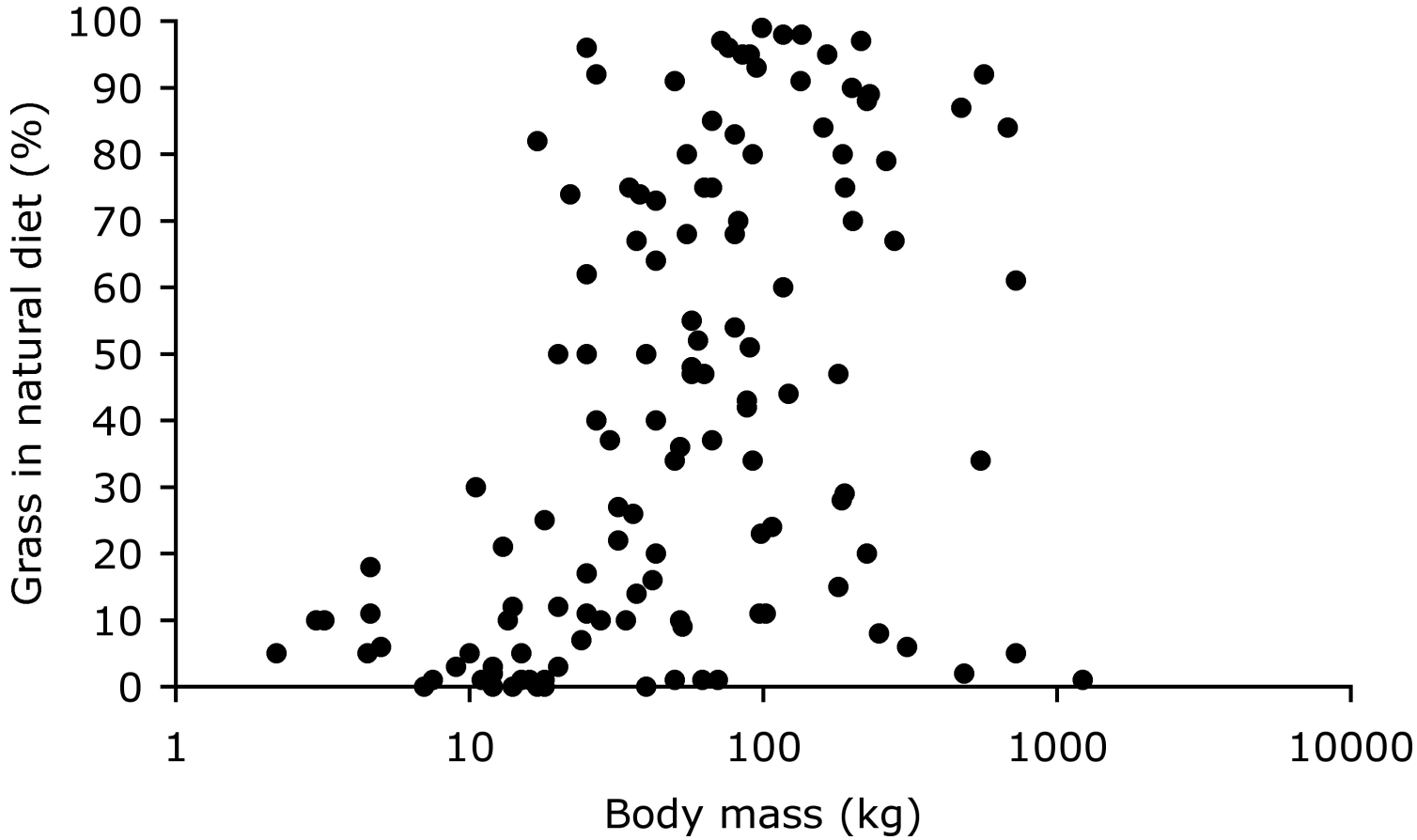
All morphological and physiological traits scale somehow with body mass.

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



Rules ?

- body mass does not explain everything



from Jäger (2010)

Allometries

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

Allometries

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

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

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

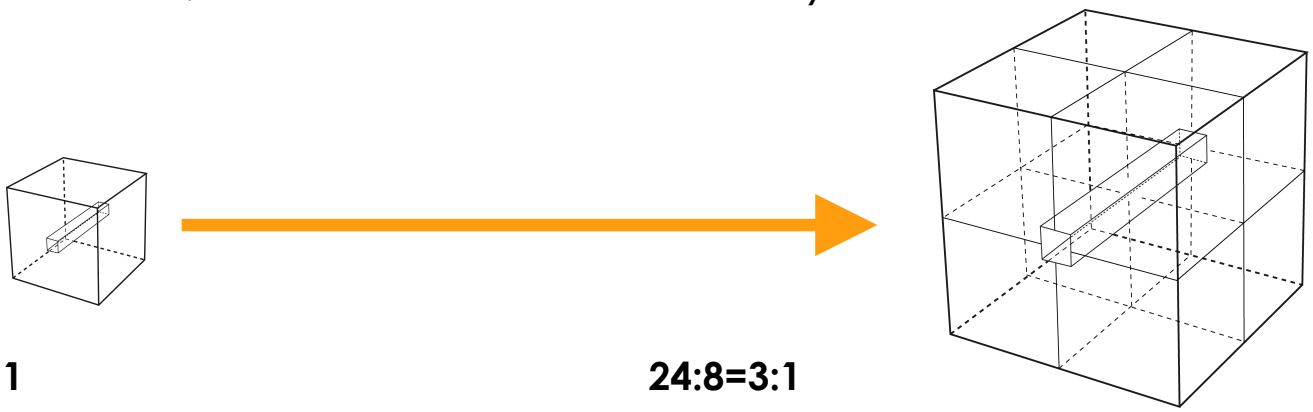
Allometries

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

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

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

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

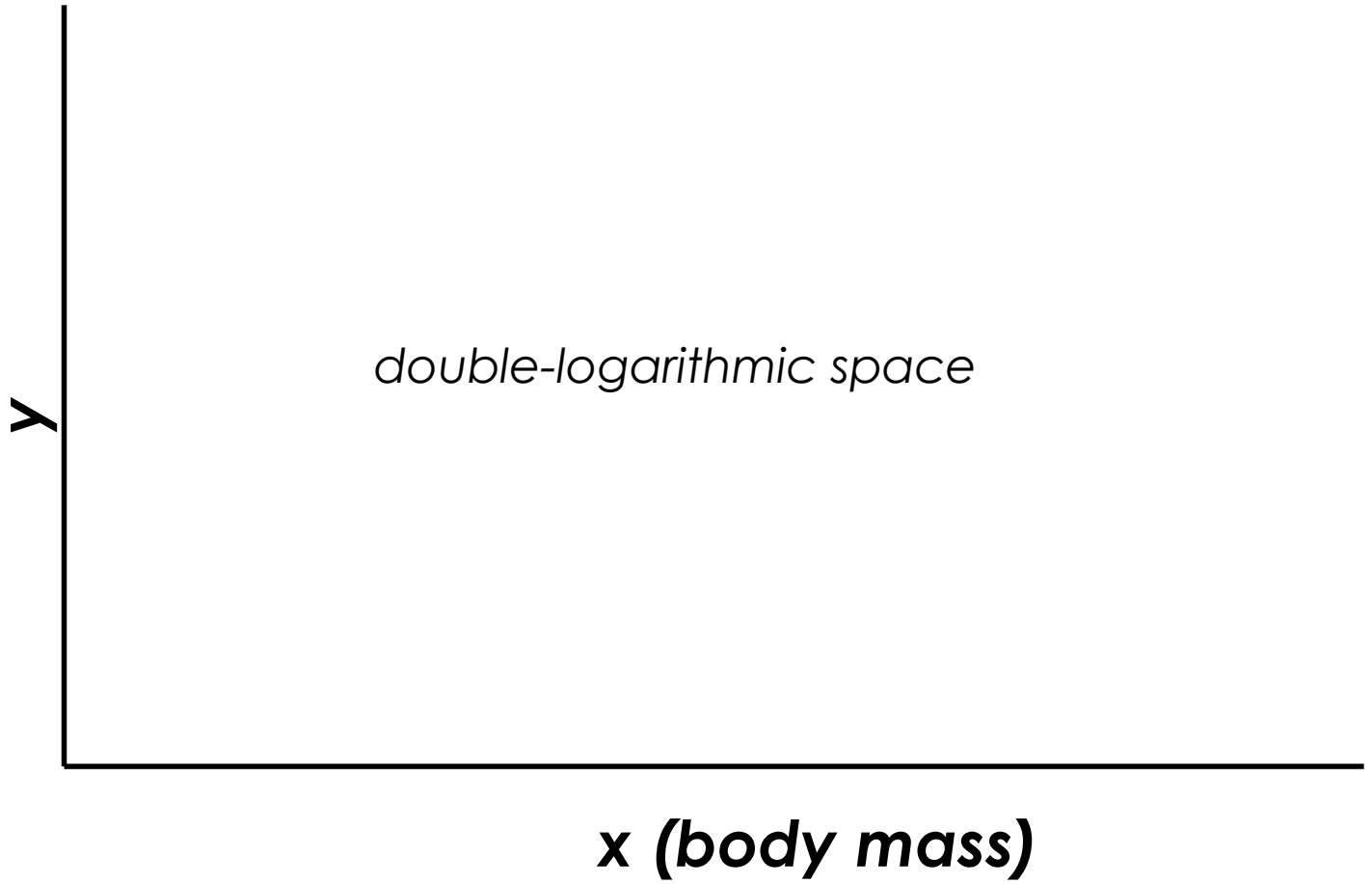


Allometries

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

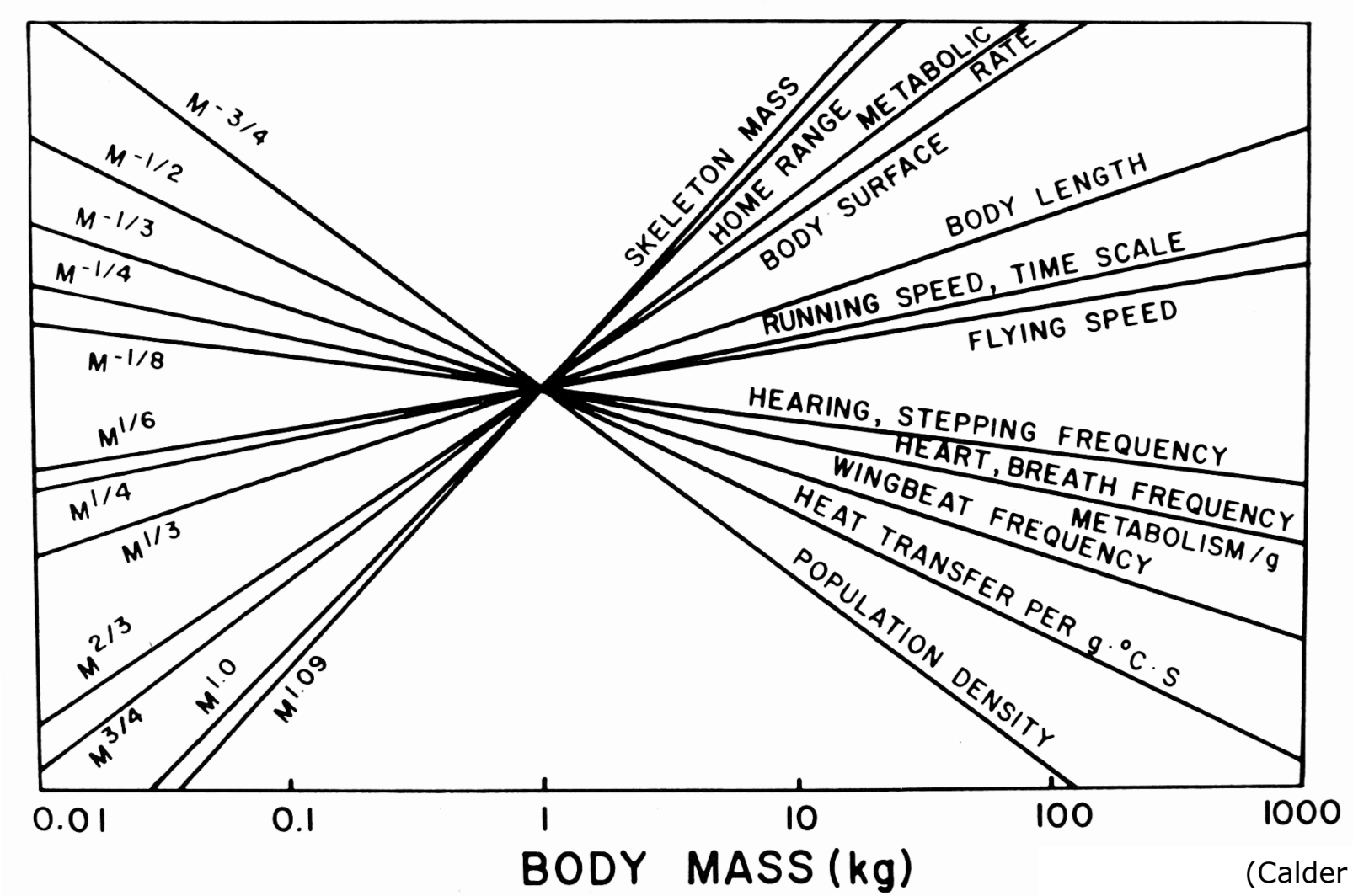
Allometries

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



Allometries

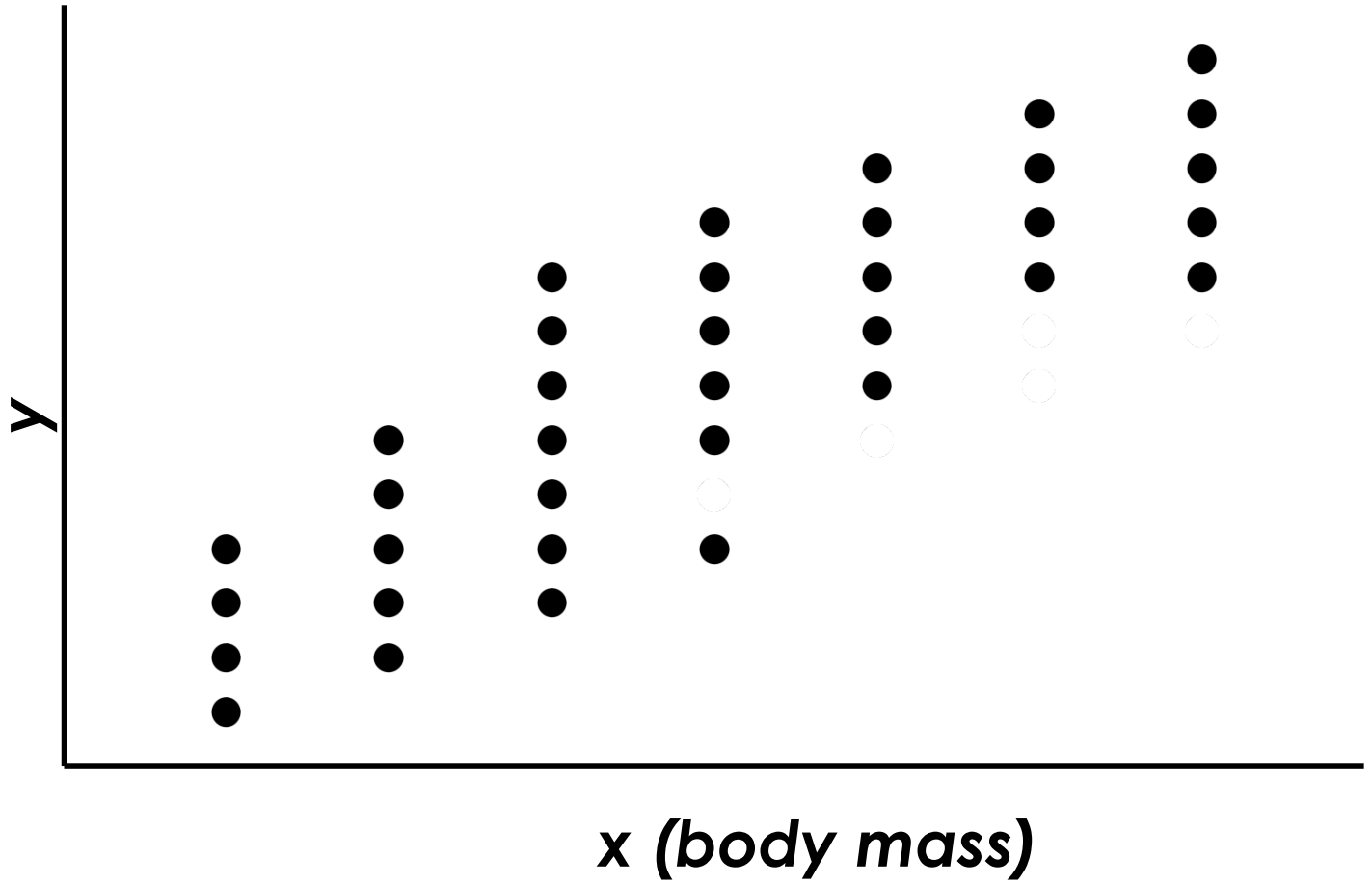
Morphological, physiological and life history variables scale with body mass.



(Calder 1983)

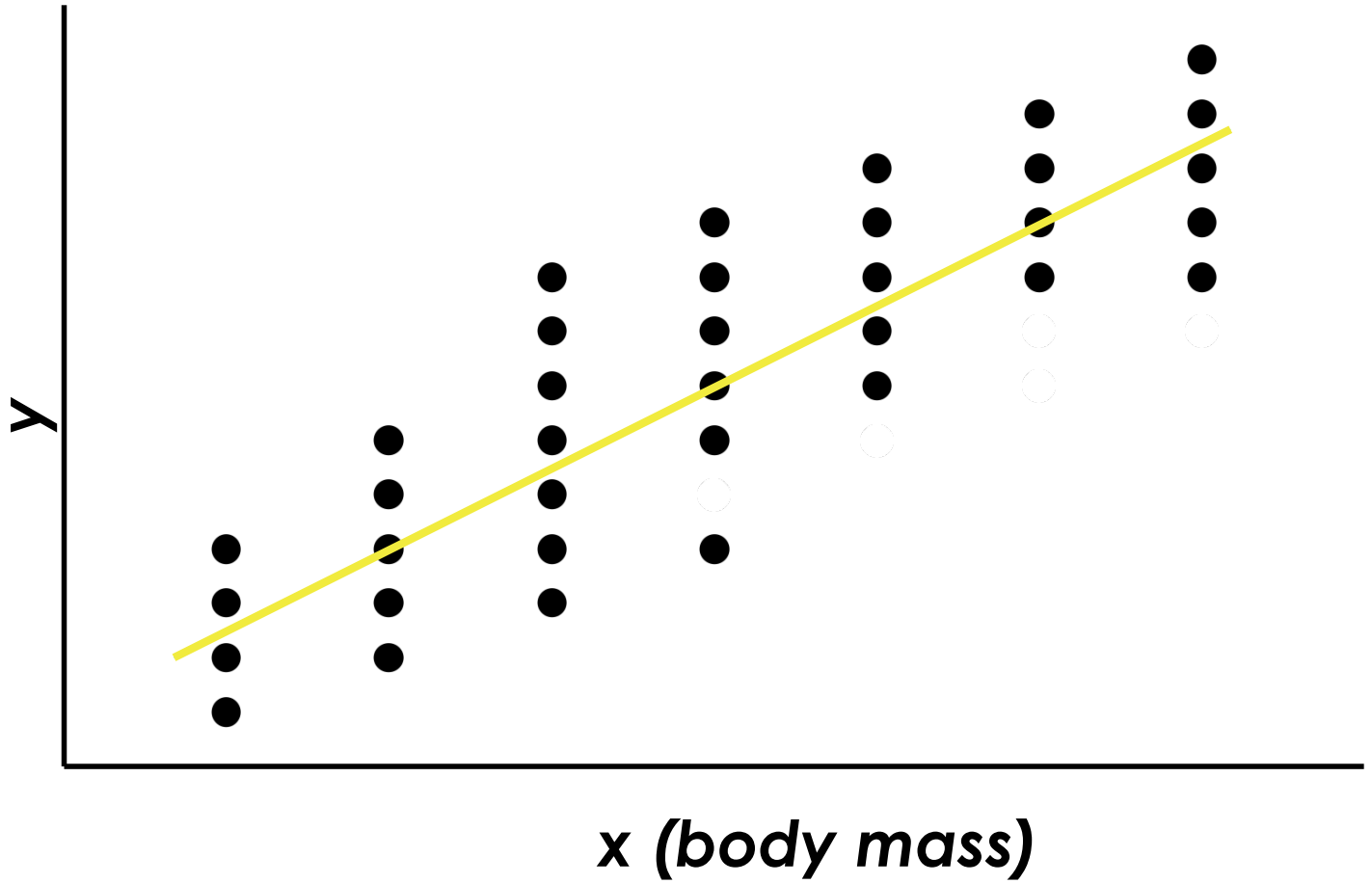
Interpreting allometries

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



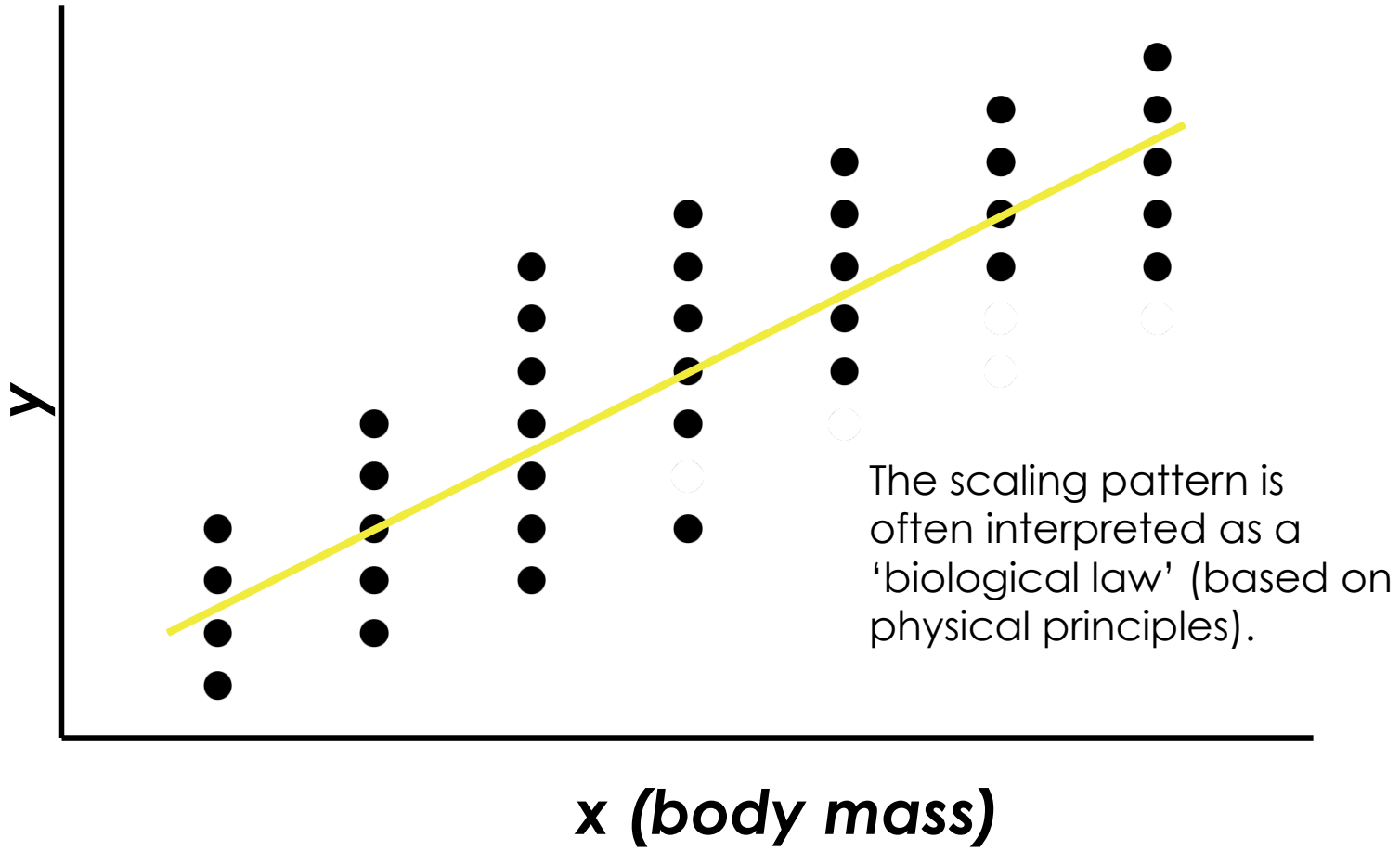
Interpreting allometries

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



Interpreting allometries

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



Using allometries

Using allometric relationships to extrapolate data for other species.

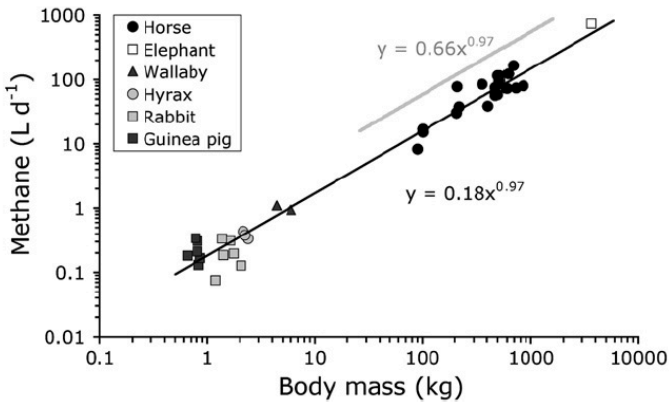
Using allometries

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



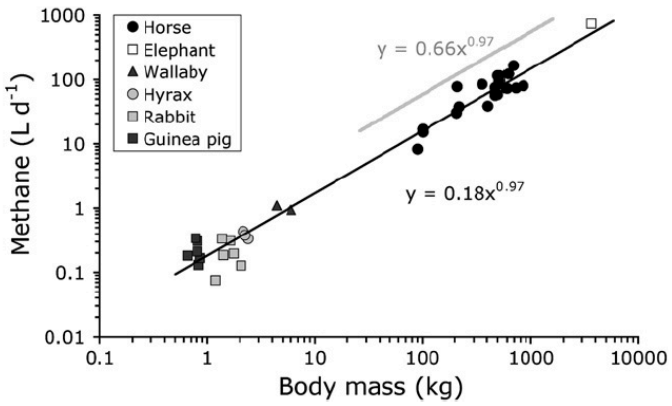
Using allometries

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]

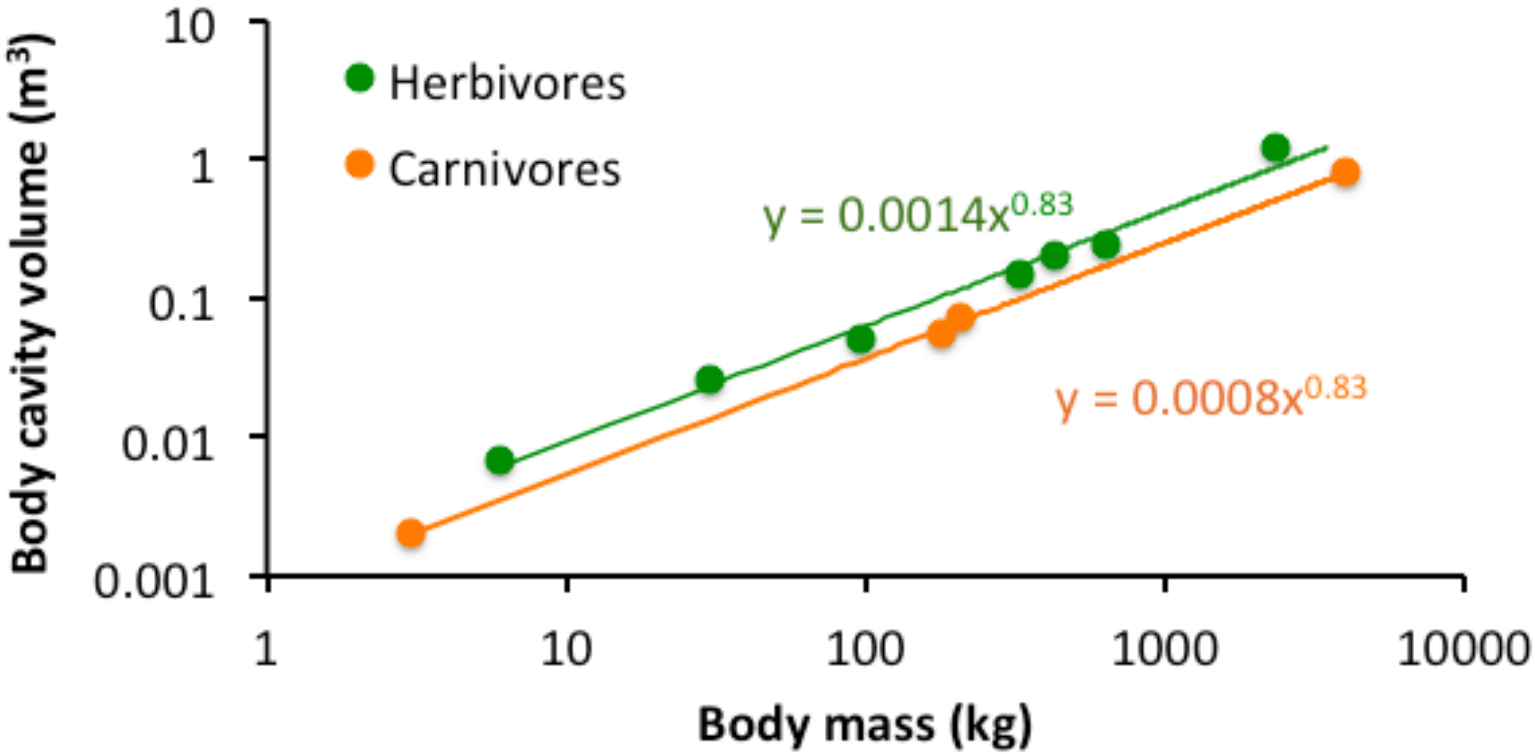
Current Biology Vol 22 No 9
R292

Using allometries

Using allometric relationships to compare different animal groups.

Using allometries

Using allometric relationships to compare different animal groups.



(work in progress)

Using allometries

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

Using allometries

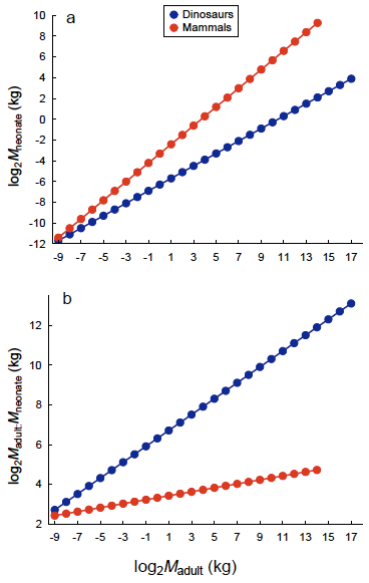
Differences in allometric relationships ***between animal groups*** can explain different ecological scenarios.

biology letters
Evolutionary biology

Biol. Lett. (2012) 8, 620–623
doi:10.1098/rsbl.2012.0240
Published online 18 April 2012

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]



Using allometries

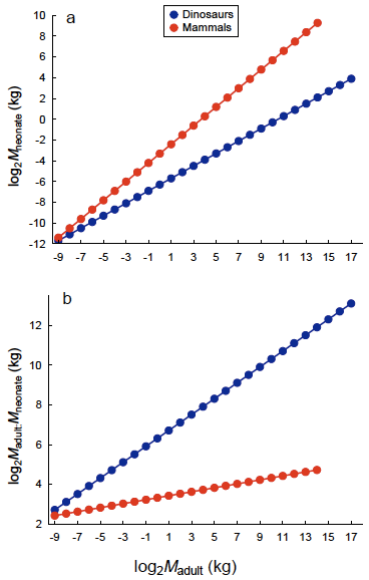
Differences in allometric relationships ***between animal groups*** can explain different ecological scenarios.

biology letters
Evolutionary biology

Biol. Lett. (2012) 8, 620–623
doi:10.1098/rsbl.2012.0240
Published online 18 April 2012

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]



Ecological modelling, size distributions and taphonomic size bias in dinosaur faunas: a comment on Codron *et al.* (2012)

Caleb Marshall Brown[1], Nicolás E. Campione[1], Henrique Corrêa Giacomini[1], Lorna J. O'Brien[1], Matthew J. Vavrek[2] and David C. Evans[1,2]

Ecological modelling, size distributions and taphonomic size bias in dinosaur faunas: reply to Brown *et al.*

Daryl Codron[1,2], Chris Carbone[3], Dennis W. H. Müller[1] and Marcus Clauss[1]

Allometry fallacies

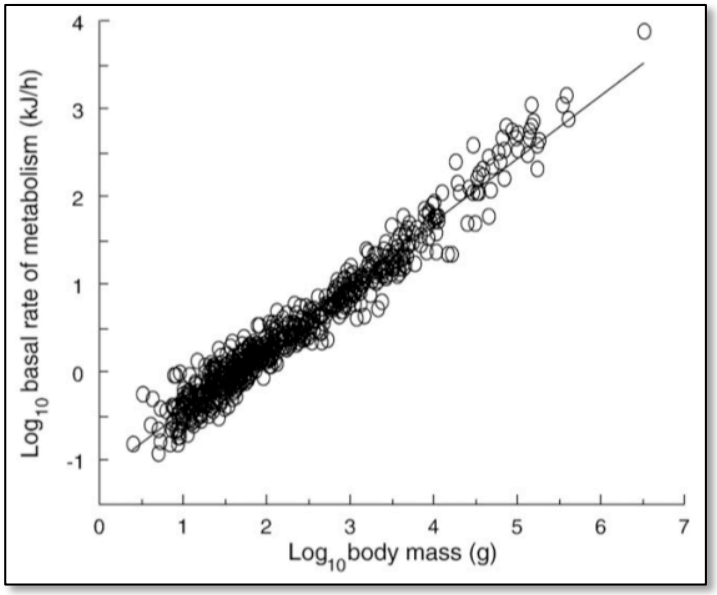
Using allometries: a call for caution

Using allometries: a call for caution

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

This can be expressed in three different ways:

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

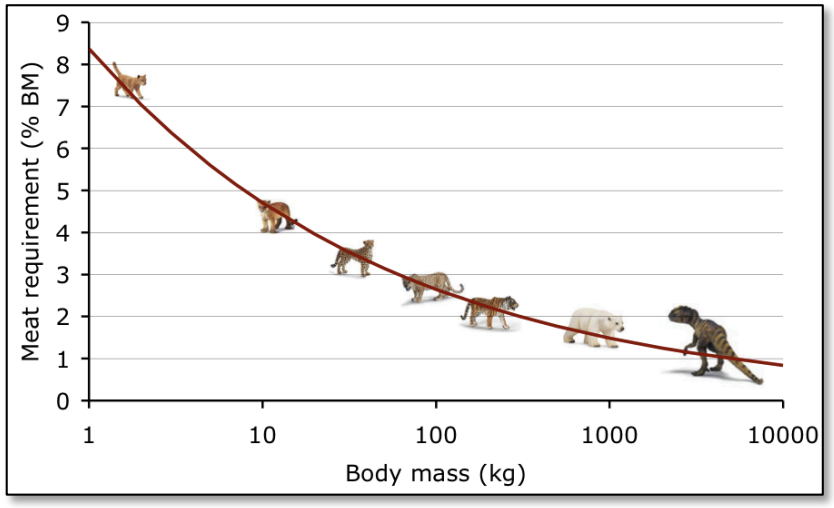


Using allometries: a call for caution

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

This can be expressed in three different ways:

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

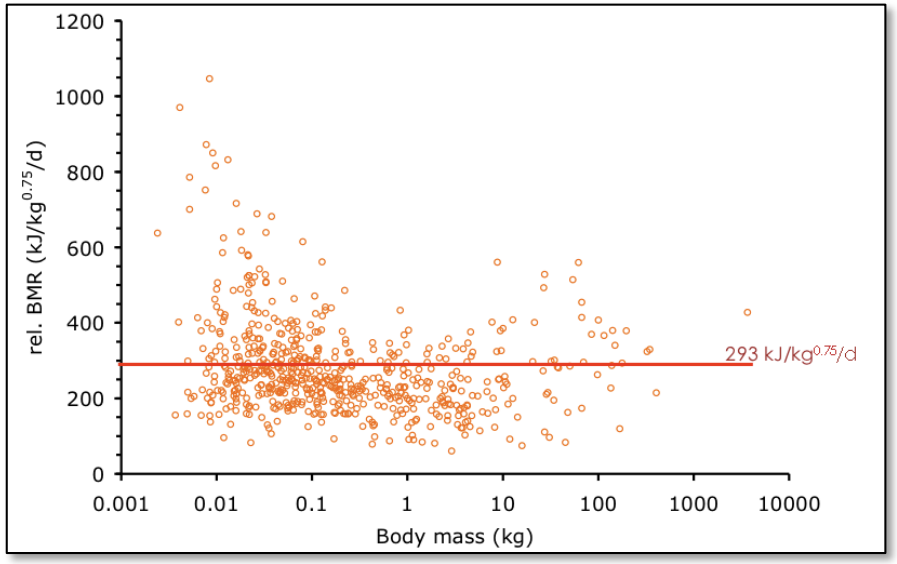


Using allometries: a call for caution

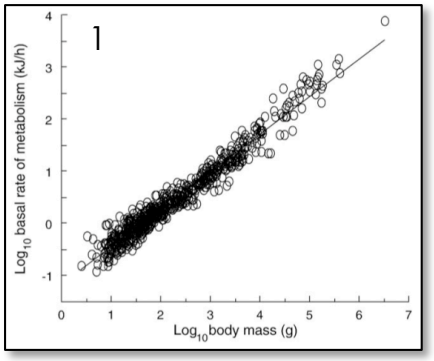
The probably most-often committed fallacy in ecophysiological manuscripts:
Metabolic rate = requirements
scale to $BM^{0.75}$

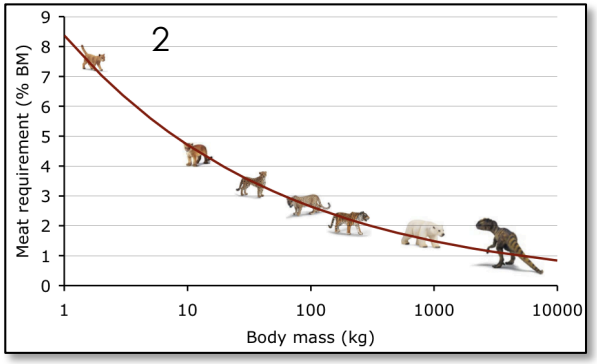
This can be expressed in three different ways:

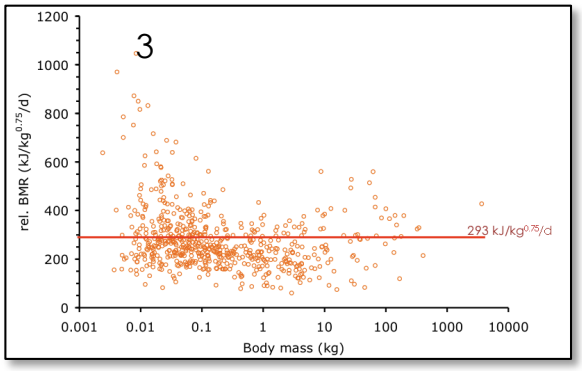
3. all animals have the same requirements (in joules per $kg^{0.75}$ (per day))



Using allometries: a call for caution







1. larger animals have higher absolute requirements (in joules (per day))
2. smaller animals have higher '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 !

Using allometries: a call for caution

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

e.g.
"Smaller animals have higher 'mass-specific' requirements" means nothing for diet quality if smaller animals also have higher 'mass-specific' food intake.

Only if the scalings of requirements and food intake differed could we postulate a consequence for diet quality.

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.

Using allometries: a call for caution

Metabolic allometry - the influence of the exponent

Mammals: $a\ BM^{0.75}$ Reptiles: $a/10\ BM^{?}$

Using allometries: a call for caution

Metabolic allometry - the influence of the exponent

Mammals: a $BM^{0.75}$

Reptiles BM$^{0.89}$

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

Reptiles BM$^{0.77}$

from Nagy et al. (1999)

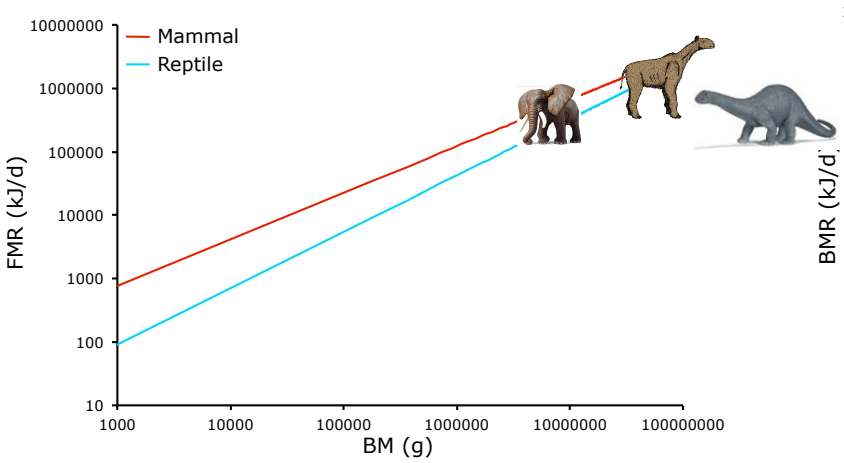
from Bennett & Dawson (1976)

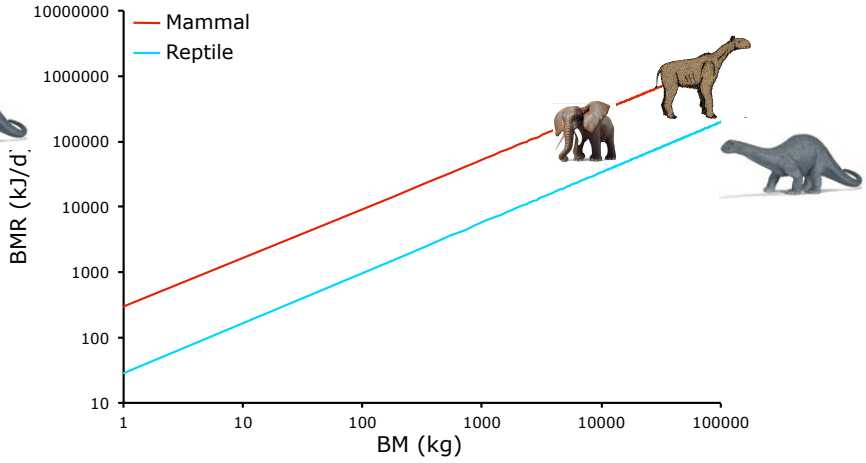
Using allometries: a call for caution

Metabolic allometry - the influence of the exponent

Mammals: a $BM^{0.75}$ Reptiles: a/10 $BM^{?}$

Reptiles $BM^{0.89}$ Reptiles $BM^{0.77}$





from Nagy et al. (1999)

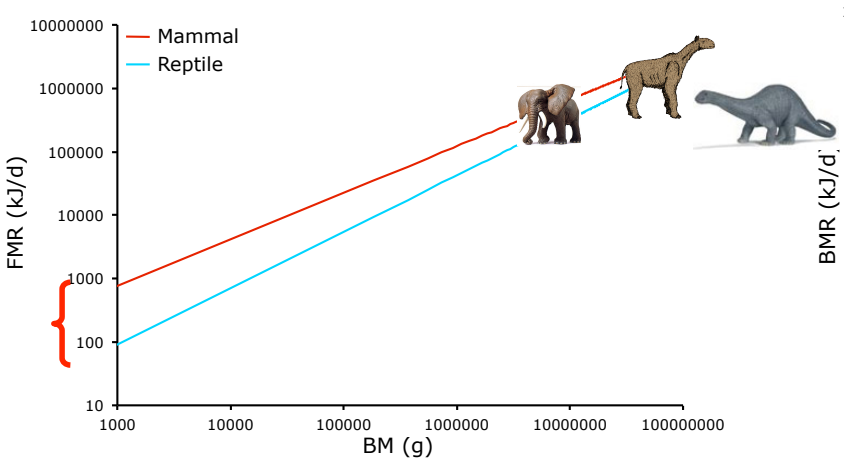
from Bennett & Dawson (1976)

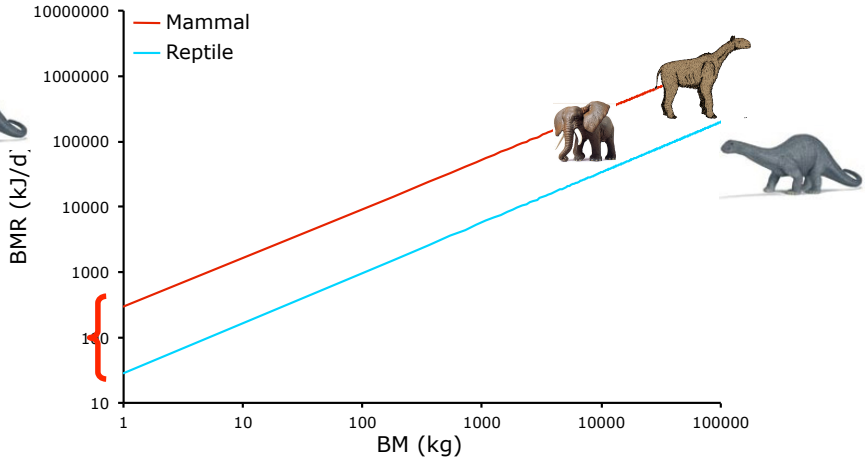
Using allometries: a call for caution

Metabolic allometry - the influence of the exponent

Mammals: a $BM^{0.75}$ Reptiles: a/10 $BM^{?}$

Reptiles $BM^{0.89}$ Reptiles $BM^{0.77}$





from Nagy et al. (1999)

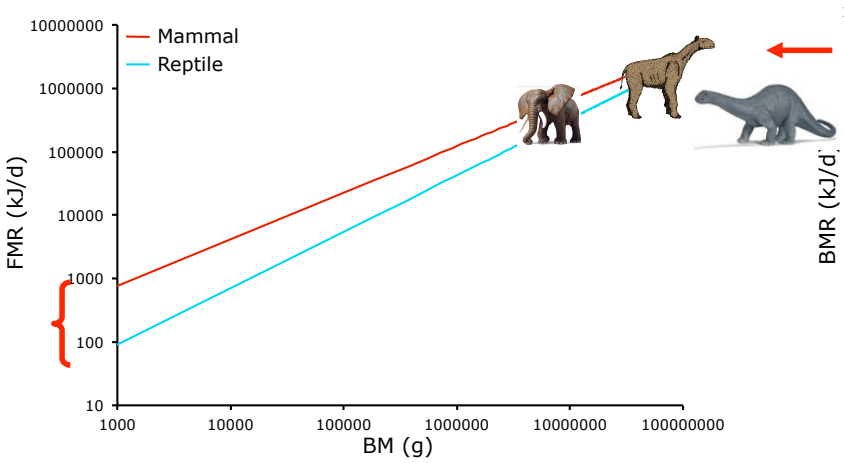
from Bennett & Dawson (1976)

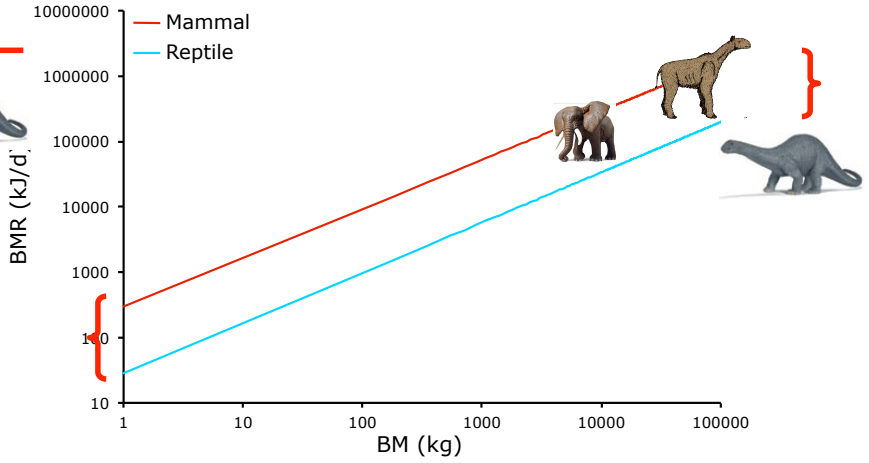
Using allometries: a call for caution

Metabolic allometry - the influence of the exponent

Mammals: a $BM^{0.75}$ Reptiles: a/10 $BM^{?}$

Reptiles $BM^{0.89}$ Reptiles $BM^{0.77}$



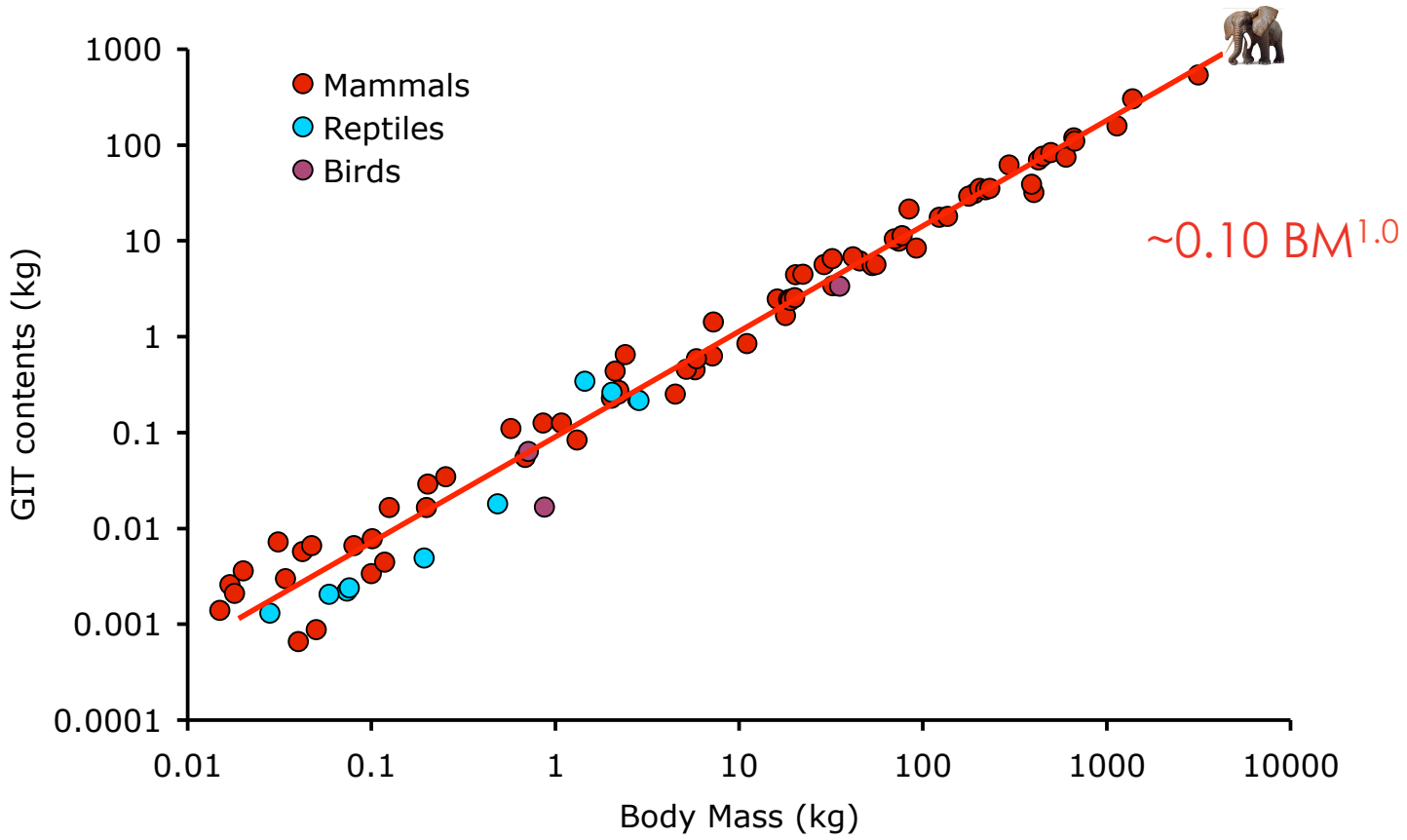


from Nagy et al. (1999)

from Bennett & Dawson (1976)

Using allometries: a call for caution

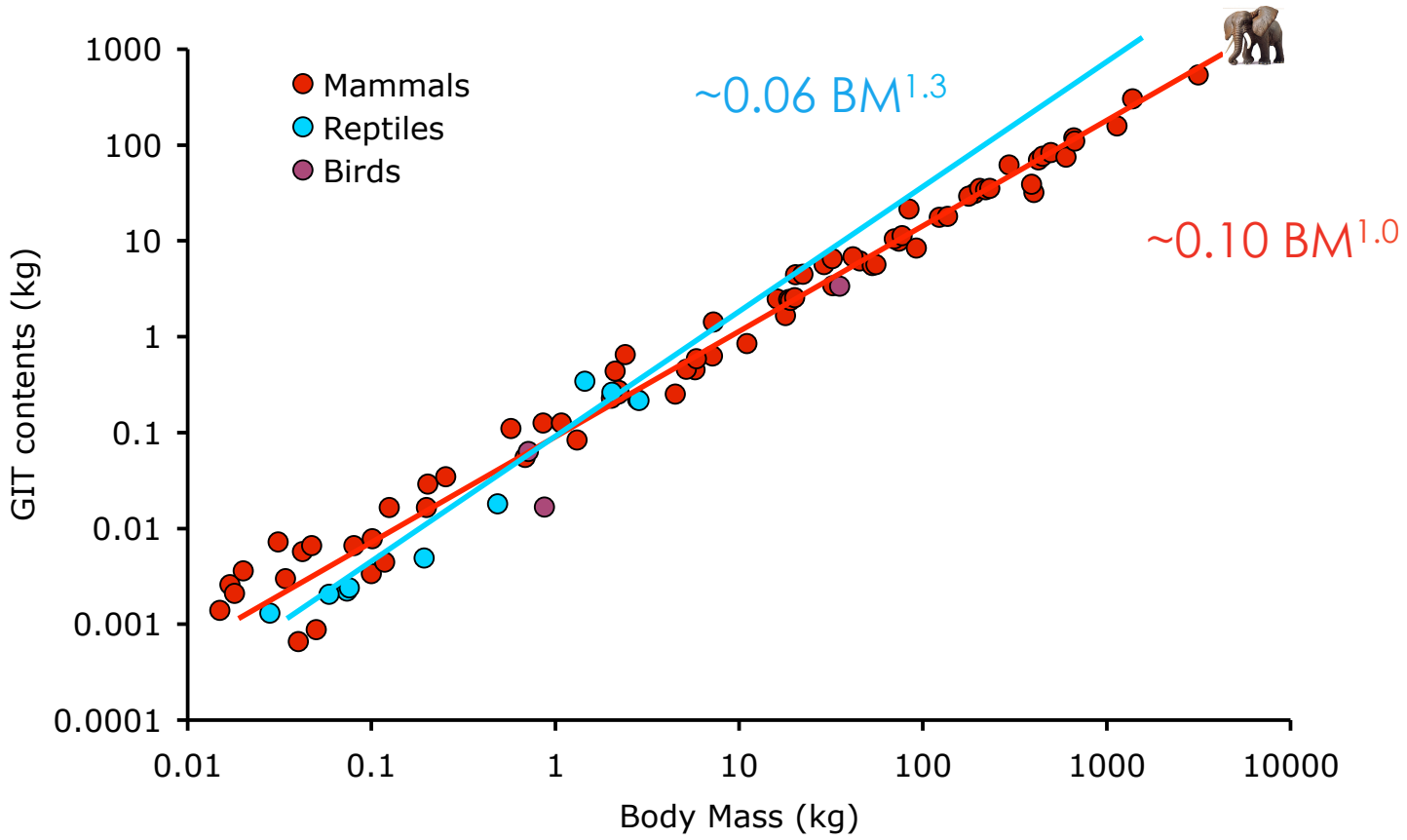
Gut capacity



from Franz et al. (2009)

Using allometries: a call for caution

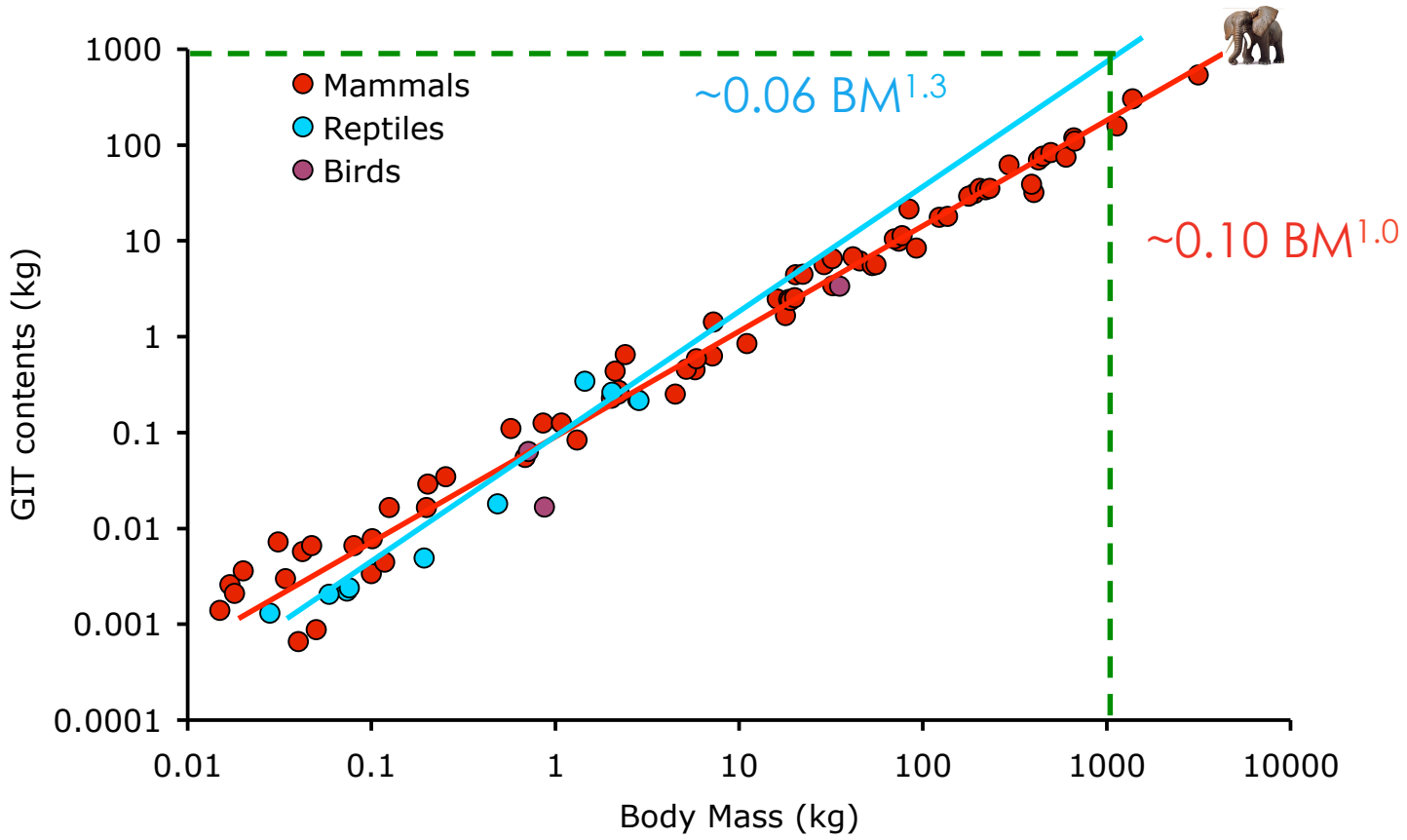
Gut capacity



from Franz et al. (2009)

Using allometries: a call for caution

Gut capacity



from Franz et al. (2009)

Using allometries: a call for caution

Functional Ecology

British Ecological Society

Functional Ecology 2013, **27**, 131–135

doi: 10.1111/1365-2435.12033

PERSPECTIVES

High C/N ratio (not low-energy content) of vegetation may have driven gigantism in sauropod dinosaurs and perhaps omnivory and/or endothermy in their juveniles

David M. Wilkinson*,[1] and Graeme D. Ruxton[2]

In addition, we use recently published allometric equations for herbivore nitrogen and carbon use to make tentative calculations which suggest that if Mesozoic C/N ratios were greater than extant ones, this would have selected for one of two strategies: gigantism in ectothermic herbivores or endothermy (and selective foraging on high N material) in very small herbivores.

Using allometries: a call for caution

Functional Ecology

British Ecological Society

Functional Ecology 2013, **27**, 131–135 doi: 10.1111/1365-2435.12033

PERSPECTIVES

High C/N ratio (not low-energy content) of vegetation may have driven gigantism in sauropod dinosaurs and perhaps omnivory and/or endothermy in their juveniles

David M. Wilkinson*,[1] and Graeme D. Ruxton[2]

Ecology Letters, (2008) **11**: 785–792 doi: 10.1111/j.1461-0248.2008.01180.x

LETTER

Stoichiometry of endothermy: shifting the quest from nitrogen to carbon

Marcel Klaassen[1,2]* and
Bart A. Nolet[1]

Using allometries: a call for caution

Ecology Letters, (2008) **11**: 785–792 doi: 10.1111/j.1461-0248.2008.01180.x

LETTER

Stoichiometry of endothermy: shifting the quest from nitrogen to carbon

Marcel Klaassen[1,2]* and
Bart A. Nolet[1]

Abstract

Reptiles

$MNR = 108\ M^{0.473}$ ($n = 3$, $R^2 = 0.837$)	Data and references in Appendix S1
$BMR = 27\ M^{0.77}$ ($n = 44$, $R^2 = 0.828$)	Bennett & Dawson (1976)*†
$FMR = 91\ M^{0.889}$ ($n = 55$, $R^2 = 0.945$)	Nagy (2005)
$MNR : BMR = 4.00\ M^{-0.297}$	
$MNR : FMR = 1.19\ M^{-0.416}$	

Eutherian mammals

$MNR = 411\ M^{0.863}$ ($n = 11$, $R^2 = 0.980$)	Data and references in Appendix S1
$BMR = 241\ M^{0.705}$ ($n = 625$, $R^2 = 0.952$)	Duncan *et al.* (2007)
$FMR = 872\ M^{0.772}$ ($n = 58$, $R^2 = 0.959$)	Nagy *et al.* (1999)
$MNR : BMR = 1.71\ M^{0.158}$	
$MNR : FMR = 0.47\ M^{0.091}$	

Using allometries: a call for caution

Ecology Letters, (2008) **11**: 785–792 doi: 10.1111/j.1461-0248.2008.01180.x

LETTER

Stoichiometry of endothermy: shifting the quest from nitrogen to carbon

Marcel Klaassen[1,2]* and
Bart A. Nolet[1]

Abstract

Reptiles

$MNR = 108\ M^{0.473}$ ($n = 3$, $R^2 = 0.837$)	Data and references in Appendix S1
$BMR = 27\ M^{0.77}$ ($n = 44$, $R^2 = 0.828$)	Bennett & Dawson (1976)*†
$FMR = 91\ M^{0.889}$ ($n = 55$, $R^2 = 0.945$)	Nagy (2005)
$MNR : BMR = 4.00\ M^{-0.297}$	
$MNR : FMR = 1.19\ M^{-0.416}$	

Eutherian mammals

$MNR = 411\ M^{0.863}$ ($n = 11$, $R^2 = 0.980$)	Data and references in Appendix S1
$BMR = 241\ M^{0.705}$ ($n = 625$, $R^2 = 0.952$)	Duncan *et al.* (2007)
$FMR = 872\ M^{0.772}$ ($n = 58$, $R^2 = 0.959$)	Nagy *et al.* (1999)
$MNR : BMR = 1.71\ M^{0.158}$	
$MNR : FMR = 0.47\ M^{0.091}$	

Using allometries: a call for caution

Reptiles

$MNR = 108\ M^{0.47}$

$FMR = 91\ M^{0.89}$

$MNR/FMR = 1.19\ M^{-0.42}$

Mammals

$MNR = 411\ M^{0.86}$

$FMR = 872\ M^{0.77}$

$MNR/FMR = 0.47\ M^{0.09}$

Conclusion:
Difference in C:N ratio in plants favours different body sizes in ecto- / endo-therms

Using allometries: a call for caution

Reptiles
$MNR = 108\ M^{0.47}$
$FMR = 91\ M^{0.89}$
$MNR/FMR = 1.19\ M^{-0.42}$

Mammals
$MNR = 411\ M^{0.86}$
$FMR = 872\ M^{0.77}$
$MNR/FMR = 0.47\ M^{0.09}$

Conclusion:
Difference in C:N ratio in plants favours different body sizes in ecto- / endo-therms

The underlying Null hypothesis is that there are no differences in the exponents!

Using allometries: a call for caution

Reptiles

$MNR = 108\ M^{0.47}$

$FMR = 91\ M^{0.89}$

$MNR/FMR = 1.19\ M^{-0.42}$

Mammals

$MNR = 411\ M^{0.86}$

$FMR = 872\ M^{0.77}$

$MNR/FMR = 0.47\ M^{0.09}$

Conclusion:
Difference in C:N ratio in plants favours different body sizes in ecto- / endo-therms

The underlying Null hypothesis is that there are no differences in the exponents!

Using allometries: a call for caution

Reptiles

$MNR = 108\ M^{0.47}$

$FMR = 91\ M^{0.89}$

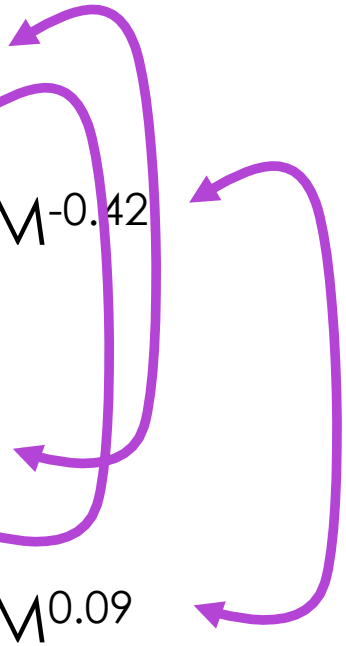
$MNR/FMR = 1.19\ M^{-0.42}$

Mammals

$MNR = 411\ M^{0.86}$

$FMR = 872\ M^{0.77}$

$MNR/FMR = 0.47\ M^{0.09}$



The underlying Null hypothesis is that there are no differences in the exponents!

Conclusion:
Difference in C:N ratio in plants favours different body sizes in ecto- / endo-therms

Using allometries: a call for caution

Reptiles
$MNR = 108\ M^{0.47}$
$FMR = 91\ M^{0.89}$
$MNR/FMR = 1.19\ M^{-0.42}$

Mammals
$MNR = 411\ M^{0.86}$
$FMR = 872\ M^{0.77}$
$MNR/FMR = 0.47\ M^{0.09}$

Conclusion:
Difference in C:N ratio in plants favours different body sizes in ecto- / endo-therms

The fundmental physiological difference (less N than energy with increasing M in reptiles, opposite in mammals) would require a very convincing explanation!

Using allometries: a call for caution

Reptiles	95%CI of exponents:
$MNR = 108\ M^{0.47}$	-2.179 to 3.126 ***(n.s.!)***
$FMR = 91\ M^{0.89}$	0.830 to 0.948
$MNR/FMR = 1.19\ M^{-0.42}$	
Mammals	
$MNR = 411\ M^{0.86}$	0.769 to 0.956
$FMR = 872\ M^{0.77}$	0.730 to 0.815
$MNR/FMR = 0.47\ M^{0.09}$	

Conclusion:
Difference in C:N ratio in plants favours different body sizes in ecto- / endo-therms

Using allometries: a call for caution

Reptiles
$MNR = 108\ M^{0.47}$
$FMR = 91\ M^{0.89}$
$MNR/FMR = 1.19\ M^{-0.42}$

95%CI of exponents:
-2.179 to 3.126 ***(n.s.!)***
0.830 to 0.948

no difference!

Mammals
$MNR = 411\ M^{0.86}$
$FMR = 872\ M^{0.77}$
$MNR/FMR = 0.47\ M^{0.09}$

0.769 to 0.956
0.730 to 0.815

Conclusion:
Difference in C:N ratio in plants favours different body sizes in ecto- / endo-therms

Using allometries: a call for caution

Reptiles
$MNR = 108\ M^{0.47}$
$FMR = 91\ M^{0.89}$
$MNR/FMR = 1.19\ M^{-0.42}$

95%CI of exponents:
-2.179 to 3.126 ***(n.s.!)***
0.830 to 0.948

no difference!

Mammals
$MNR = 411\ M^{0.86}$
$FMR = 872\ M^{0.77}$
$MNR/FMR = 0.47\ M^{0.09}$

0.769 to 0.956
0.730 to 0.815

Conclusion:
Difference in C:N ratio in plants favours different body sizes in ecto- / endo-therms

Using allometries: a call for caution

Reptiles
$MNR = 108\ M^{0.47}$
$FMR = 91\ M^{0.89}$
$MNR/FMR = 1.19\ M^{-0.42}$

95%CI of exponents:
-2.179 to 3.126 ***(n.s.!)***
0.830 to 0.948

Difference, but note the phylogenetic composition of the reptile dataset!

Mammals
$MNR = 411\ M^{0.86}$
$FMR = 872\ M^{0.77}$
$MNR/FMR = 0.47\ M^{0.09}$

0.769 to 0.956
0.730 to 0.815

Conclusion:
Difference in C:N ratio in plants favours different body sizes in ecto- / endo-therms

Using allometries: a call for caution

Reptiles
$MNR = 108\ M^{0.47}$
$FMR = 91\ M^{0.89}$
$MNR/FMR = 1.19\ M^{-0.42}$

95%CI of slopes:
-2.179 to 3.126 ***(n.s.!)***
0.830 to 0.948

Mammals
$MNR = 411\ M^{0.86}$
$FMR = 872\ M^{0.77}$
$MNR/FMR = 0.47\ M^{0.09}$

0.769 to 0.956
0.730 to 0.815

Conclusion:
Difference in C:N ratio in plants favours different body sizes in ecto- / endo-therms

Conclusion:
Difference in C:N ratio in plants has no body size effect in ecto- / endo-therms

Using allometries: a call for caution

Reptiles	95%CI of slopes:
$MNR = 108\ M^{0.47}$	-2.179 to 3.126 ***(n.s.!)***
$FMR = 91\ M^{0.89}$	0.830 to 0.948
$MNR/FMR = 1.19\ M^{-0.42}$	
Mammals	
$MNR = 411\ M^{0.86}$	0.769 to 0.956
$FMR = 872\ M^{0.77}$	0.730 to 0.815
$MNR/FMR = 0.47\ M^{0.09}$	
Conclusion: Difference in C:N ratio in plants favours different body sizes in ecto- / endo-therms	***Conclusion: (… and maybe not work with such data at all in the first place)***

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.

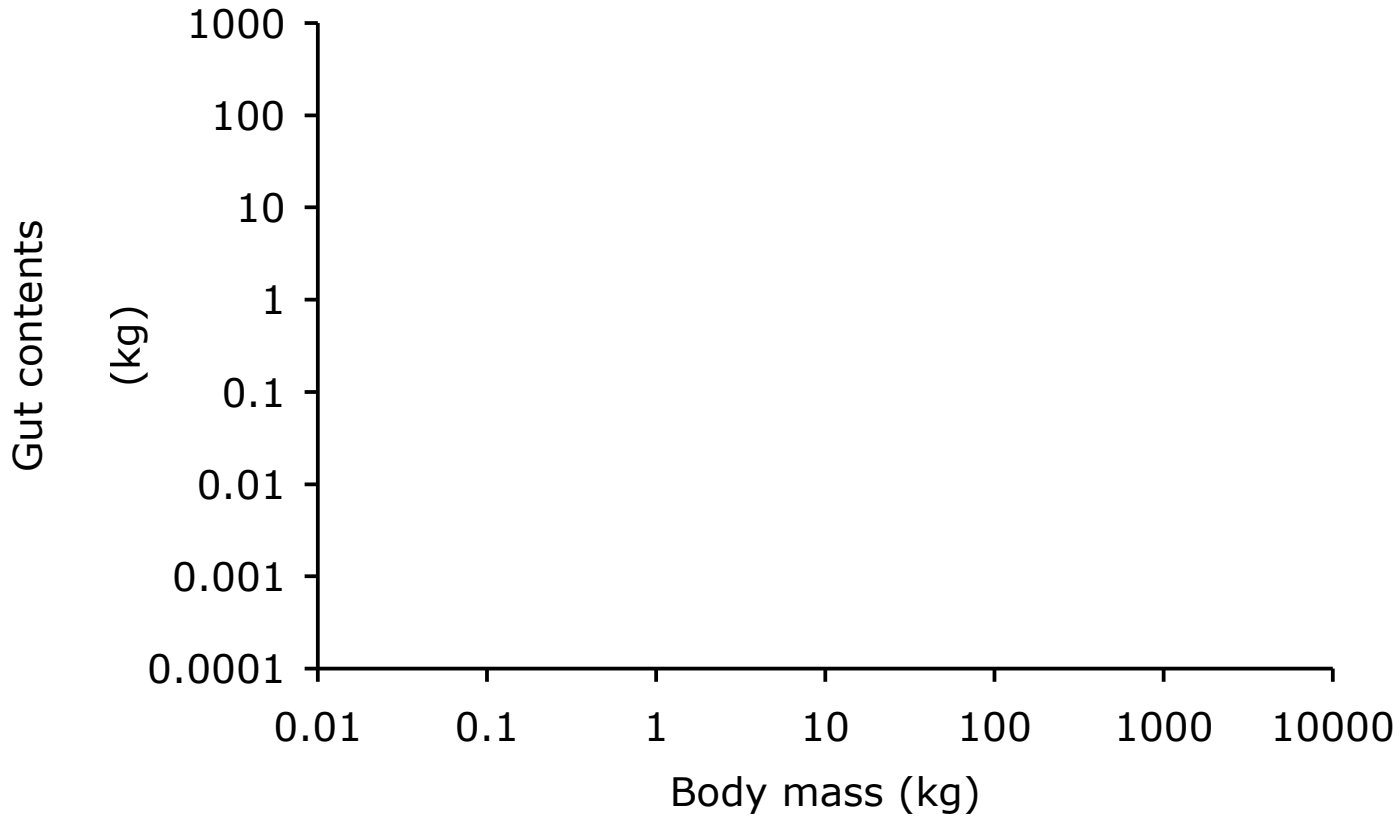
Using allometries

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)

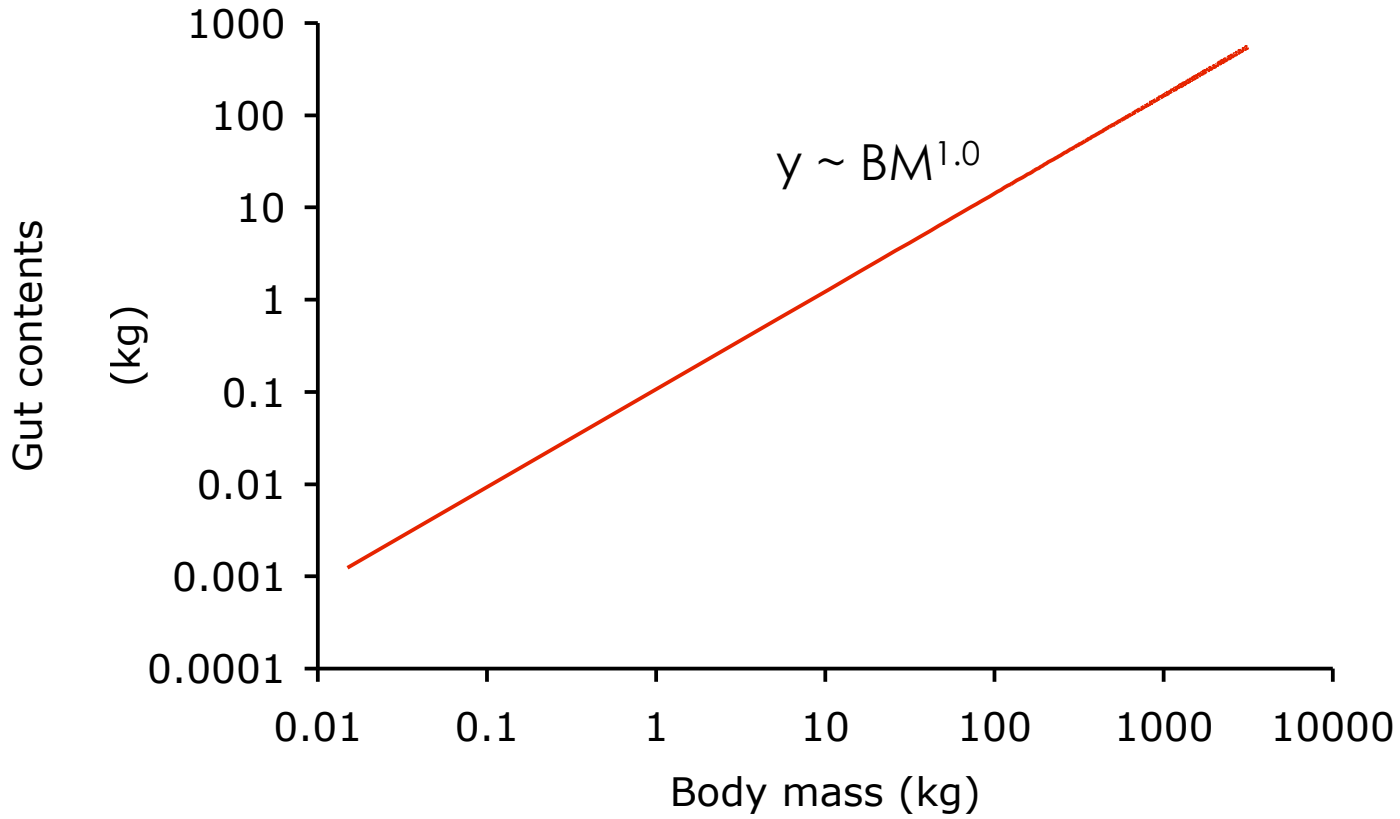
General allometric considerations



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

General allometric considerations

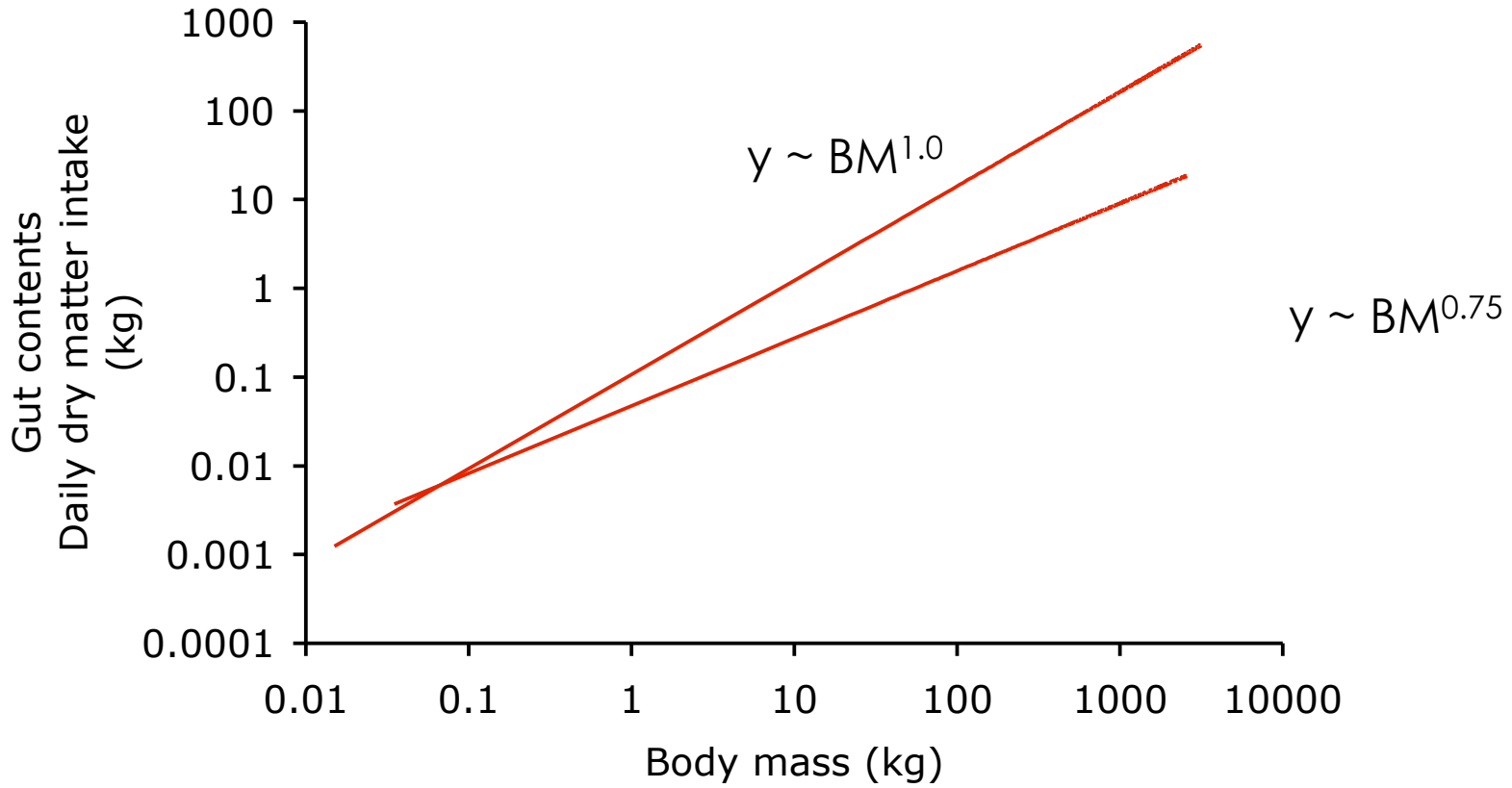
Gut capacity (measured as gut contents) scales linearly with body mass.



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

General allometric considerations

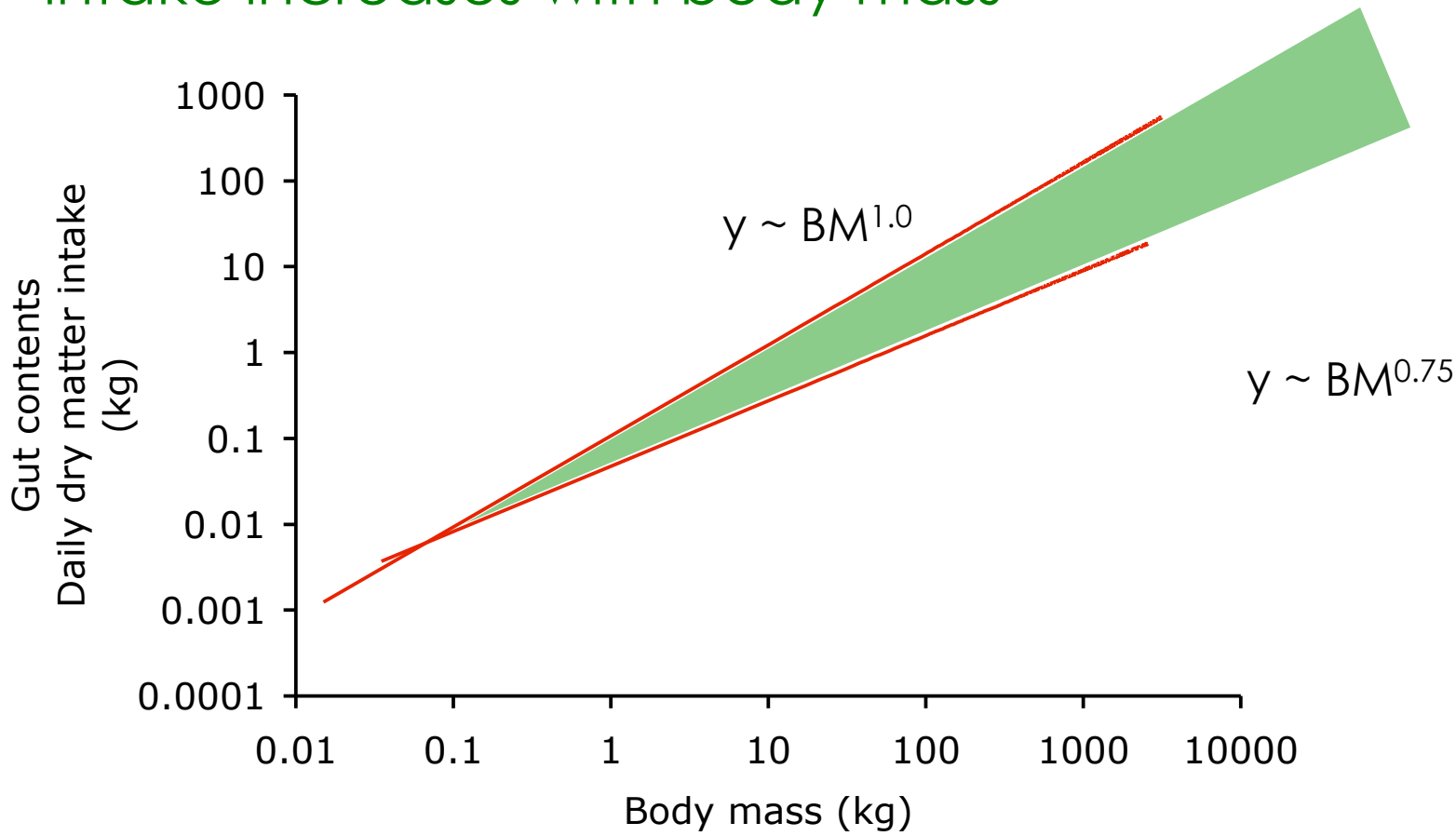
Food intake (relating to energy requirements) scales to metabolic body mass (body mass$^{0.75}$)



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

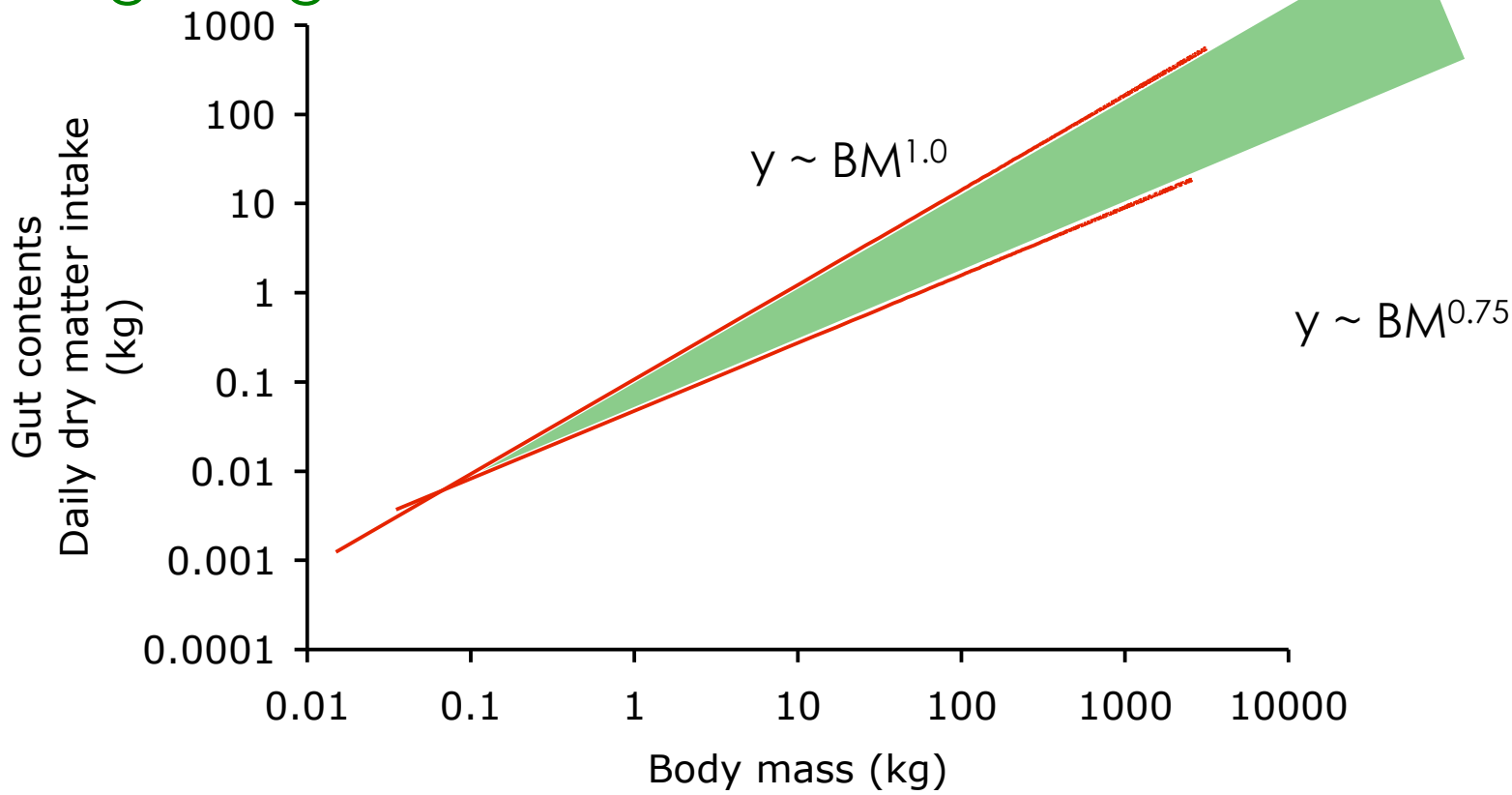


from Parra (1978), Demment & Van Soest (1985), Illius & Gordon (1992); McNab (2002)

General allometric considerations

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

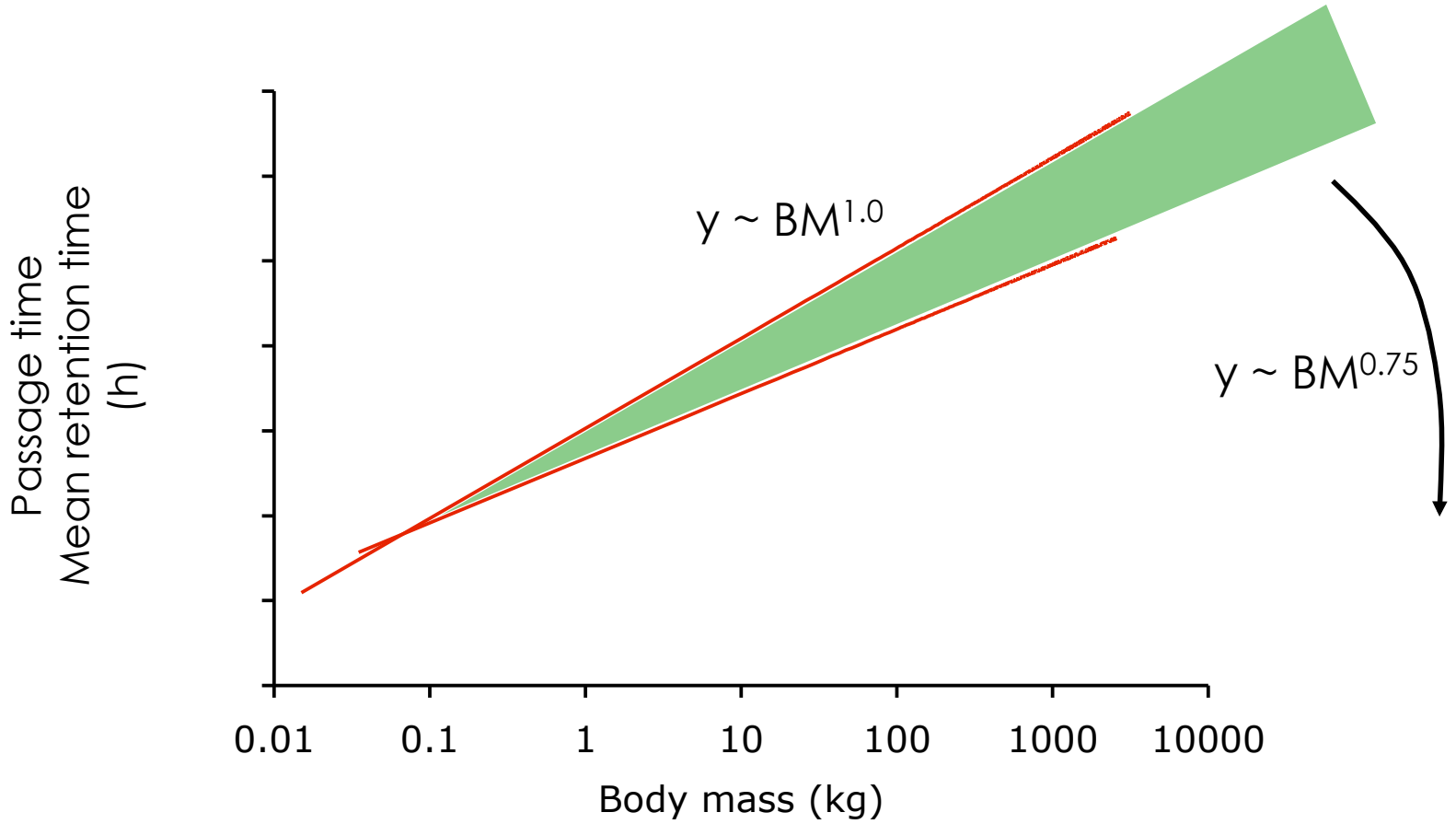
=> longer digesta retention



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

General allometric considerations

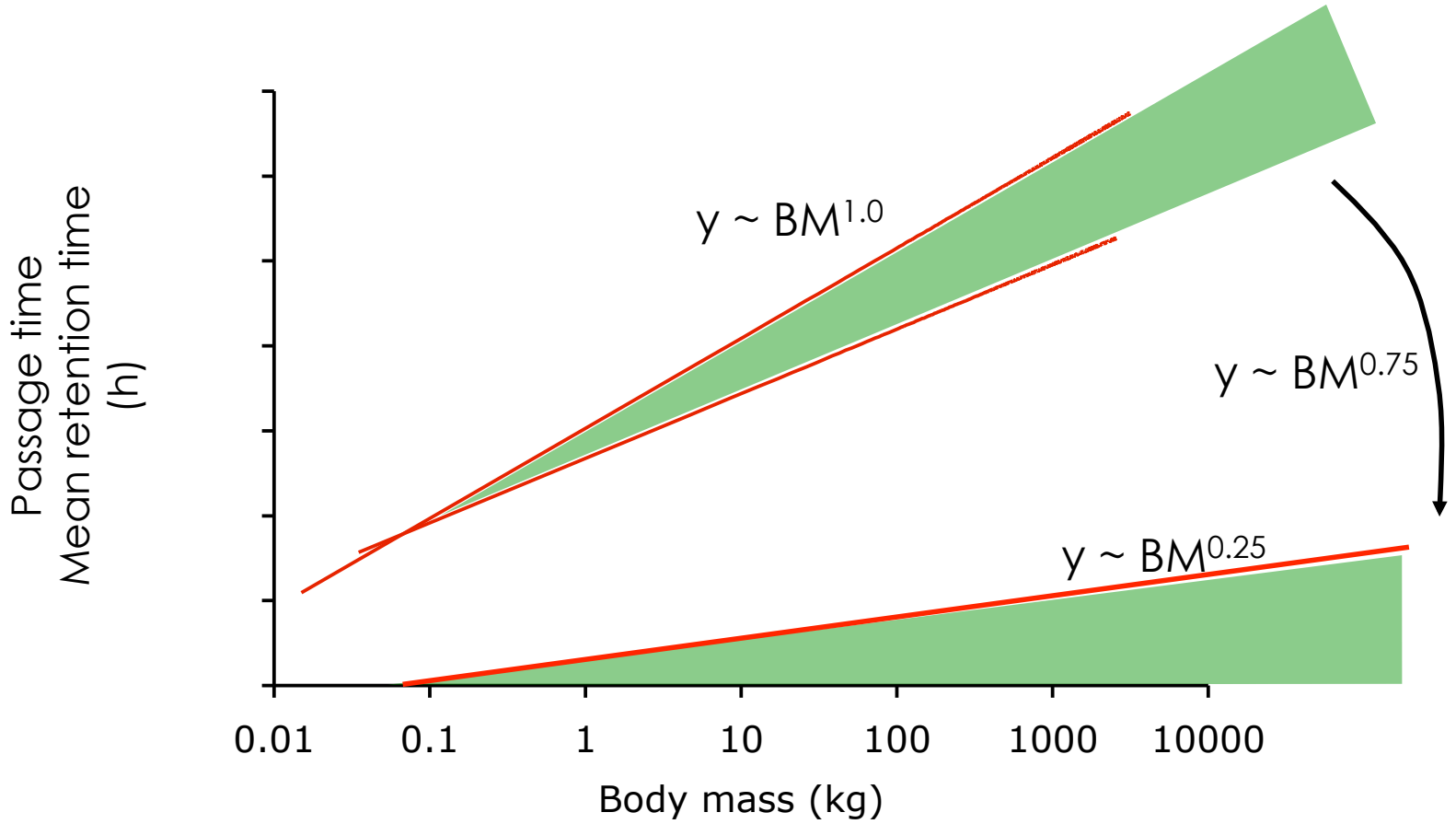
Digesta retention scales to body mass ...



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

General allometric considerations

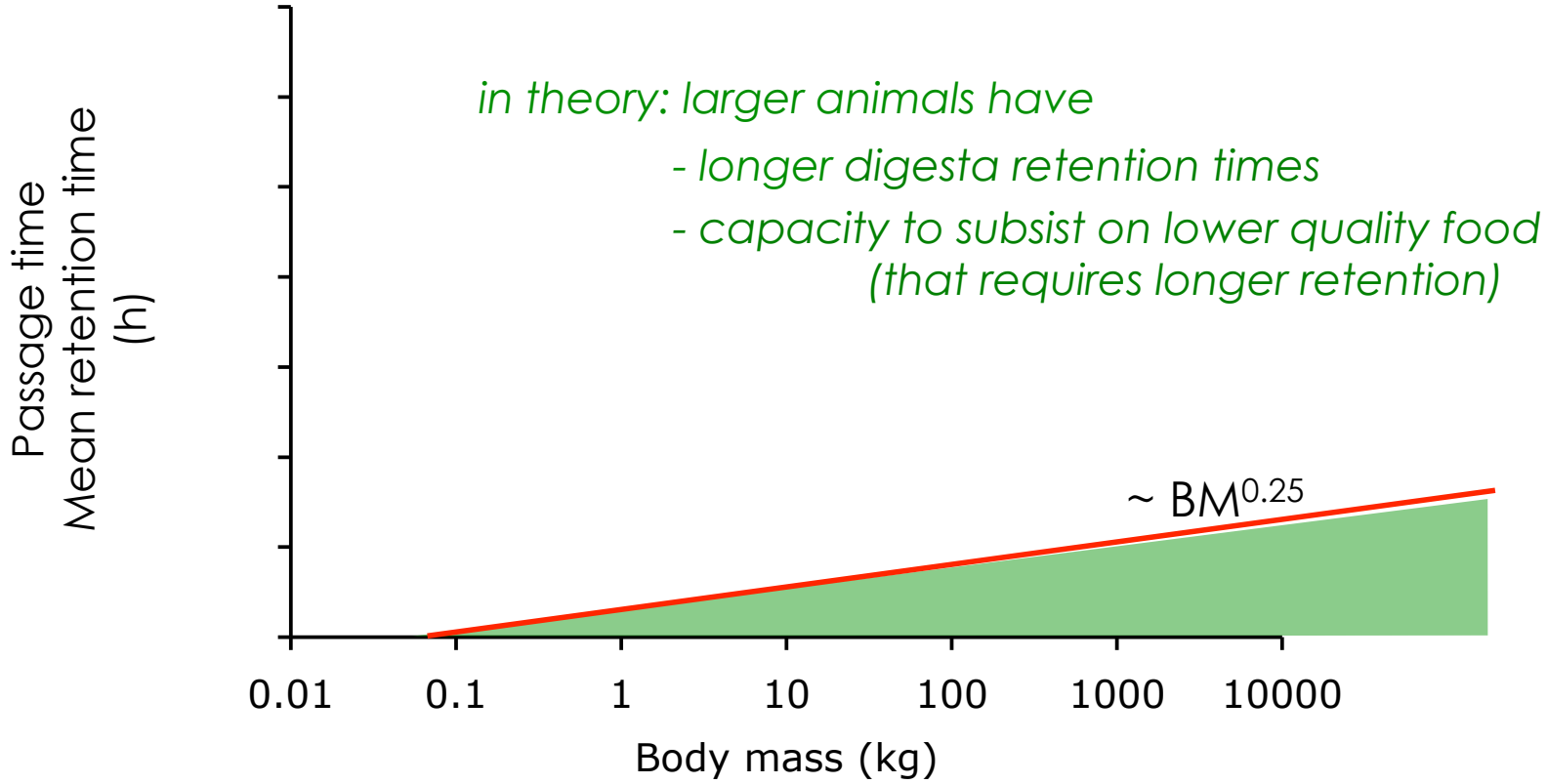
... to the power of 0.25



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)

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)

Do you believe it ?

Checking the validity of a concept

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

(vary sequence to suit your preference or intellectual capacity)

Checking the validity of a concept

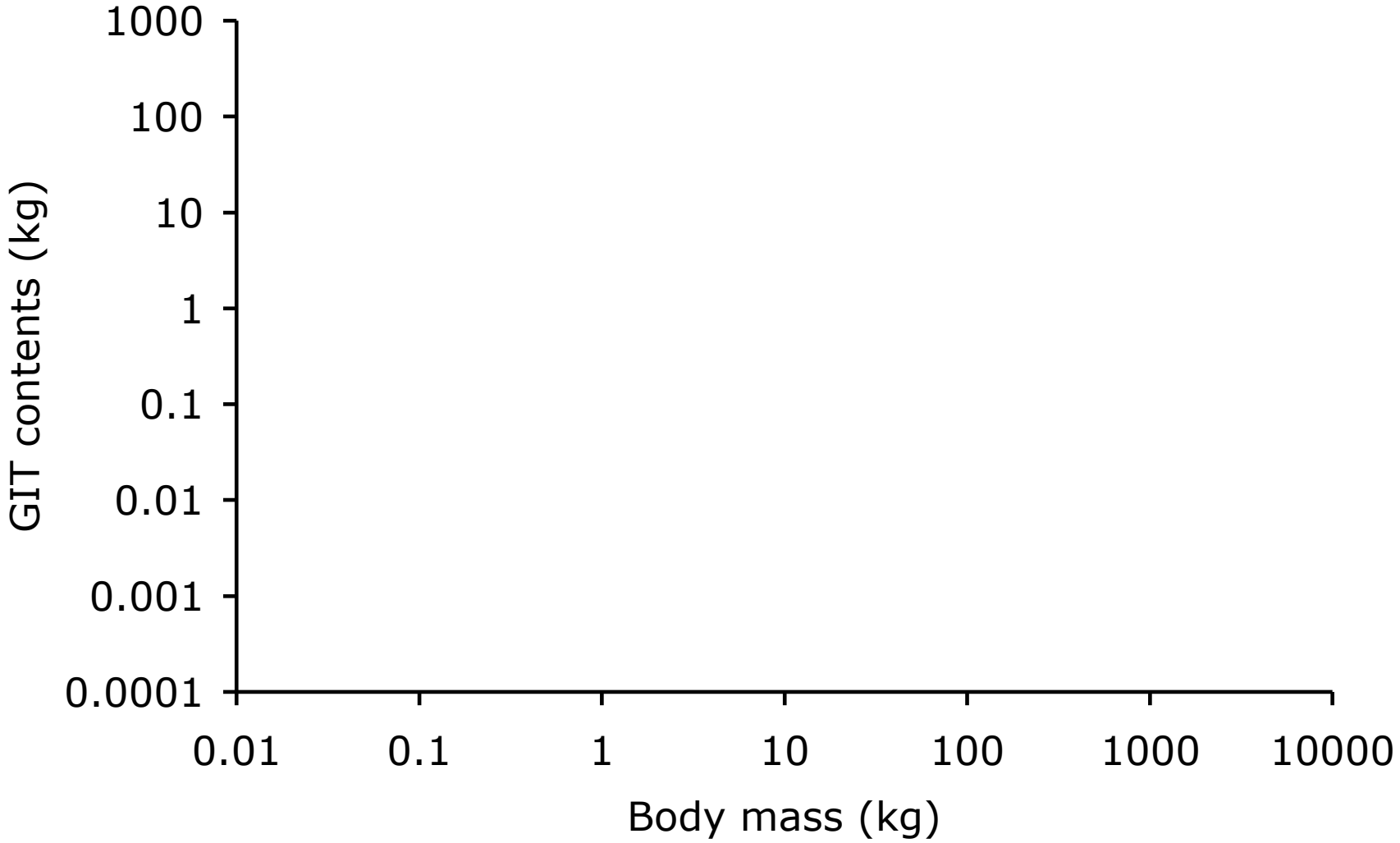
1. **Check if empirical data matches the hypothesis**
2. Check the mathematical validity
3. Check conceptual background

(vary sequence to suit your preference or intellectual capacity)

Gut capacity

Wet gut content mass

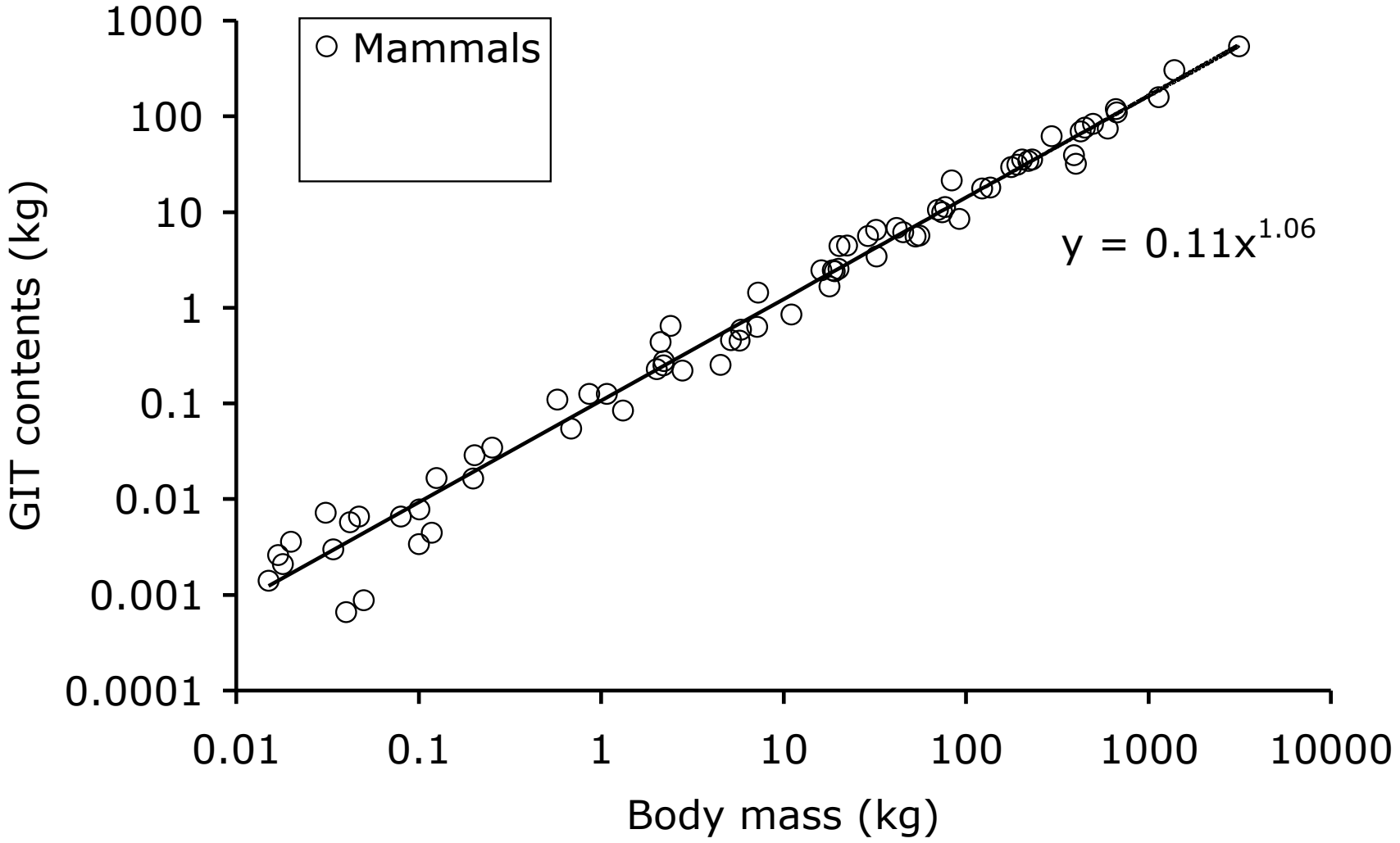
(measured by slaughtering)



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

Wet gut content mass

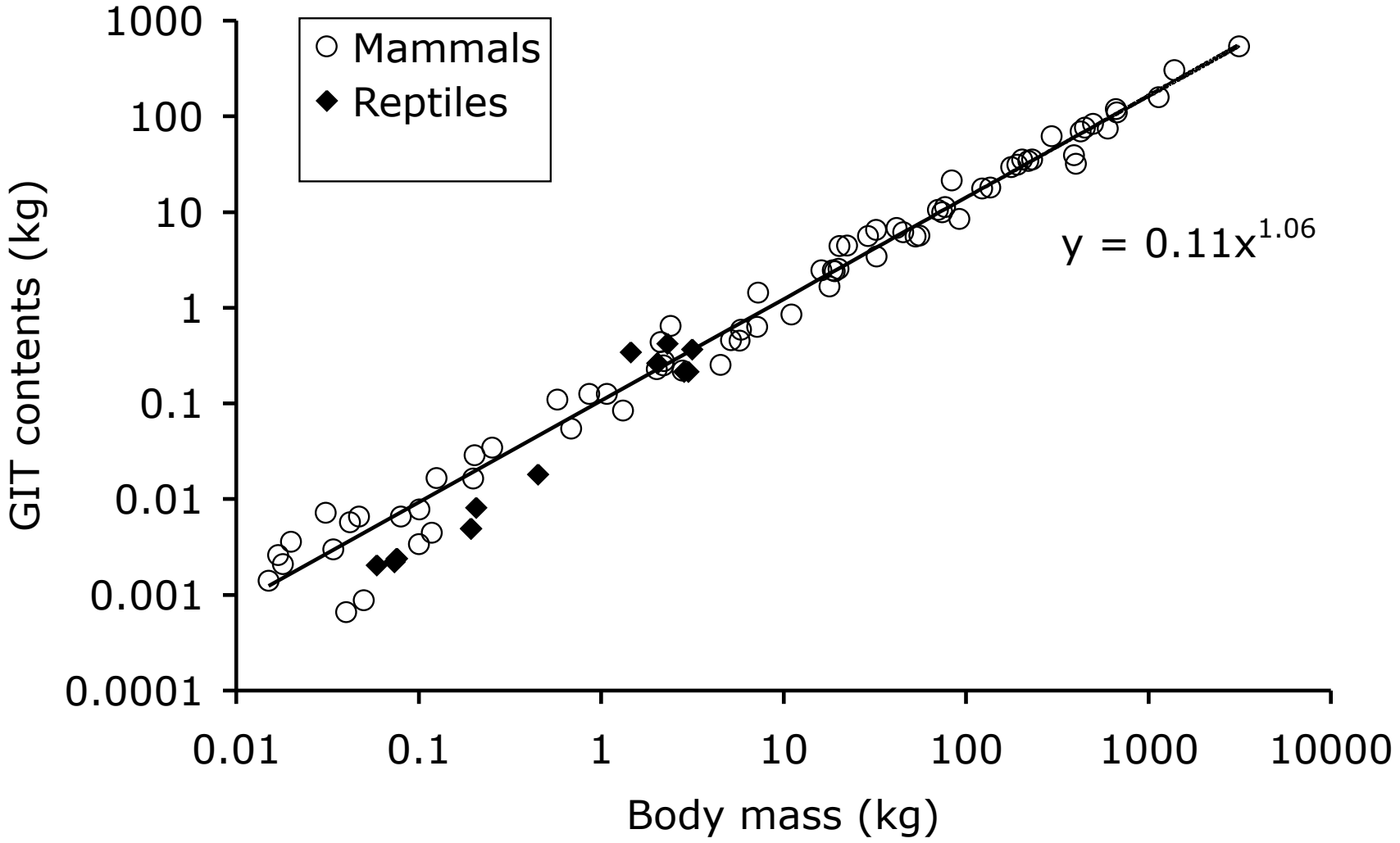
(measured by slaughtering)



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

Wet gut content mass

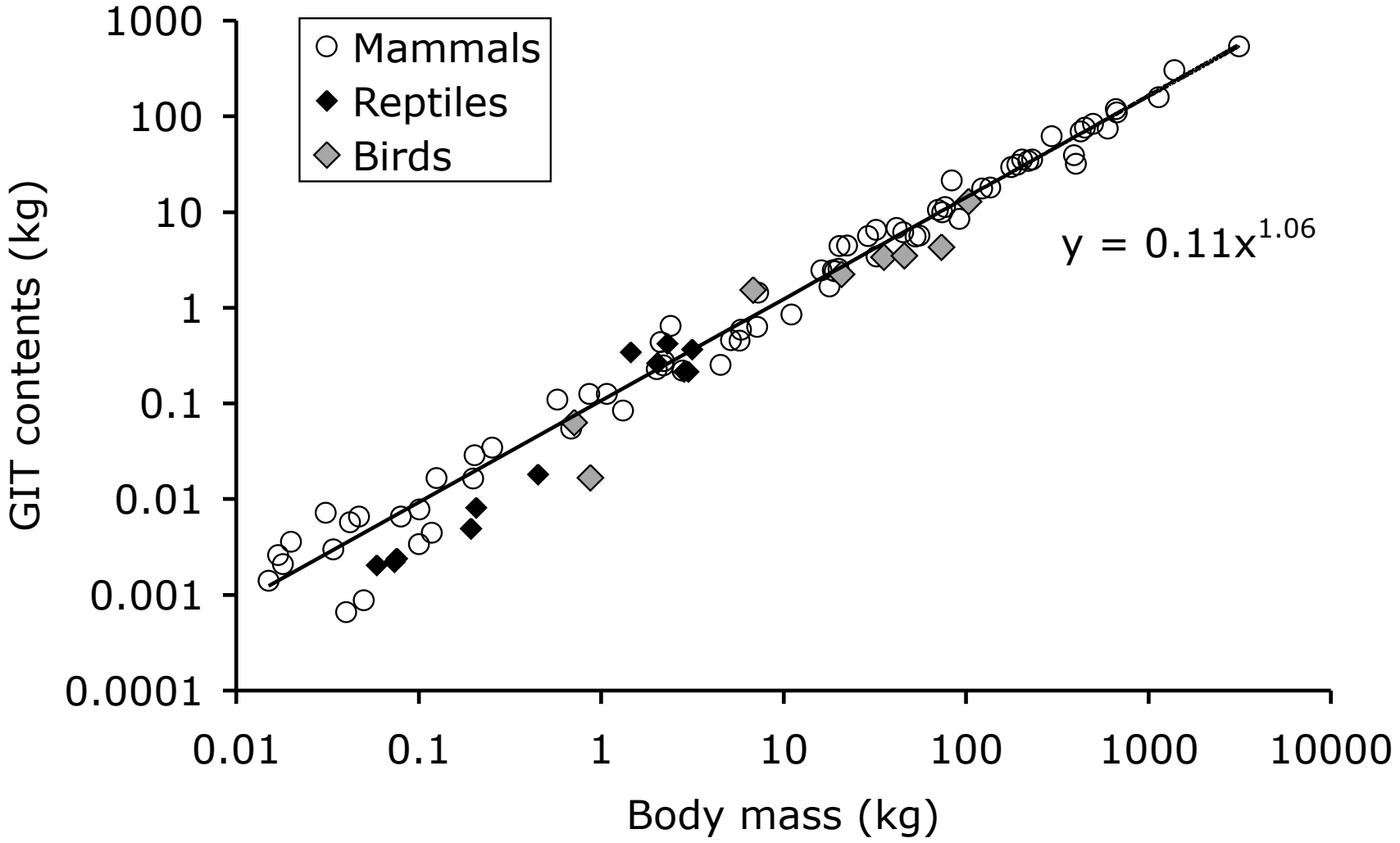
(measured by slaughtering)



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

Wet gut content mass

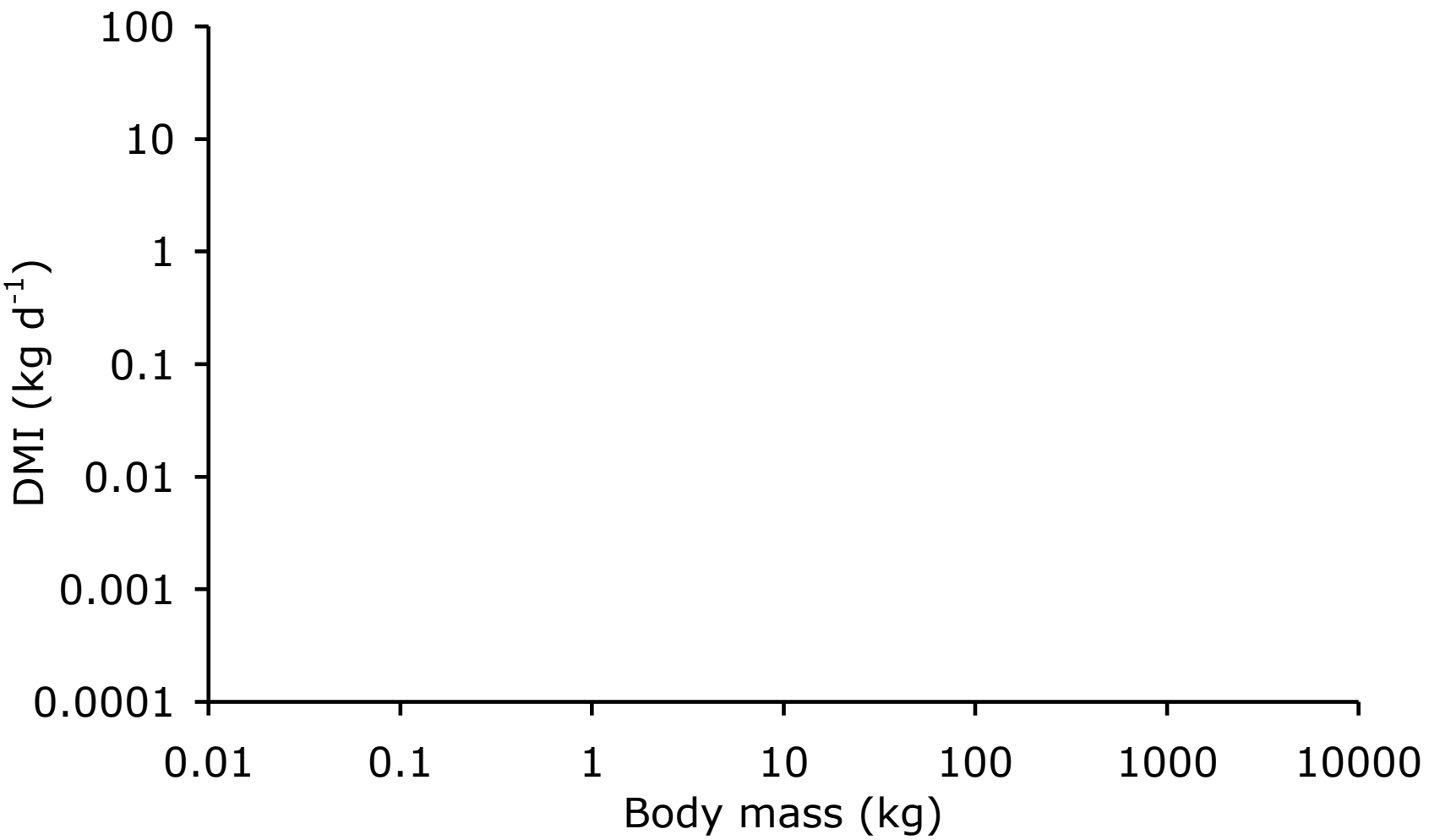
(measured by slaughtering)



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

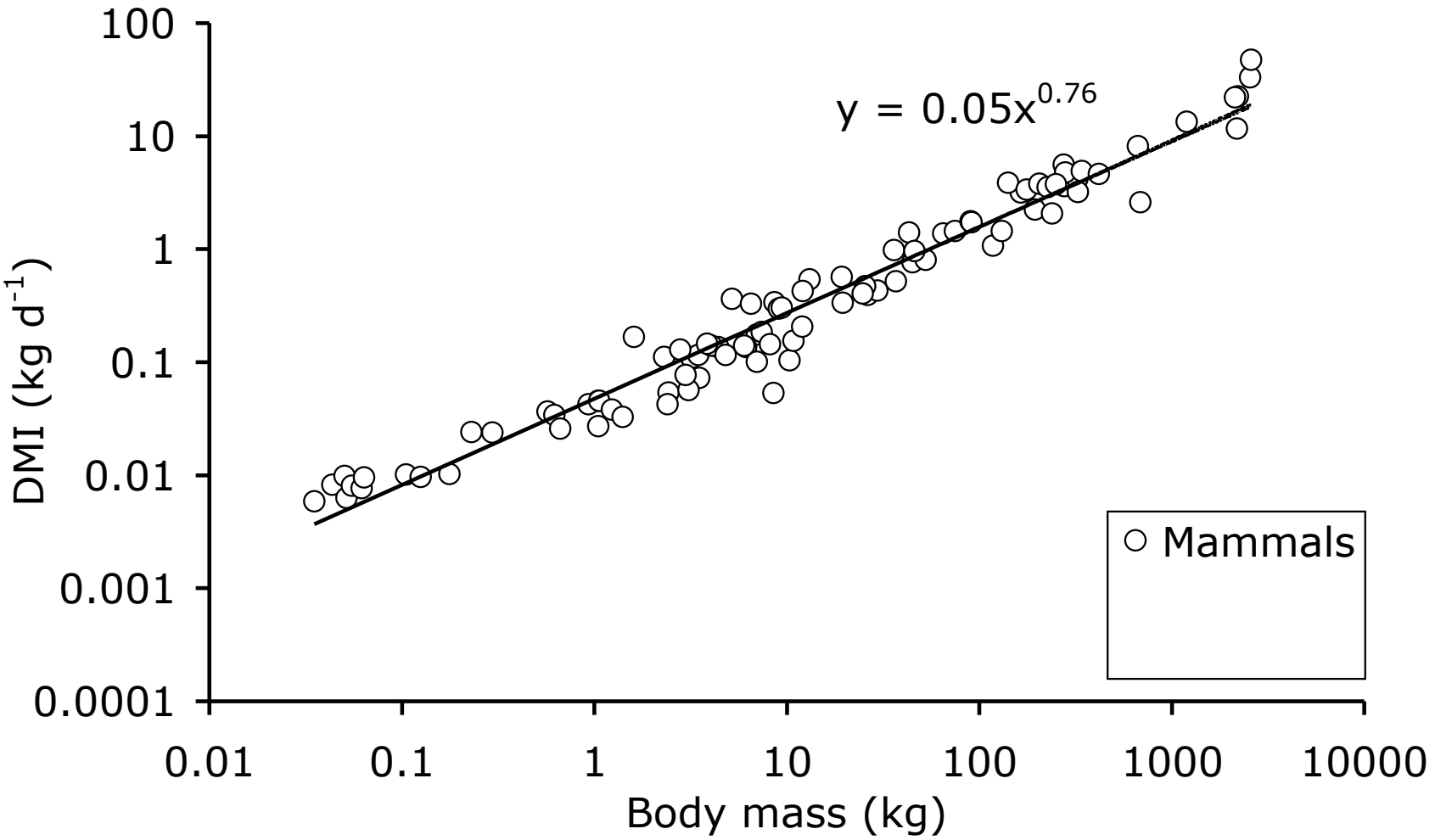
Food intake

Food intake



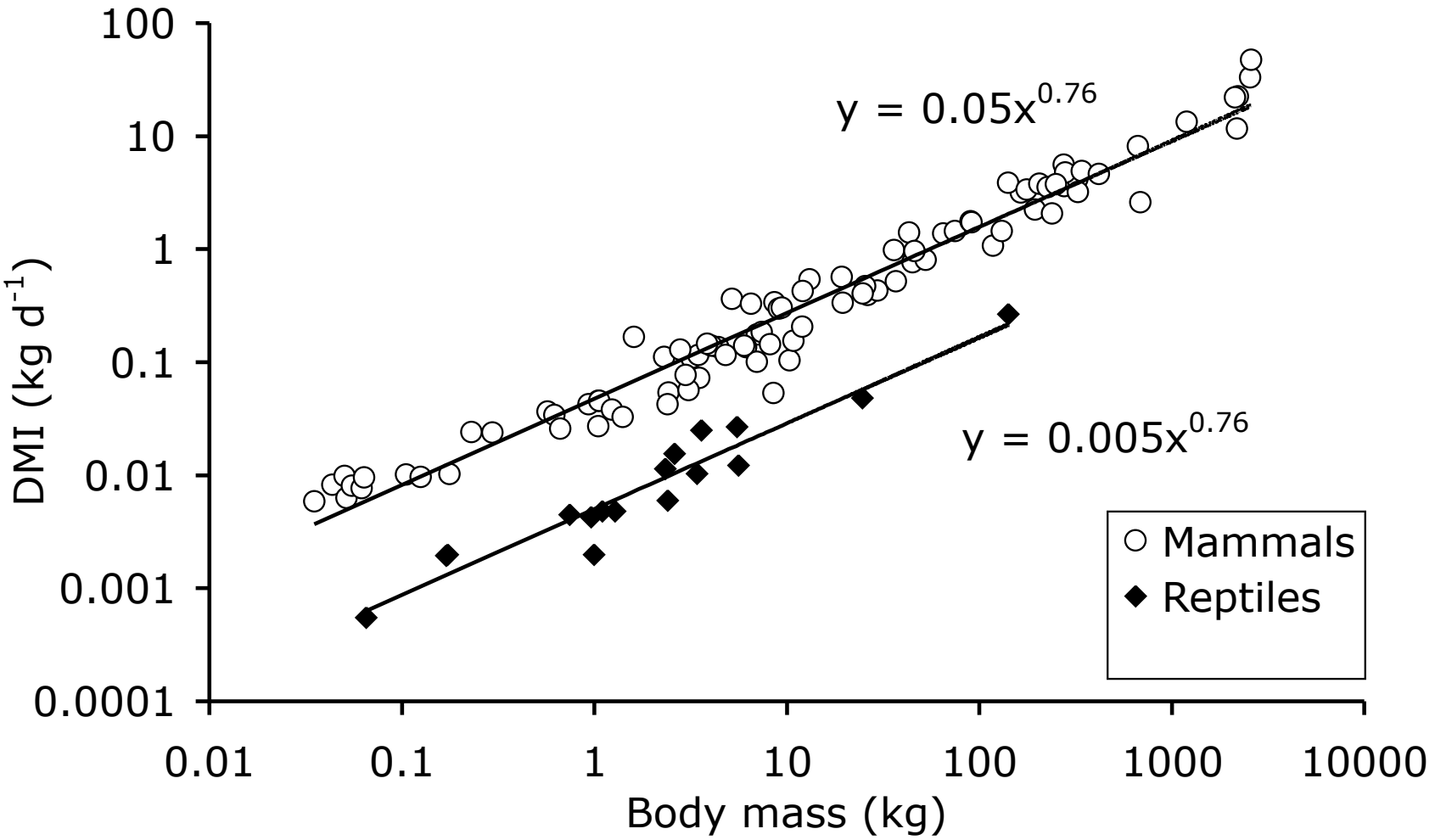
mammal data collection Clauss et al. (2007), reptile from Franz et al. (2009), bird from Fritz et al. (subm.)

Food intake



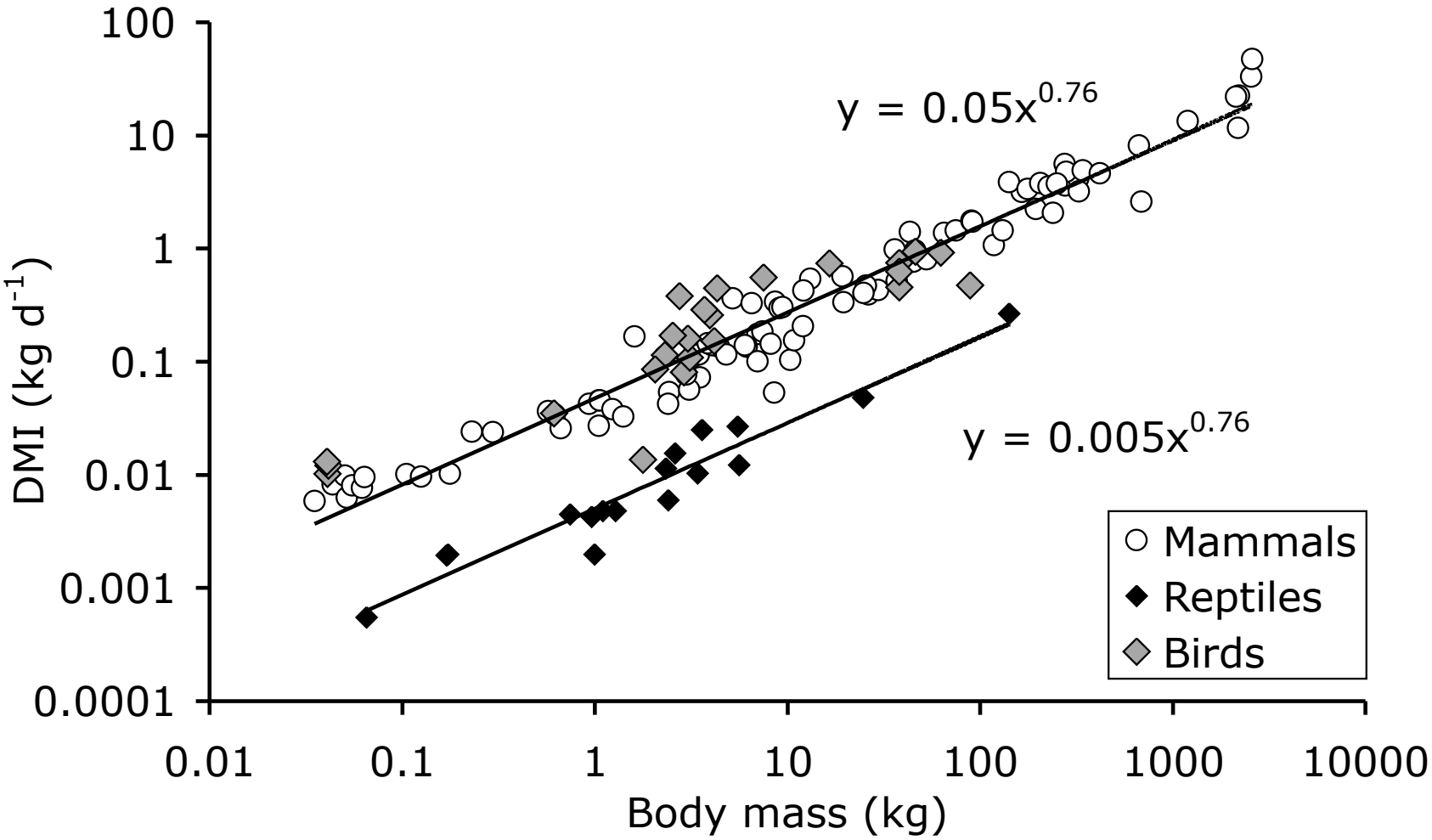
mammal data collection Clauss et al. (2007), reptile from Franz et al. (2009), bird from Fritz et al. (2012)

Food intake



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

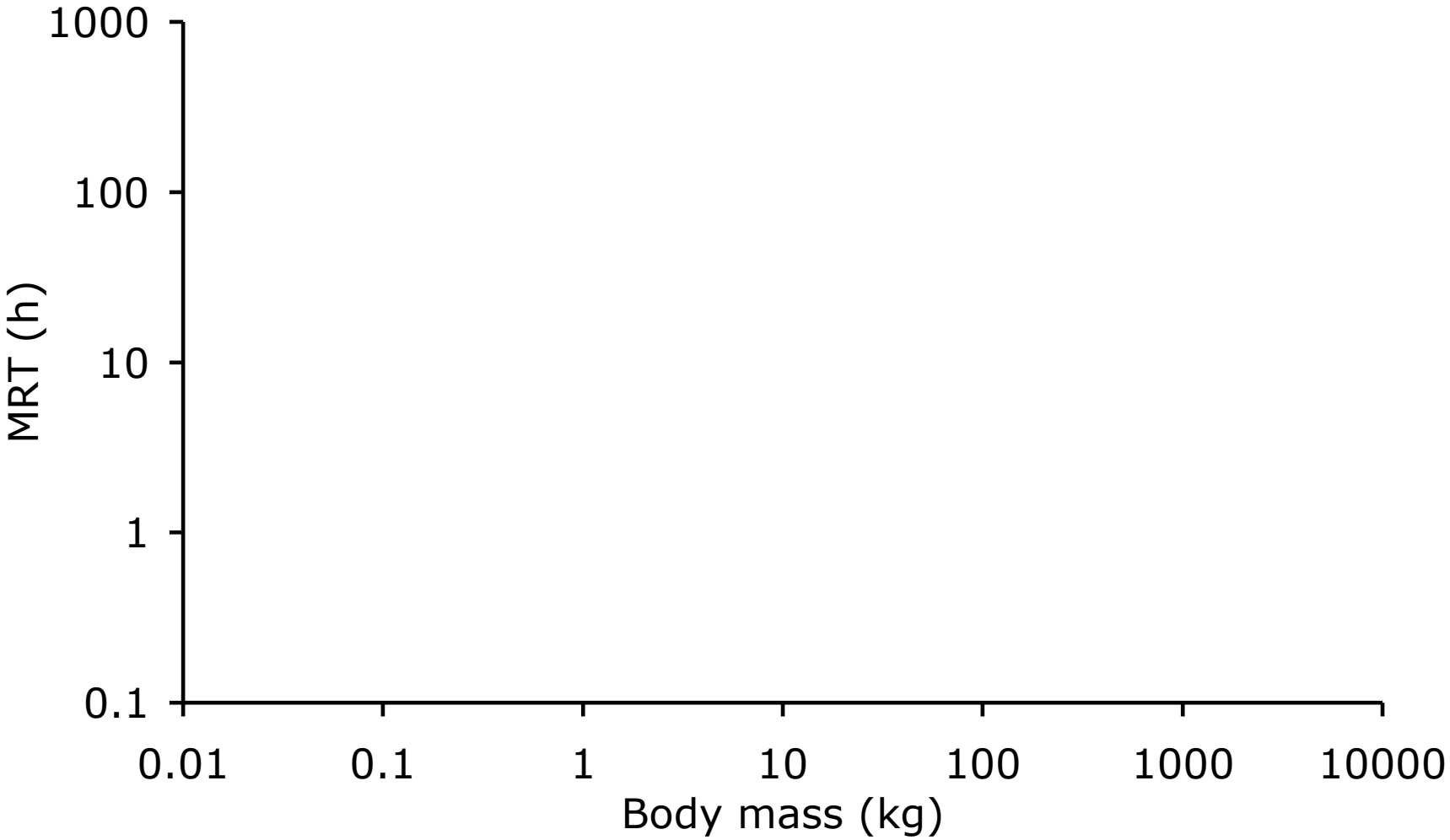
Food intake



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

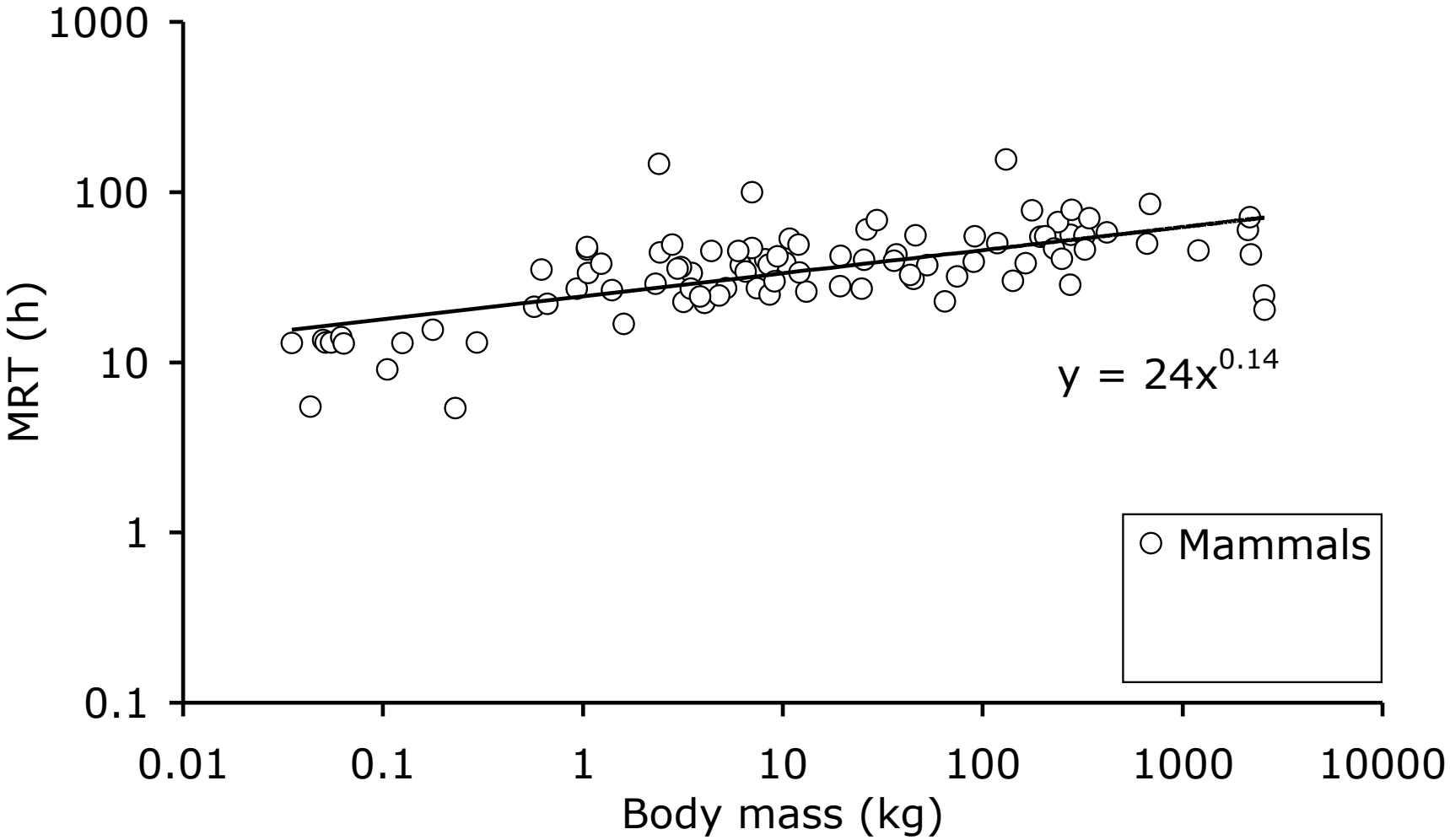
Digesta retention

Mean retention time



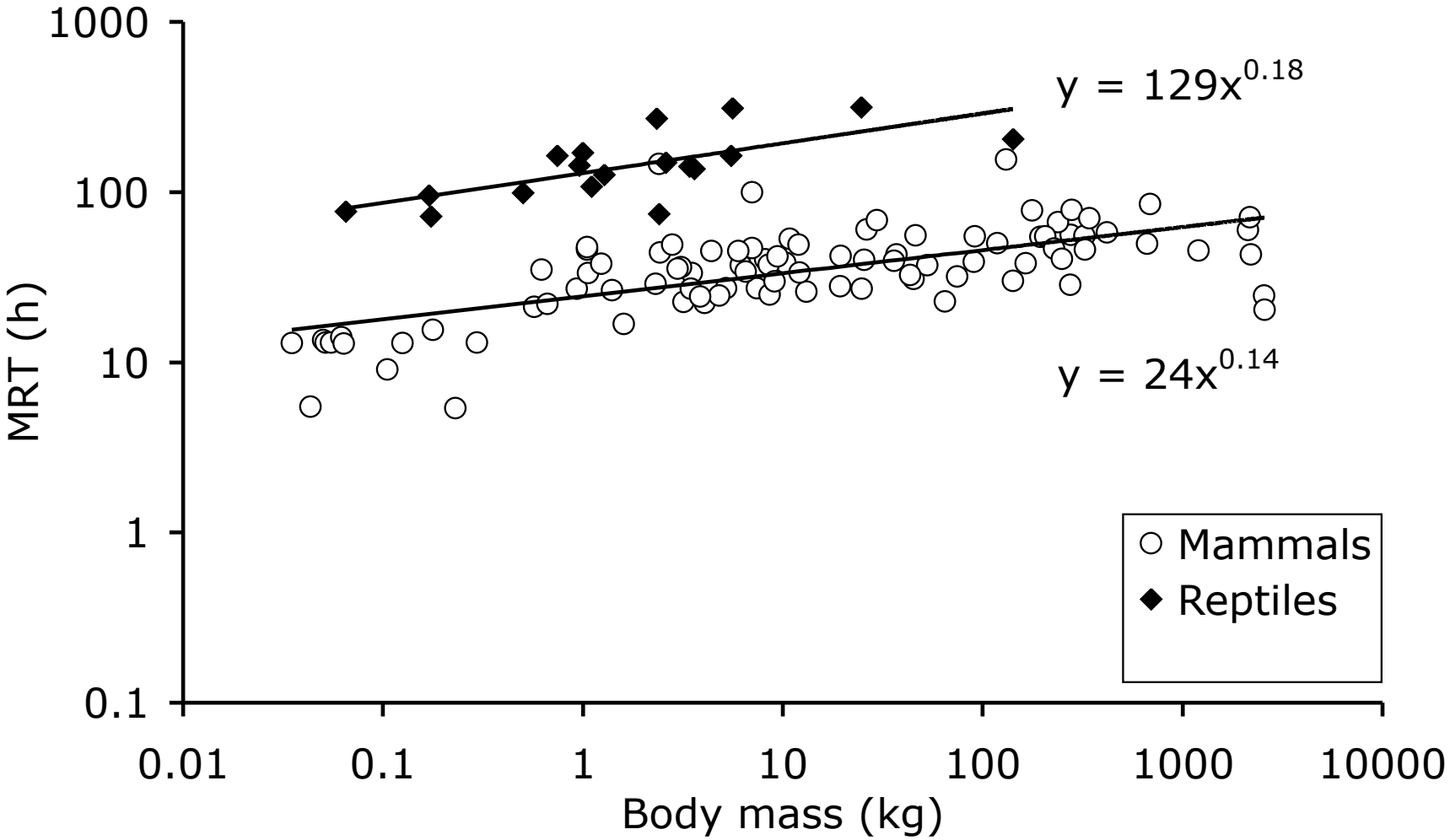
mammal data collection Clauss et al. (2007), reptile from Franz et al. (2009), bird from Fritz et al. (2012)

Mean retention time



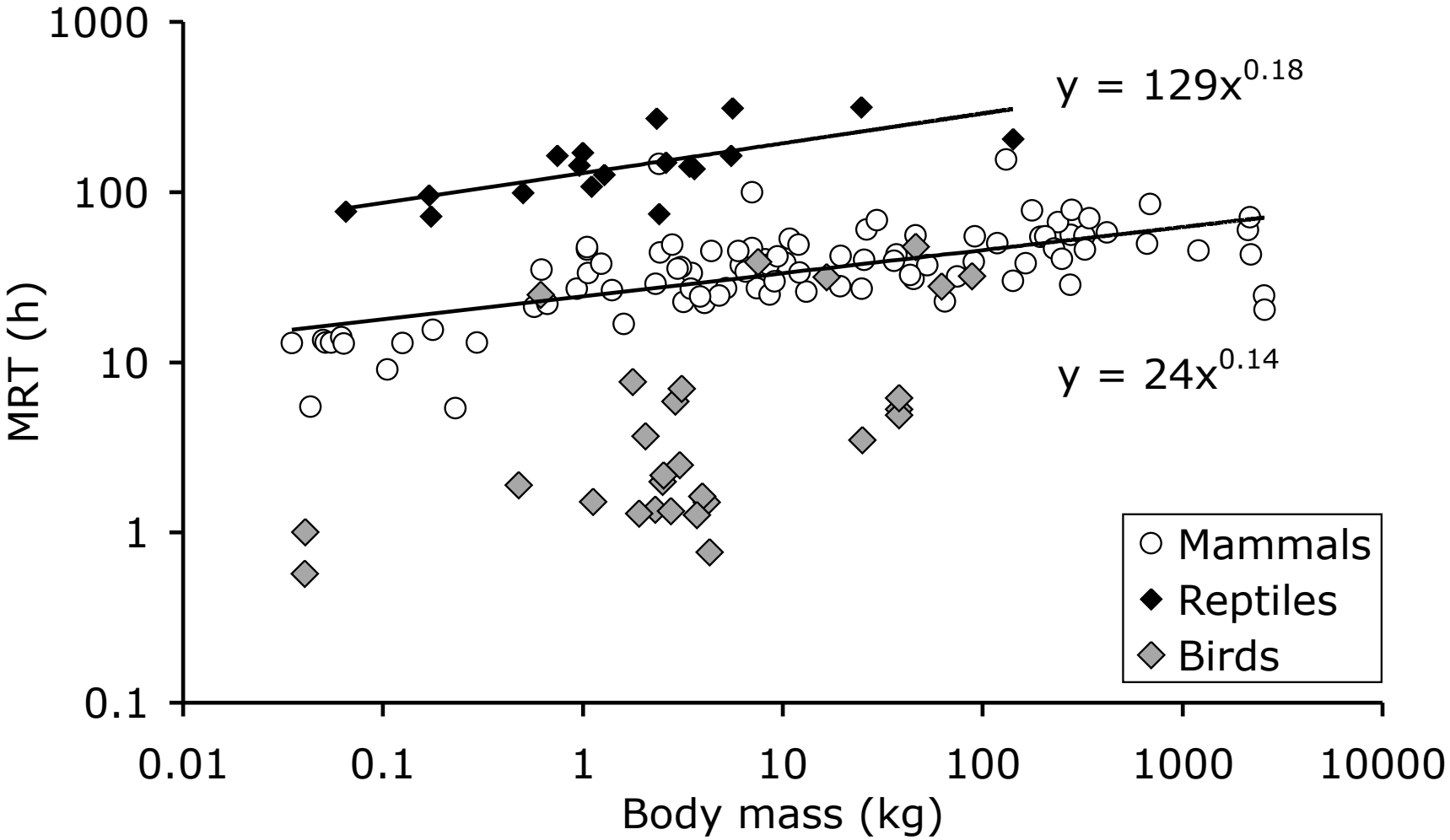
mammal data collection Clauss et al. (2007), reptile from Franz et al. (2009), bird from Fritz et al. (2012)

Mean retention time



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

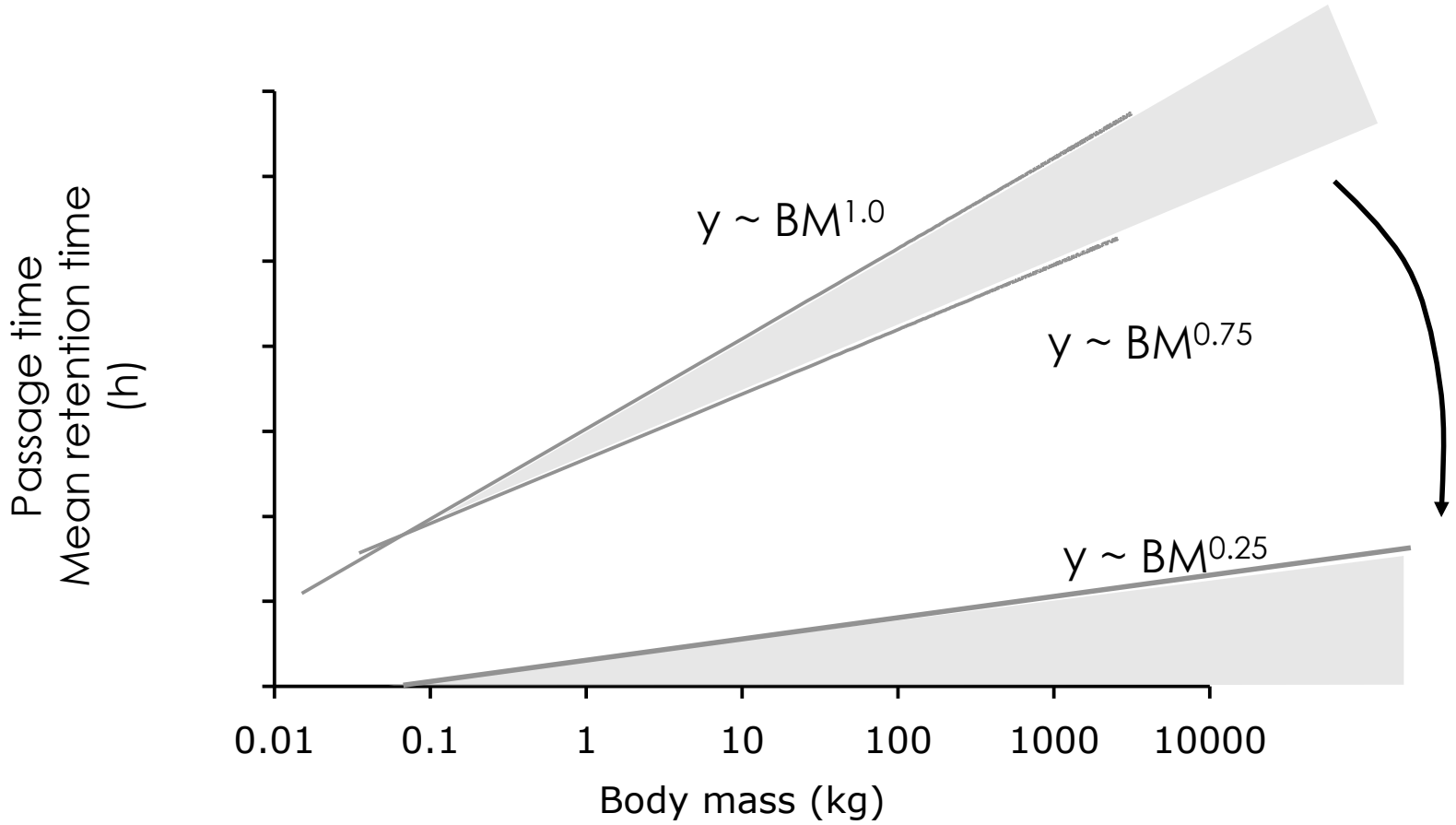
Mean retention time



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

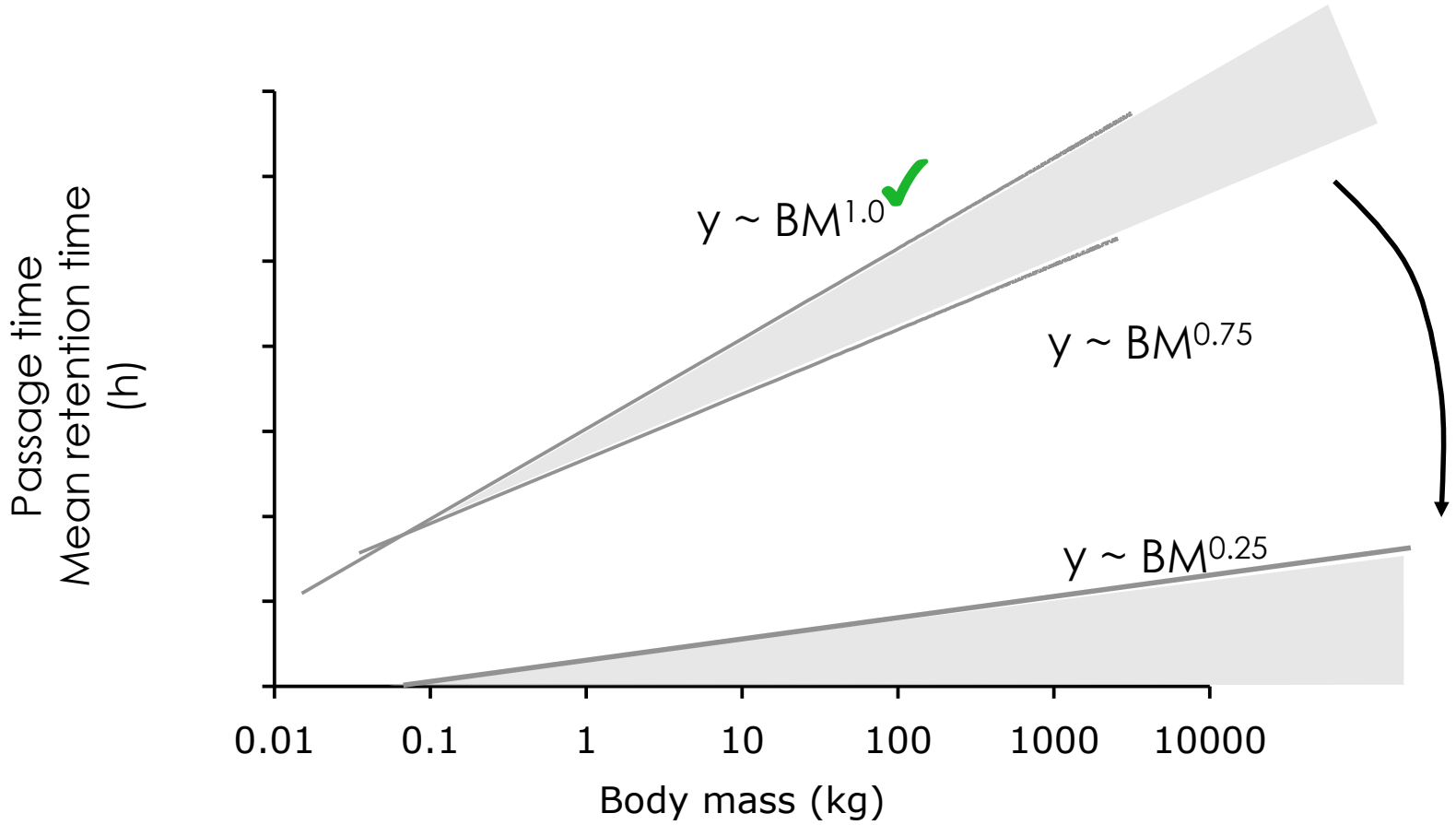
So what now?

General allometric considerations



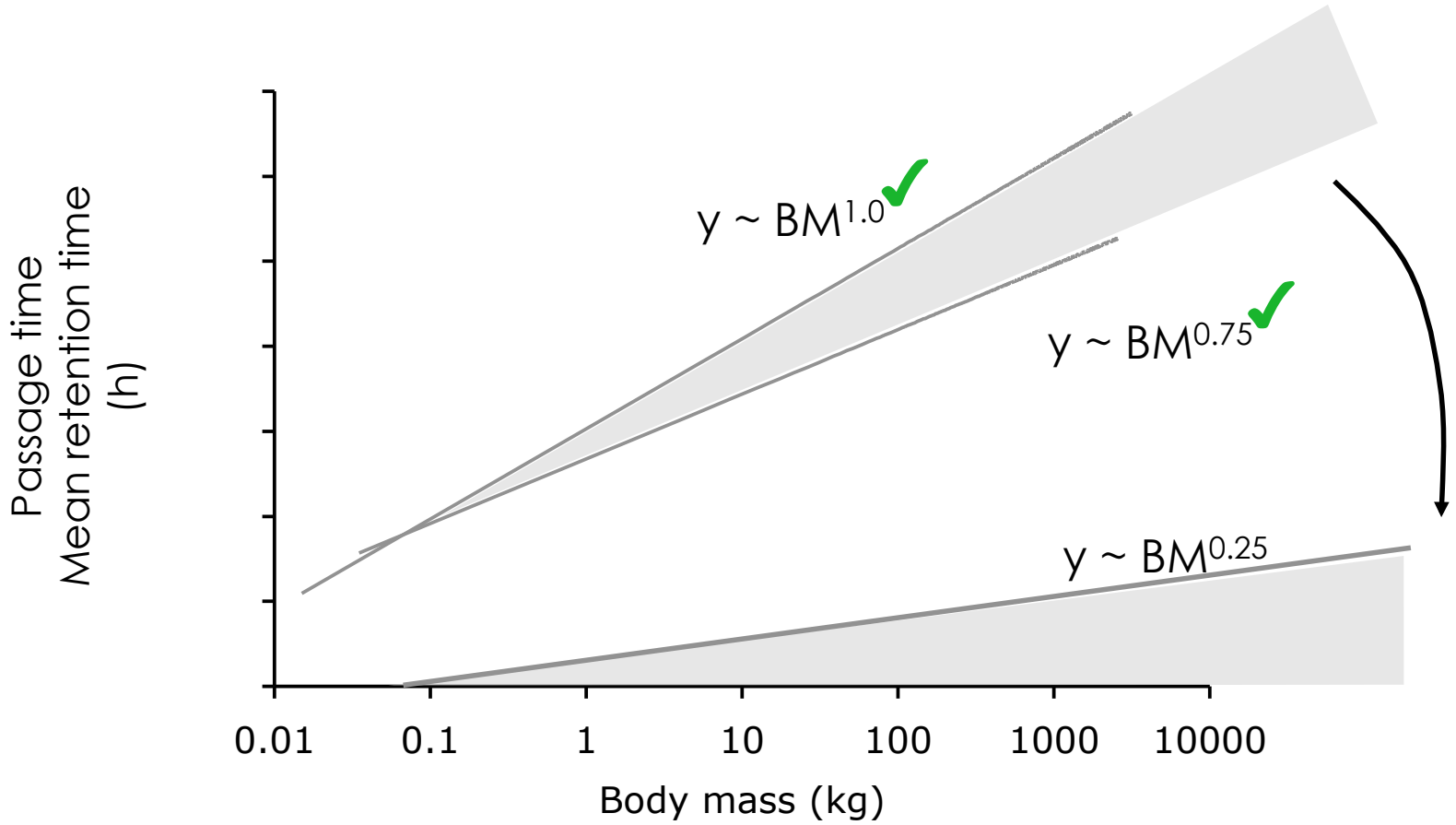
from Parra (1978), Demment & Van Soest (1985), Illius & Gordon (1992); McNab (2002)

General allometric considerations



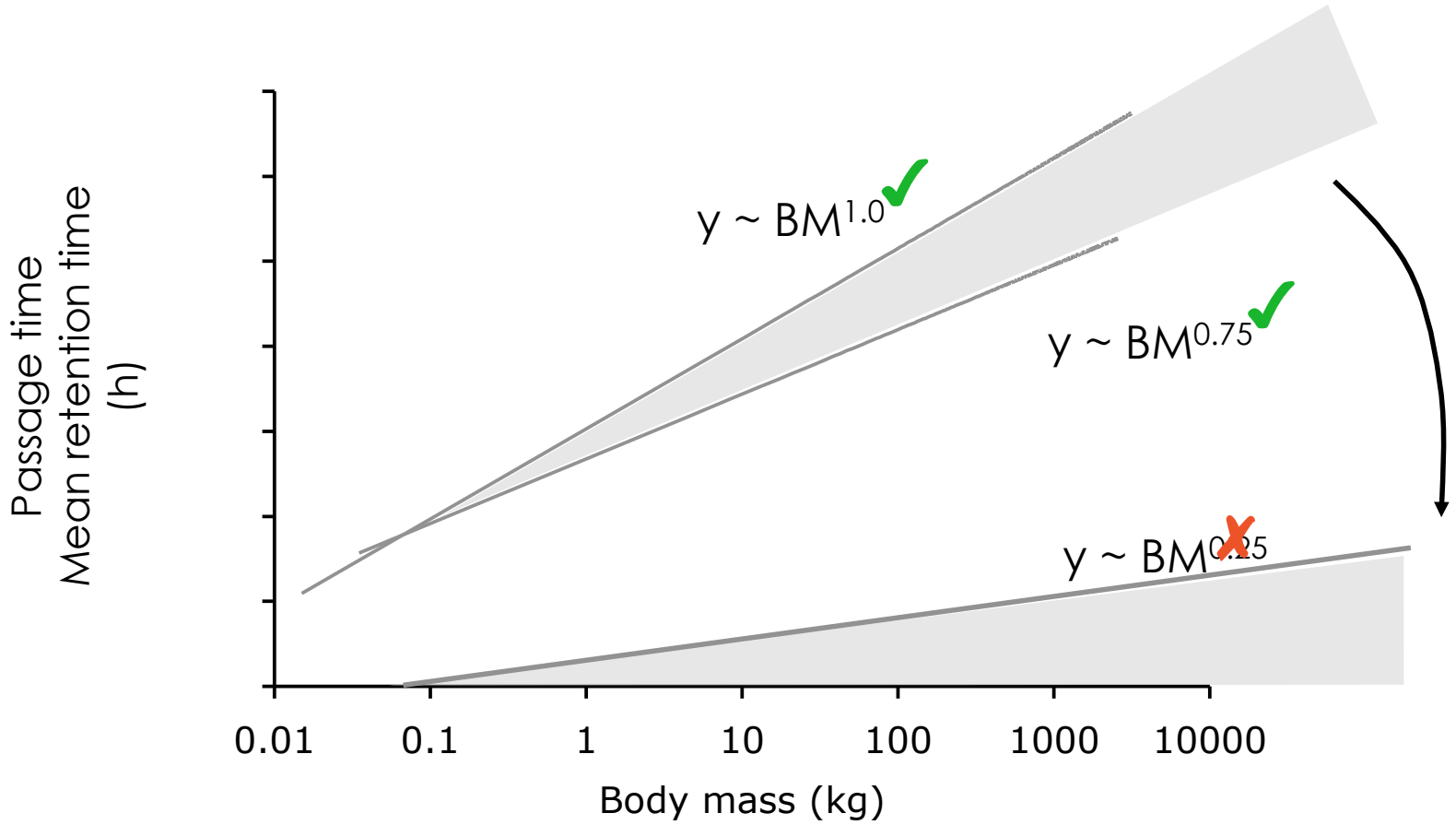
from Parra (1978), Demment & Van Soest (1985), Illius & Gordon (1992); McNab (2002)

General allometric considerations



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

General allometric considerations



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

A serious problem

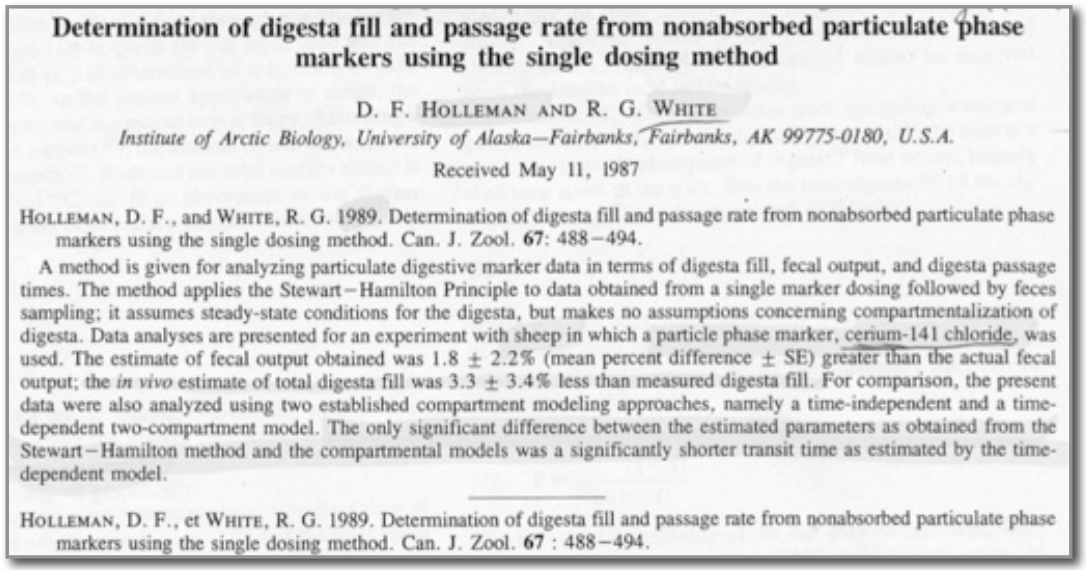
If gut capacity scales to $BM^{1.0}$, and food intake to $BM^{0.75}$, then a lack of scaling of retention time to $BM^{0.25}$ begs for an explanation!

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

Using a single dataset

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

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



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

D. F. HOLLEMAN AND R. G. WHITE

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

Received May 11, 1987

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

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

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

Contents lists available at SciVerse ScienceDirect

Comparative Biochemistry and Physiology, Part A

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

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

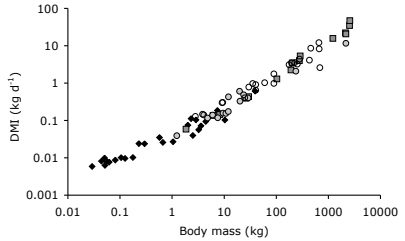
Dennis W.H. Müller [a,b], Daryl Codron [a,c], Carlo Meloro [d], Adam Munn [e], Angela Schwarm [f], Jürgen Hummel [g,h], Marcus Clauss [a,*]

Using a single dataset

Measurement	Scaling (95%CI)

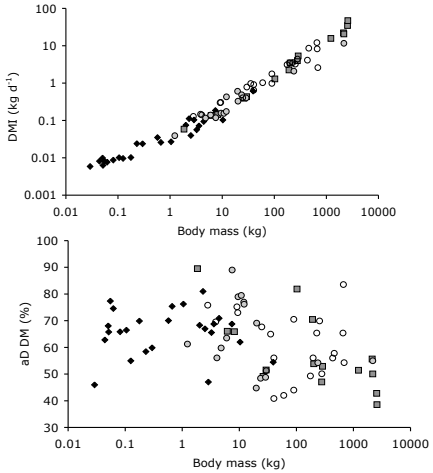
Using a single dataset

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



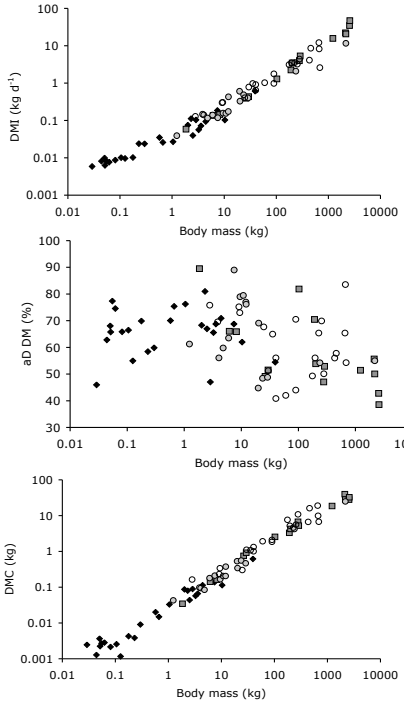
Using a single dataset

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



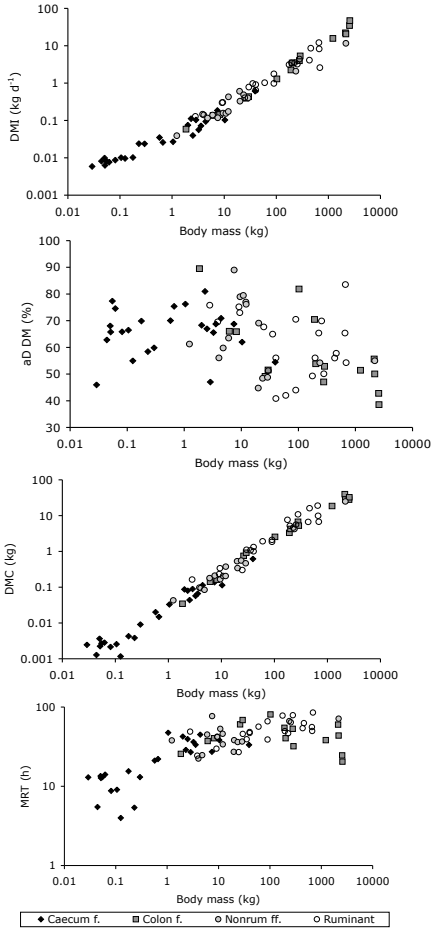
Using a single dataset

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)



Using a single dataset

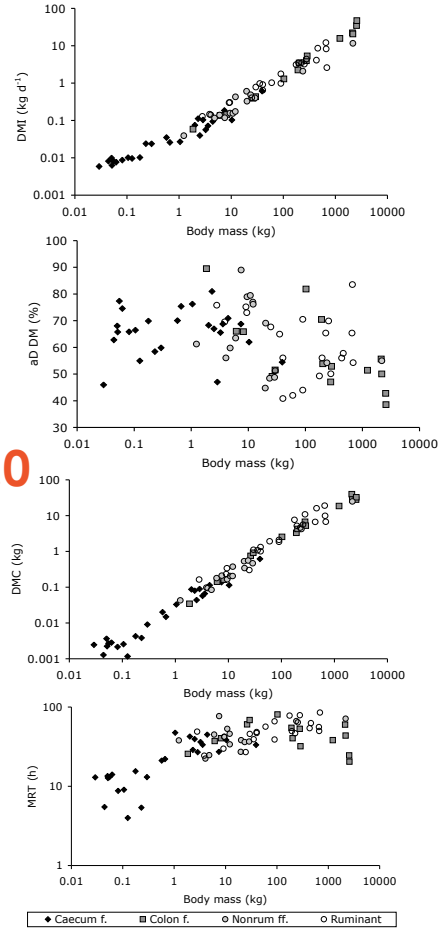
Measurement	Scaling (95%CI)
Dry matter intake	0.76 (0.73-0.79)
Digestibility	-0.03 (-0.04--0.01)
Dry matter gut fill	0.93 (0.90-0.96)
Particle retention time	0.16 (0.12-0.19)



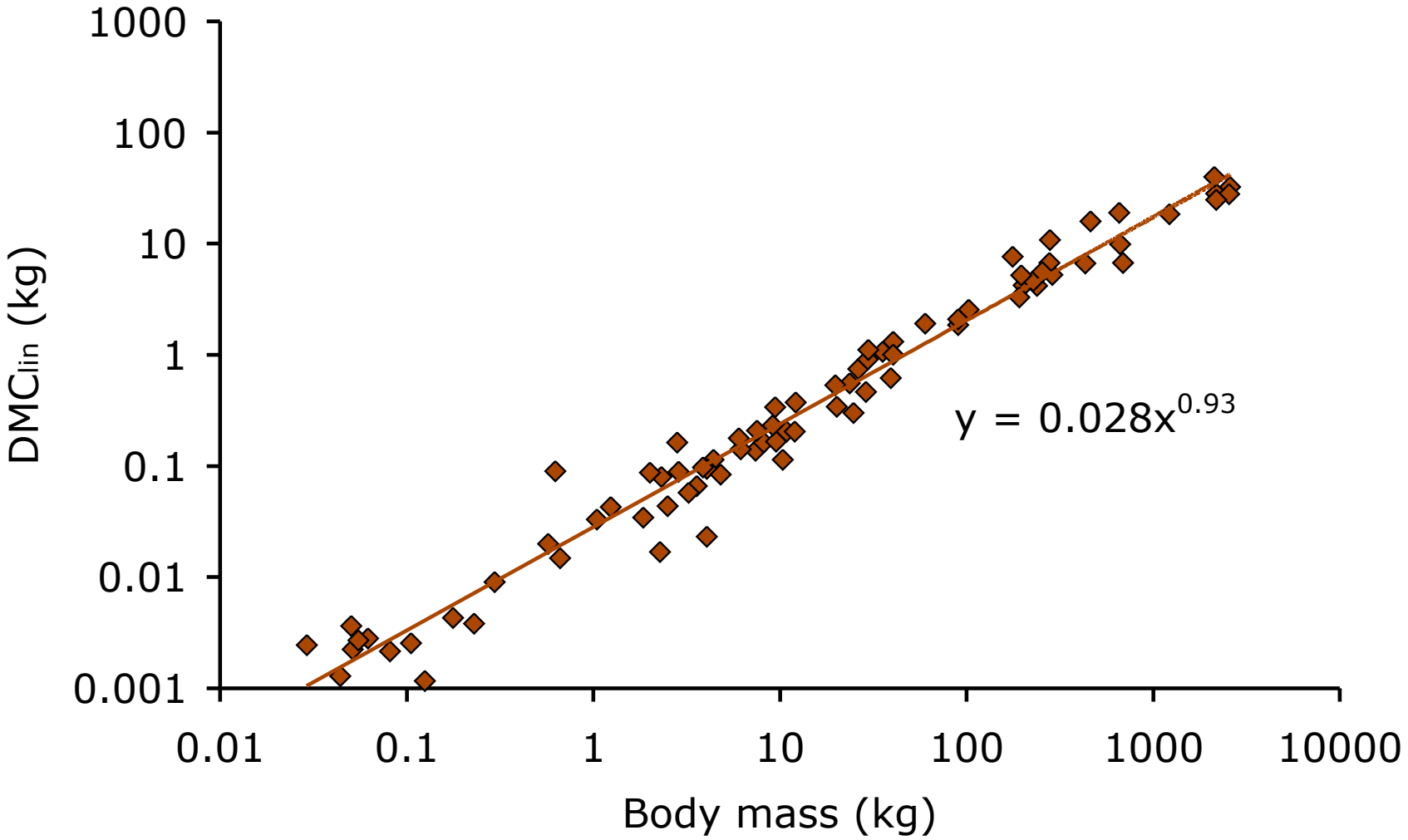
The *really real* exponents

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

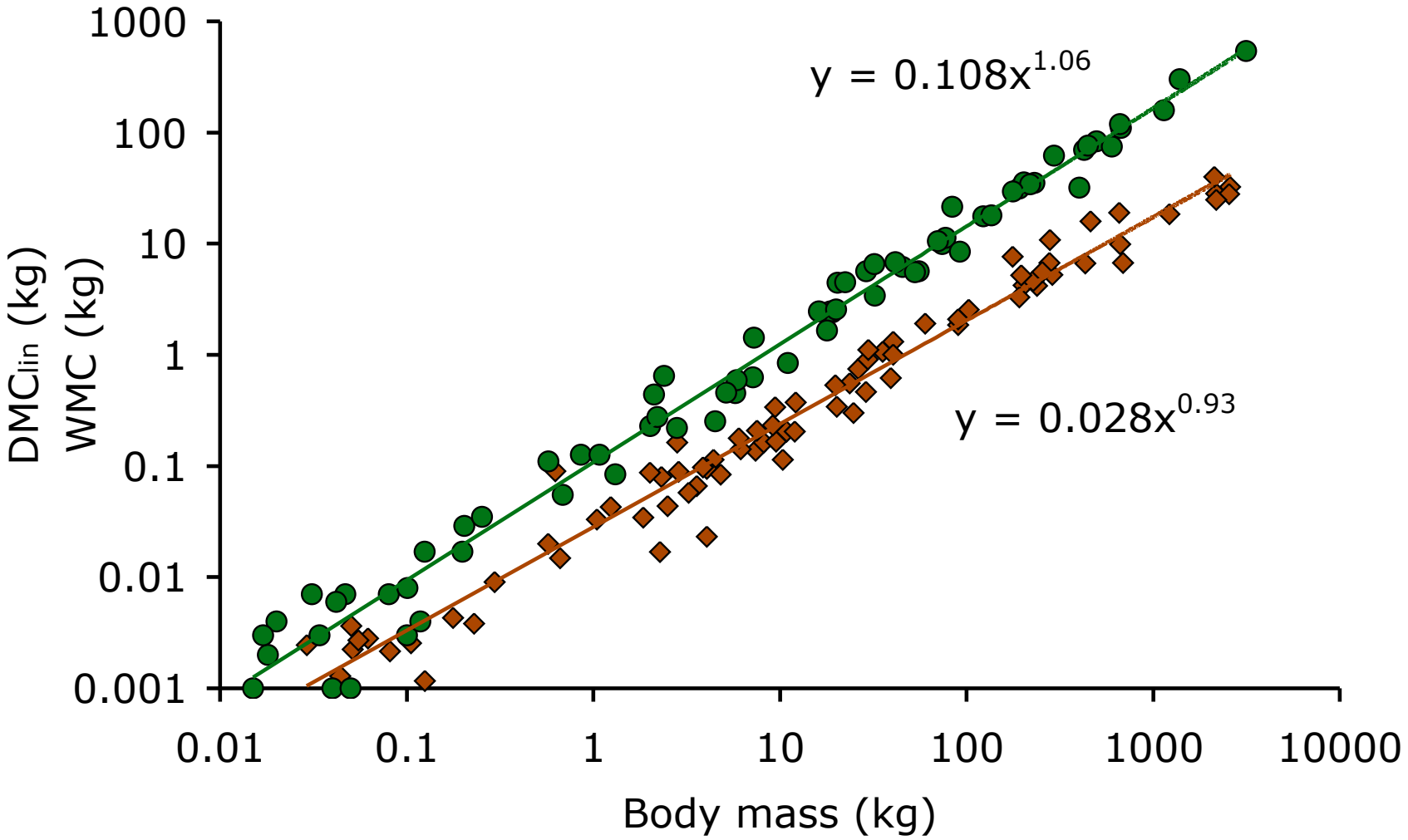


Gut moisture content



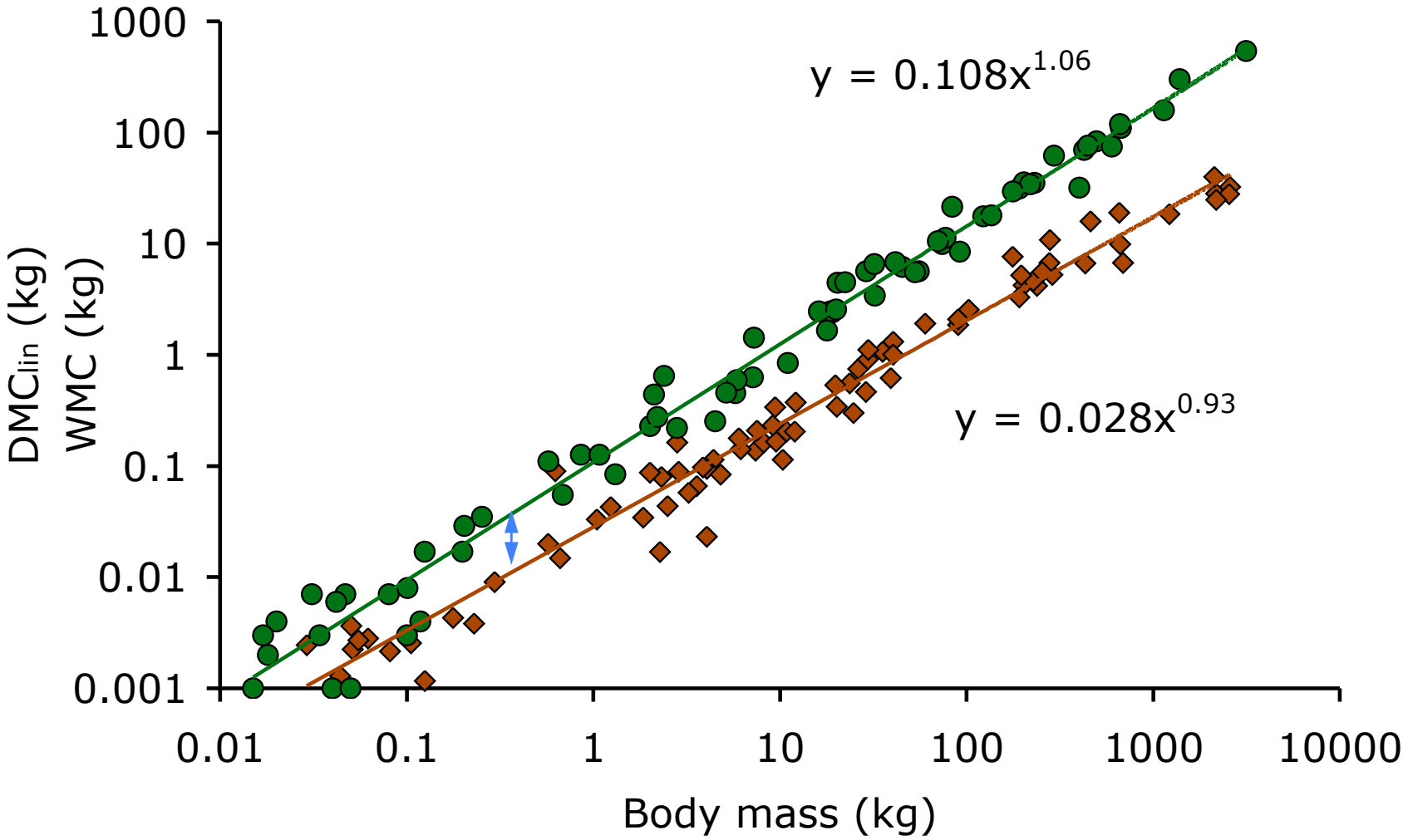
from Müller et al. (subm.)

Gut moisture content



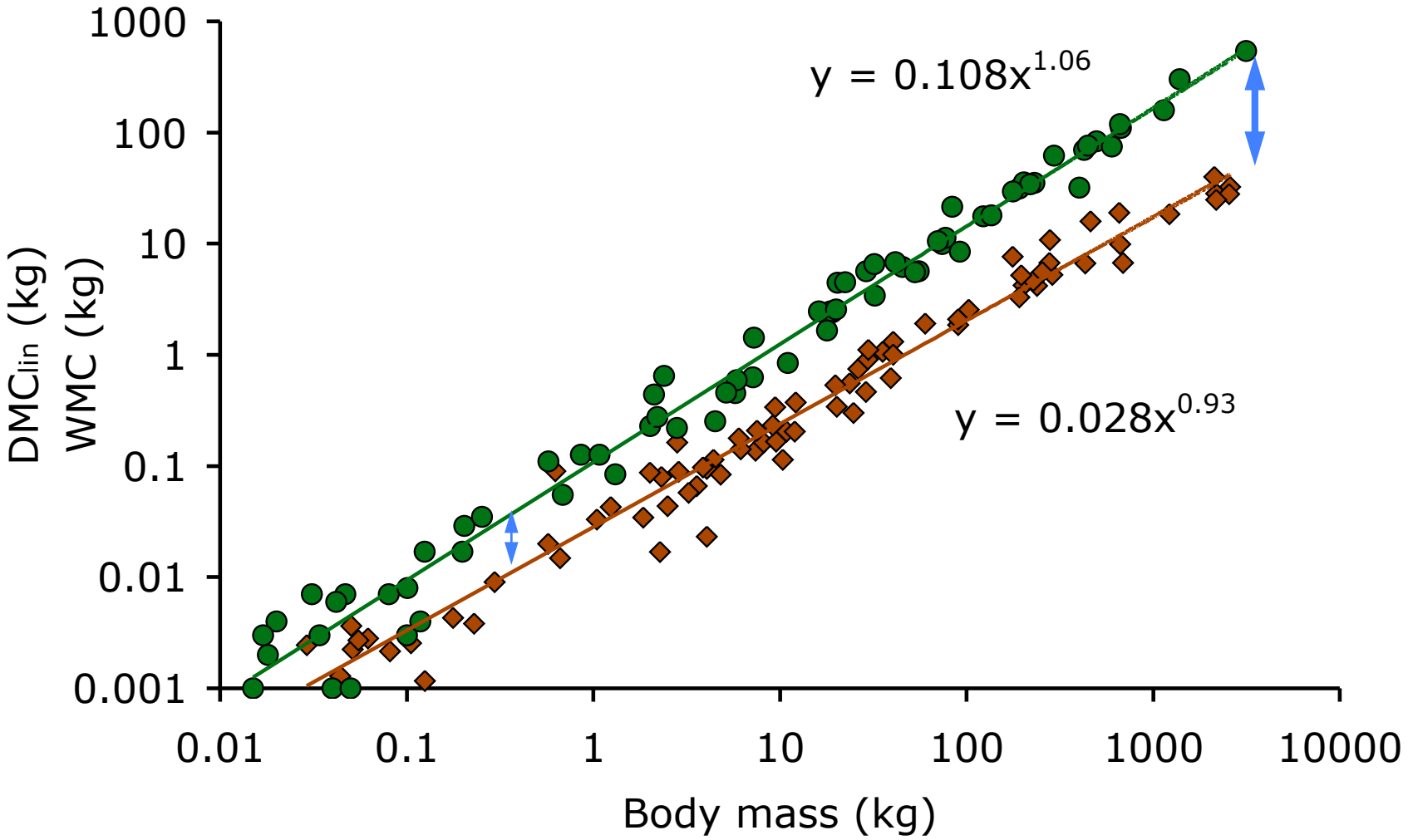
from Müller et al. (subm.)

Gut moisture content



from Müller et al. (subm.)

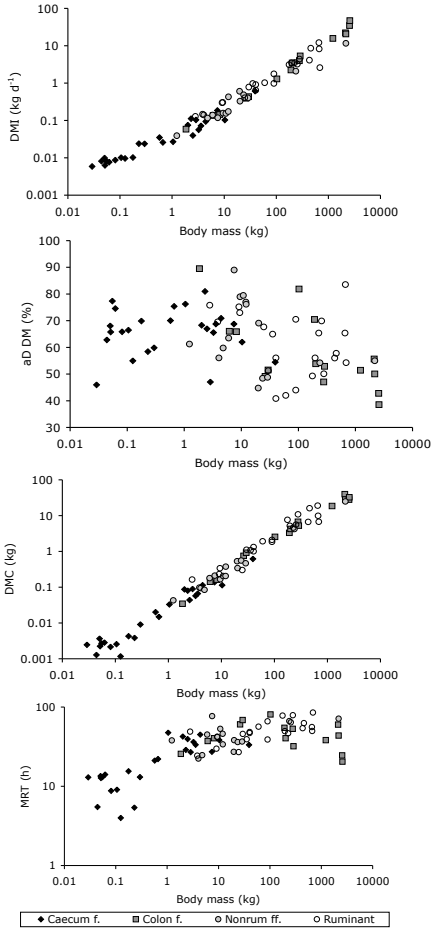
Gut moisture content



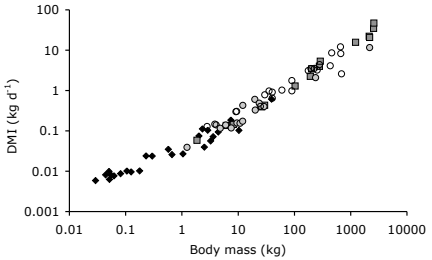
from Müller et al. (subm.)

The *really real* exponents

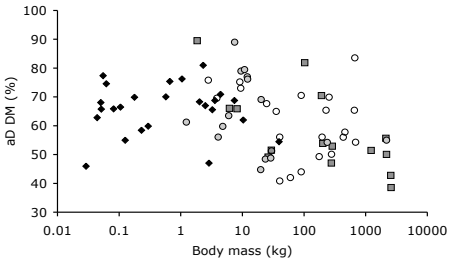
Measurement	Scaling (95%CI)
Dry matter intake	0.76 (0.73-0.79)
Digestibility	-0.03 (-0.04--0.01)
Dry matter gut fill	0.93 (0.90-0.96)
Particle retention time	0.16 (0.12-0.19)



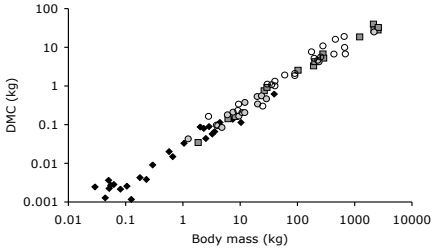
The curvature in herbivore digestive physiology



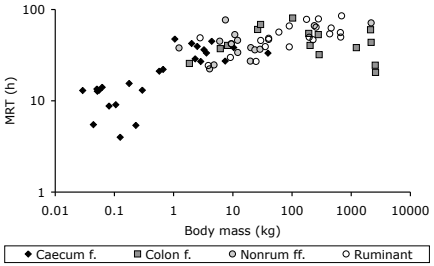
Dry matter intake



Digestibility

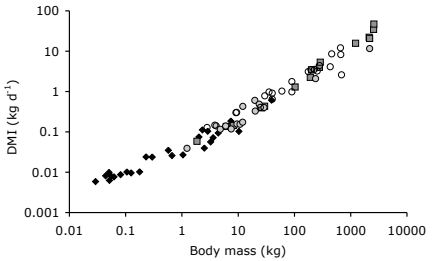


Dry matter gut content

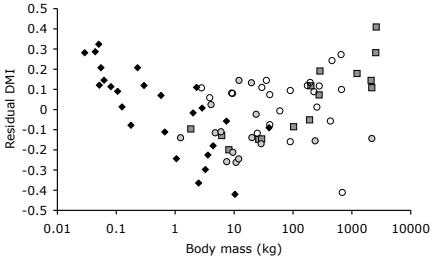


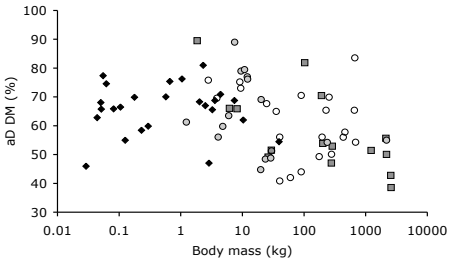
Particle retention time

The curvature in herbivore digestive physiology - plotting residuals

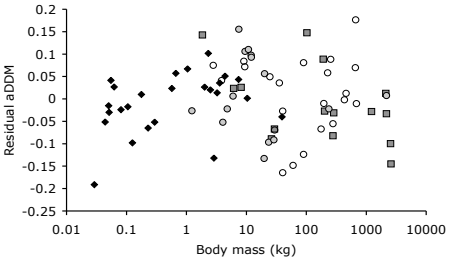


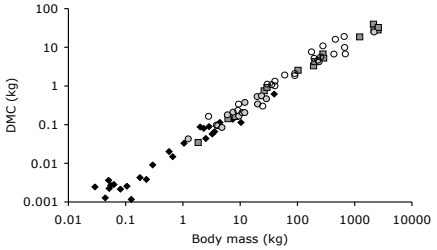
Dry matter intake



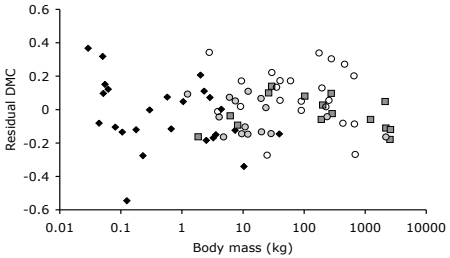


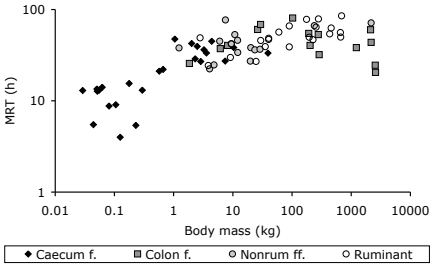
Digestibility



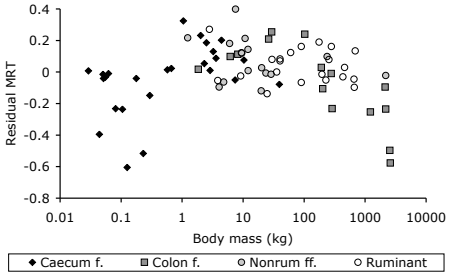


Dry matter gut content

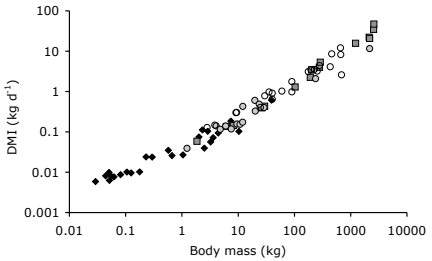




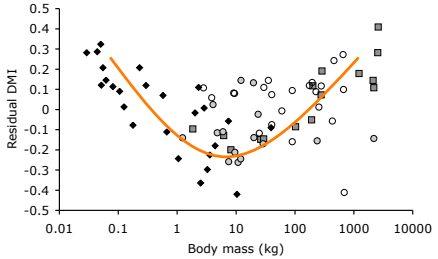
Particle retention time

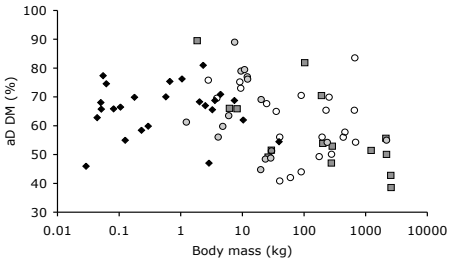


The curvature in herbivore digestive physiology - plotting residuals

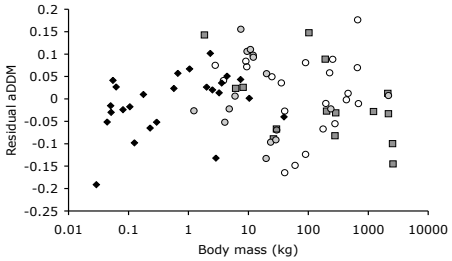


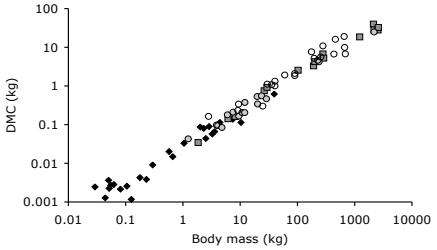
Dry matter intake



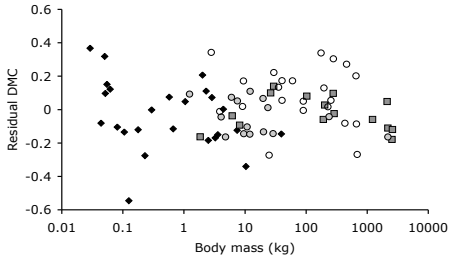


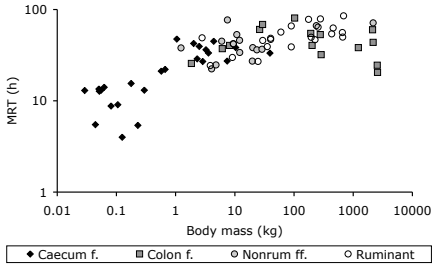
Digestibility



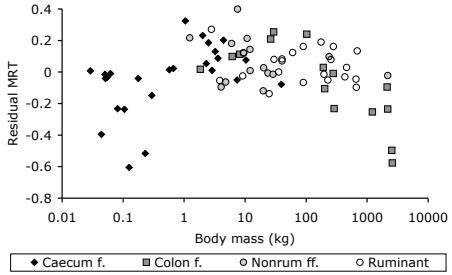


Dry matter gut content

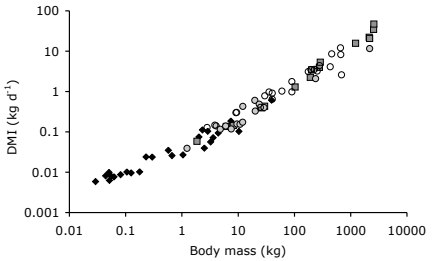




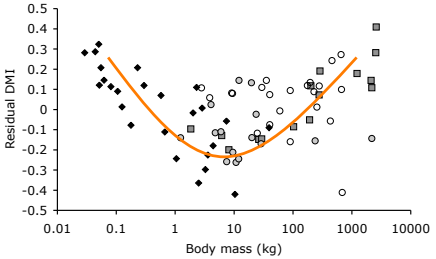
Particle retention time

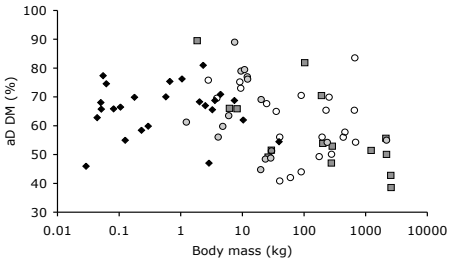


The curvature in herbivore digestive physiology - plotting residuals

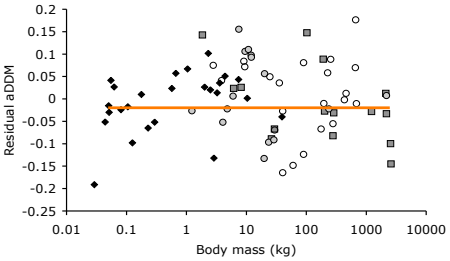


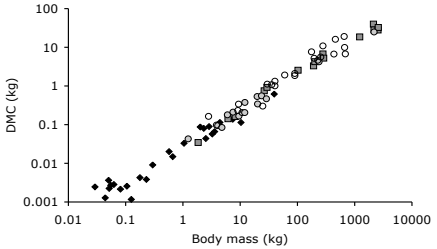
Dry matter intake



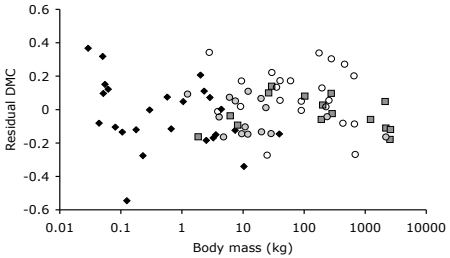


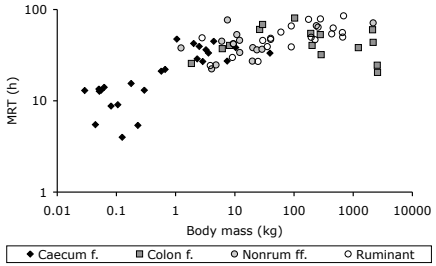
Digestibility



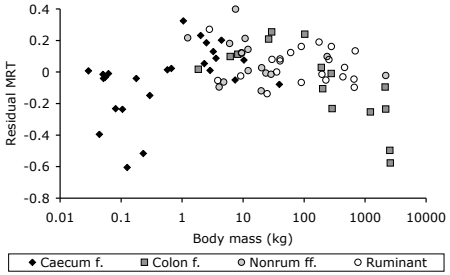


Dry matter gut content

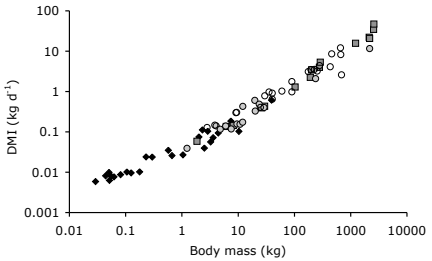




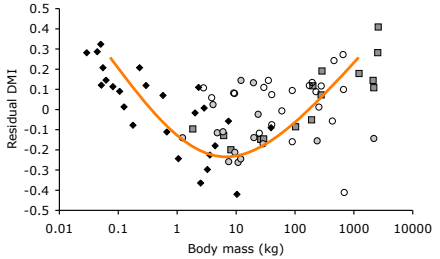
Particle retention time

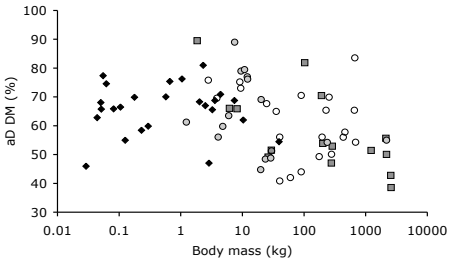


The curvature in herbivore digestive physiology - plotting residuals

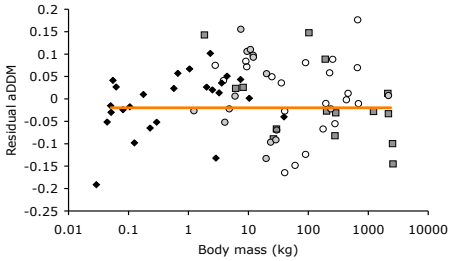


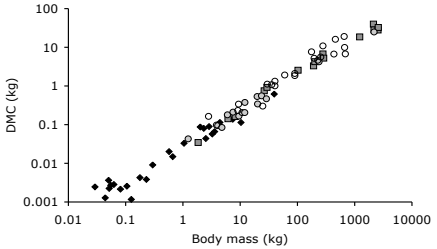
Dry matter intake



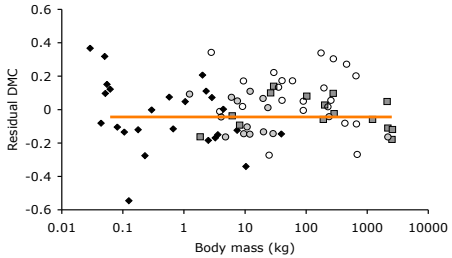


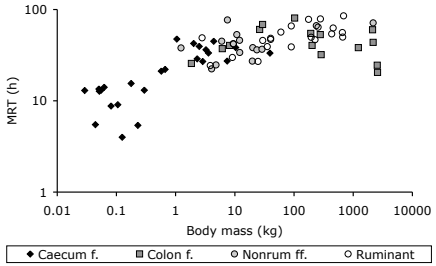
Digestibility



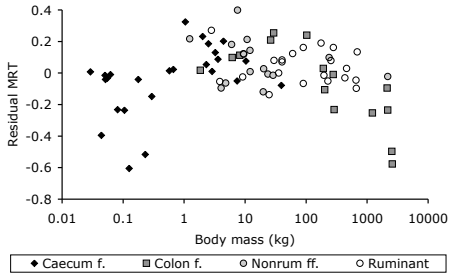


Dry matter gut content

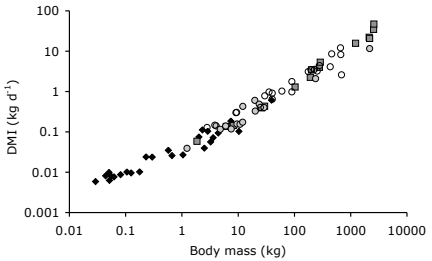




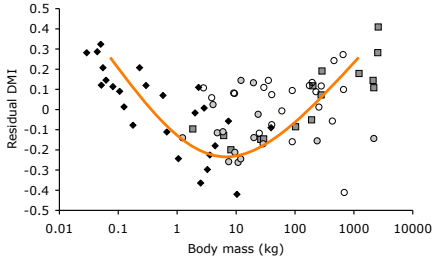
Particle retention time

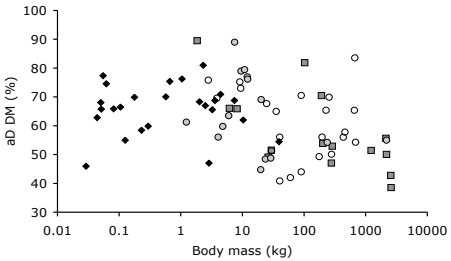


The curvature in herbivore digestive physiology - plotting residuals

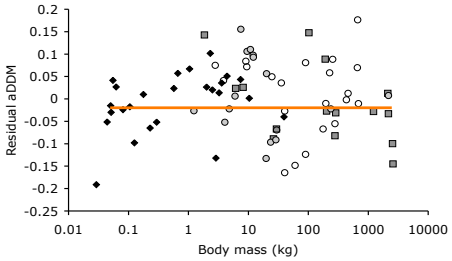


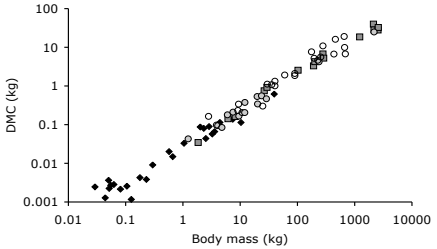
Dry matter intake



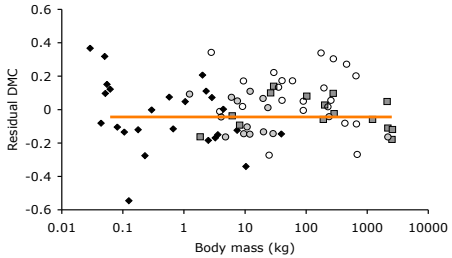


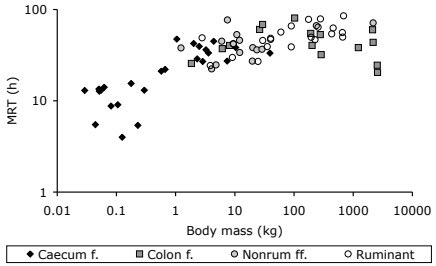
Digestibility



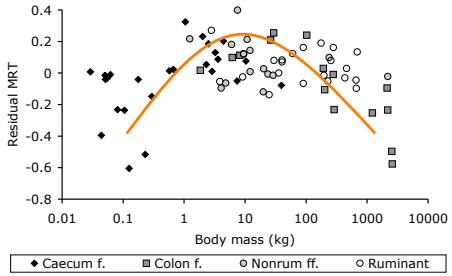


Dry matter gut content

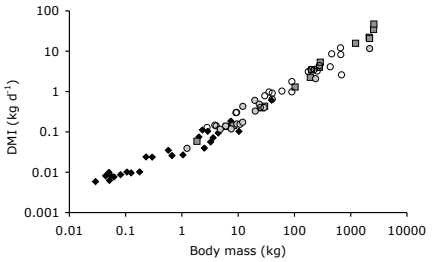




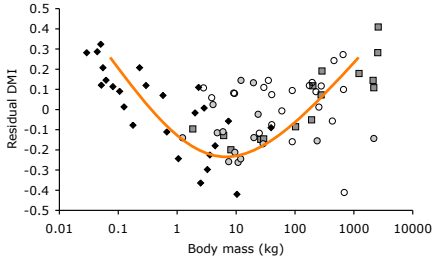
Particle retention time



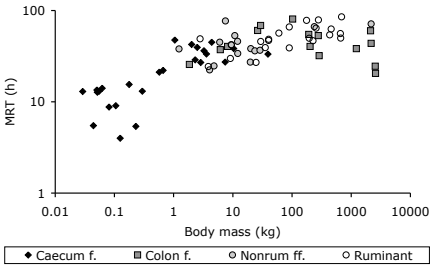
The curvature in herbivore digestive physiology - plotting residuals



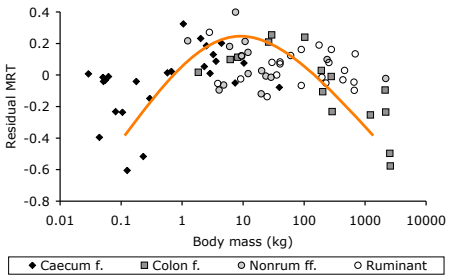
Dry matter intake



corresponding inverse curvatures



Particle retention time



The *really real* exponents

Measurement	Scaling (95%CI)	
	> 1 Litter size	= 1
Dry matter intake	0.66 (0.63-0.70)	0.86 (0.82-0.91)
Digestibility	-0.02 (-0.05--0.01)	-0.05 (-0.07--0.03)
Dry matter gut fill	0.91 (0.83-0.99)	0.94 (0.89-0.98)
Particle retention time	0.23 (0.16-0.31)	0.05 (0.01-0.09)
	< 10 kg body mass	> 10 kg
Dry matter intake	0.62 (0.57-0.68)	0.89 (0.82-0.96)
Digestibility	0.02 (-0.01-0.05)	-0.03 (-0.07-0.01)
Dry matter gut fill	0.91 (0.83-0.98)	0.92 (0.85-0.99)
Particle retention time	0.30 (0.22-0.37)	0.03 (-0.04-0.09)

The *really real* exponents

Measurement	Scaling (95%CI)	
	> 1 Litter size	= 1
Dry matter intake	0.66 (0.63-0.70)	0.86 (0.82-0.91)
Digestibility	-0.02 (-0.05--0.01)	-0.05 (-0.07--0.03)
Dry matter gut fill	0.91 (0.83-0.99)	0.94 (0.89-0.98)
Particle retention time	0.23 (0.16-0.31)	0.05 (0.01-0.09)
	< 10 kg body mass	> 10 kg
Dry matter intake	0.62 (0.57-0.68)	0.89 (0.82-0.96)
Digestibility	0.02 (-0.01-0.05)	-0.03 (-0.07-0.01)
Dry matter gut fill	0.91 (0.83-0.98)	0.92 (0.85-0.99)
Particle retention time	0.30 (0.22-0.37)	0.03 (-0.04-0.09)

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

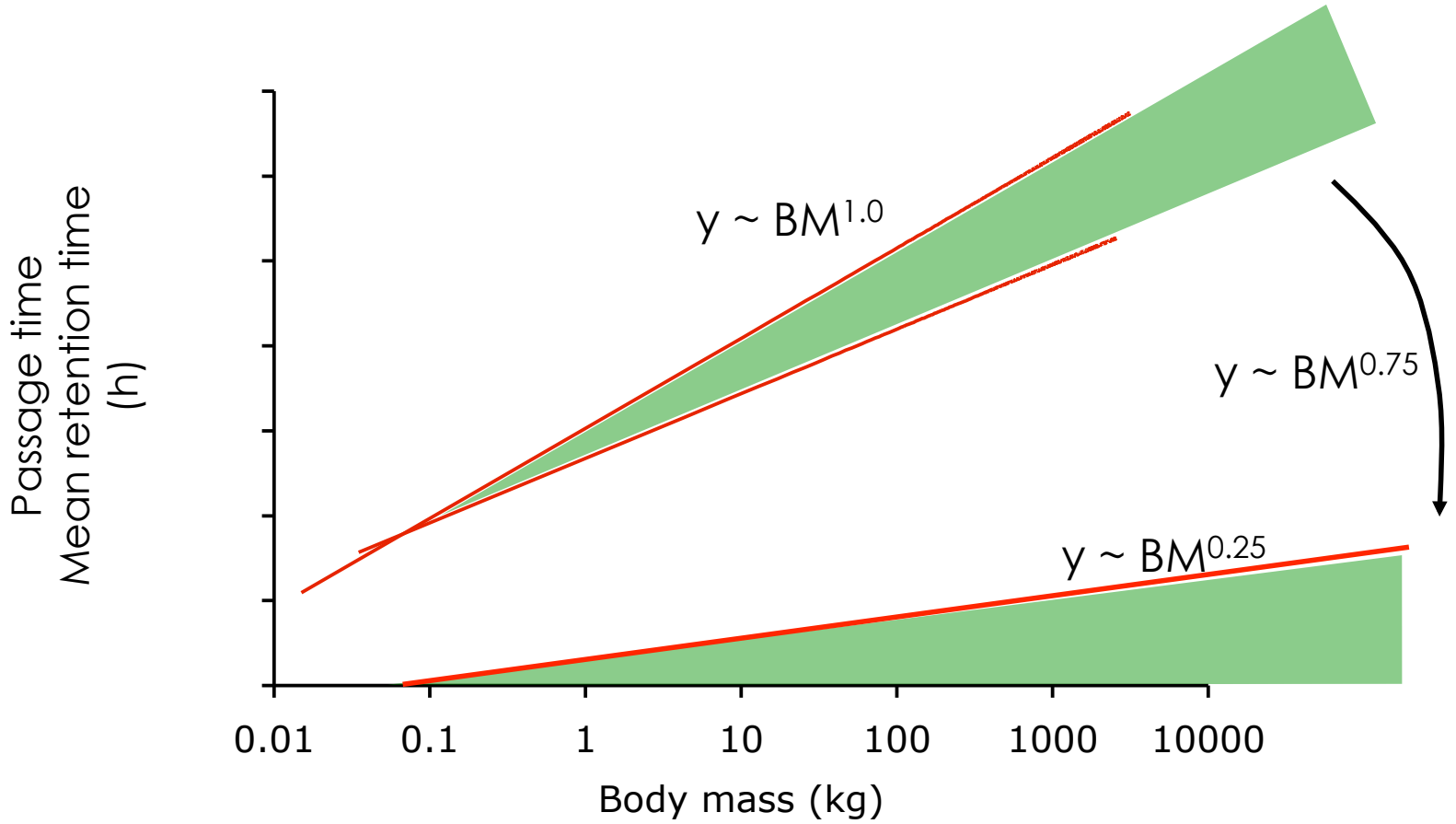
(vary sequence to suit your preference or intellectual capacity)

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)

Circular reasoning



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

A logical flaw

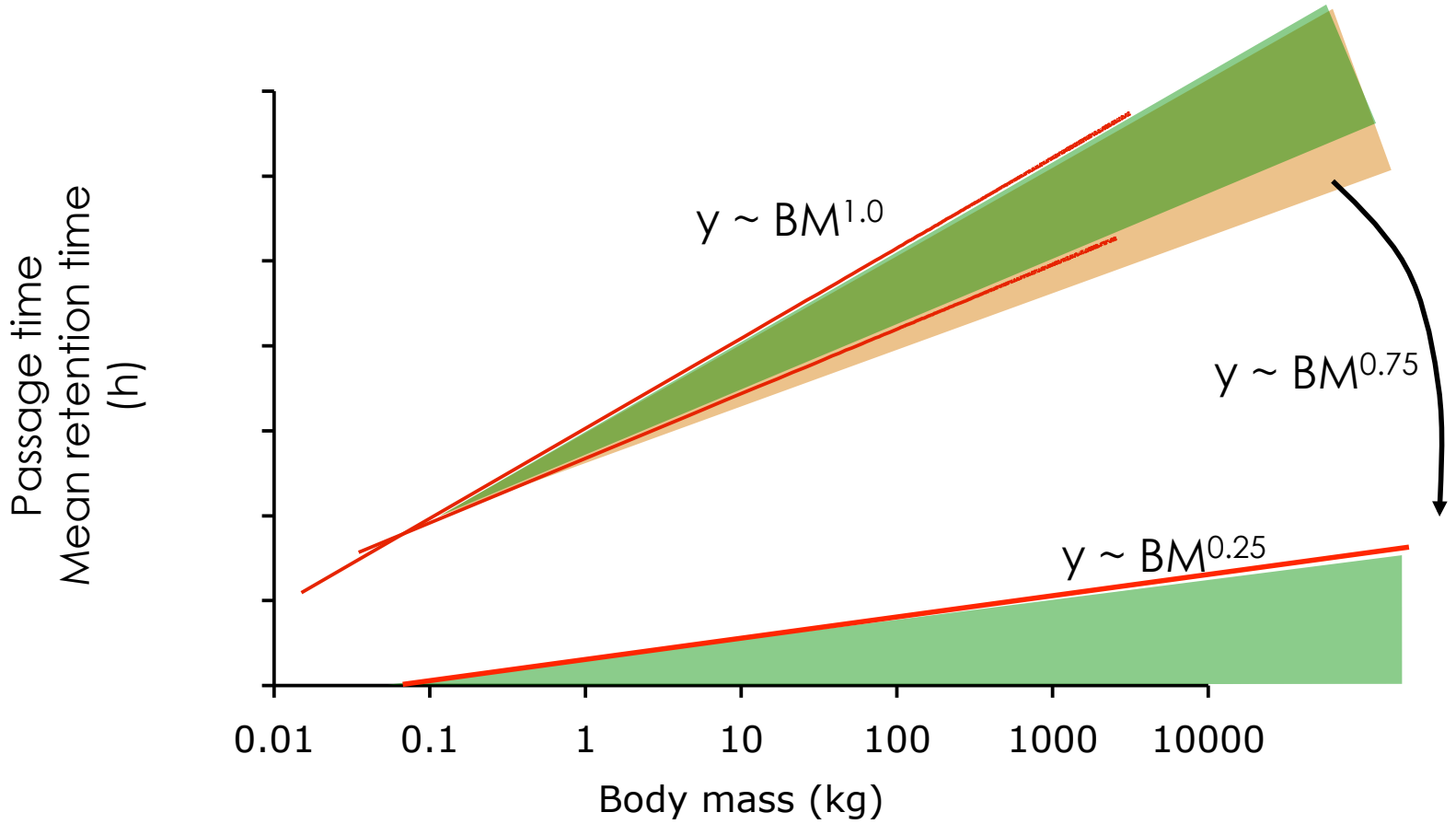
The time digesta passes through the gut depends on

- the size of the gut (capacity) BM^a
- the intake rate (how much per unit time) BM^b
- ***... and the digestibility*** (how much material disappears without 'pushing on'!) BM^c

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

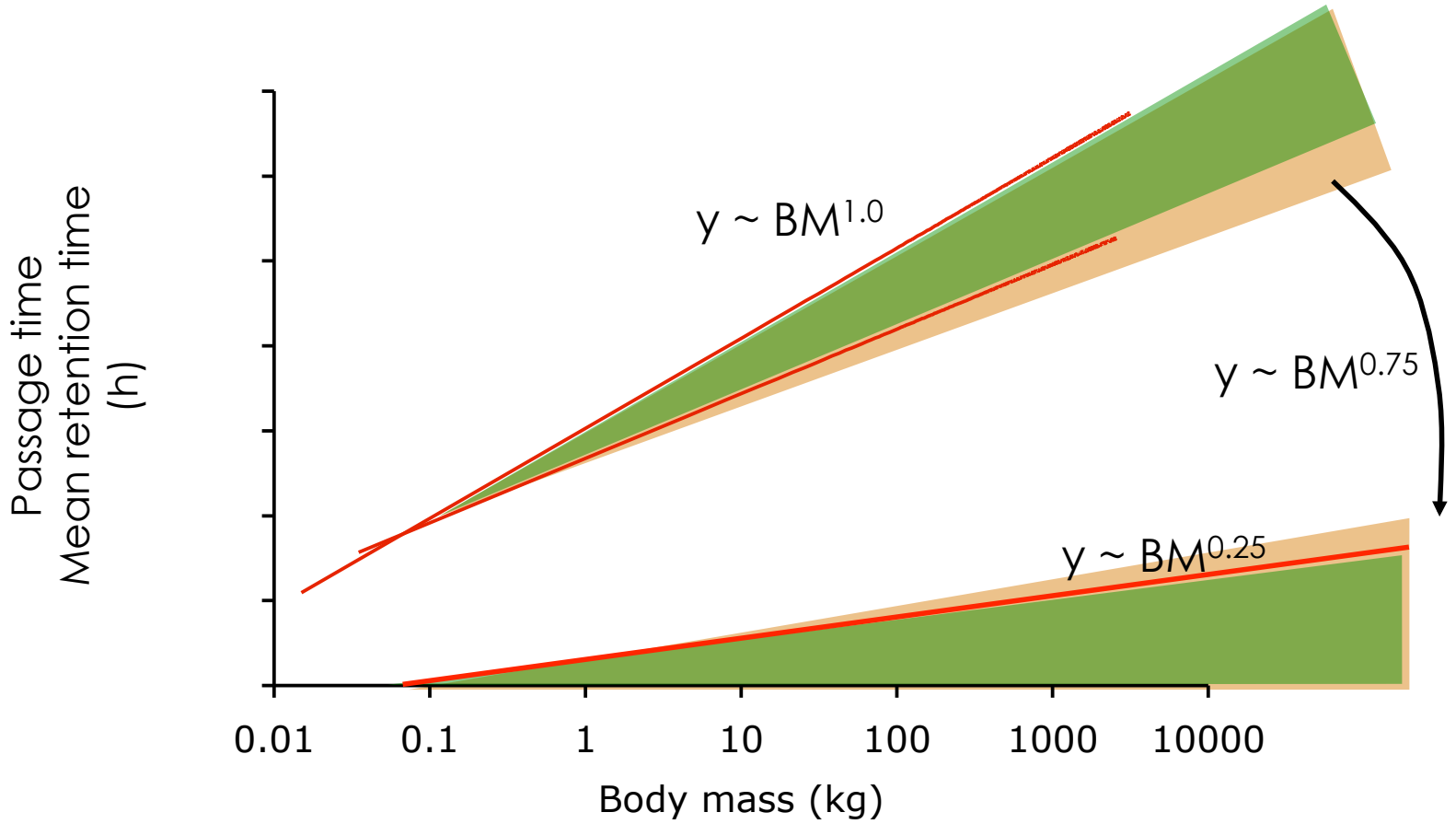
One cannot use the thus-derived scaling of MRT to make conclusions on the scaling of digestibility!

Circular reasoning



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

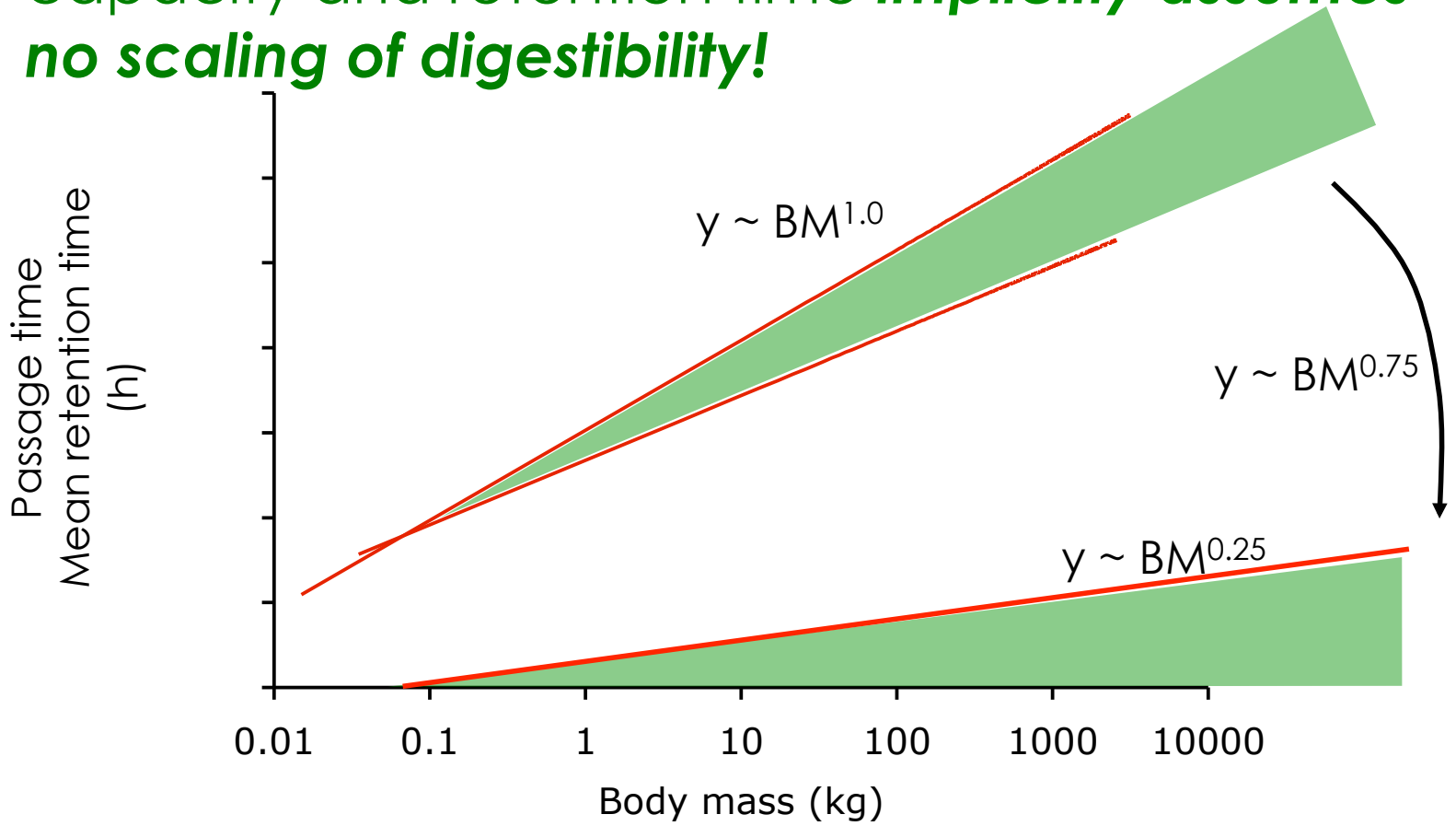
Circular reasoning



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

Circular reasoning

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



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

Checking the validity of a concept

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)

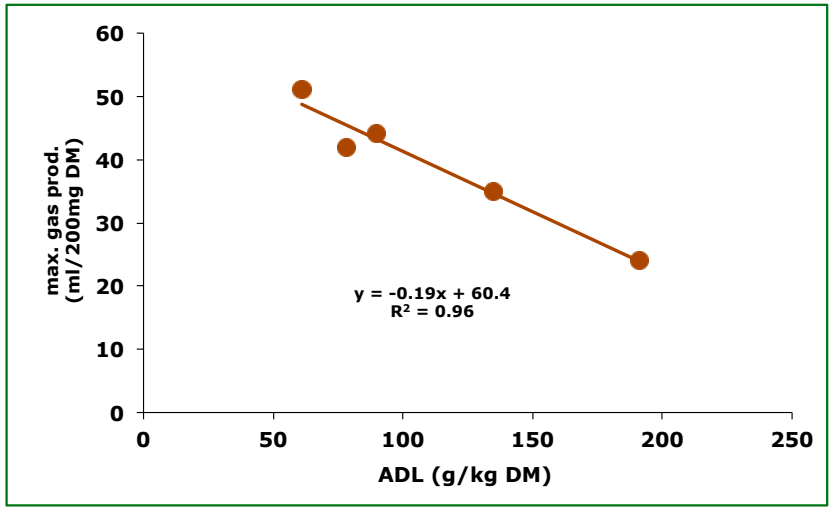
Checking the validity of a concept

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

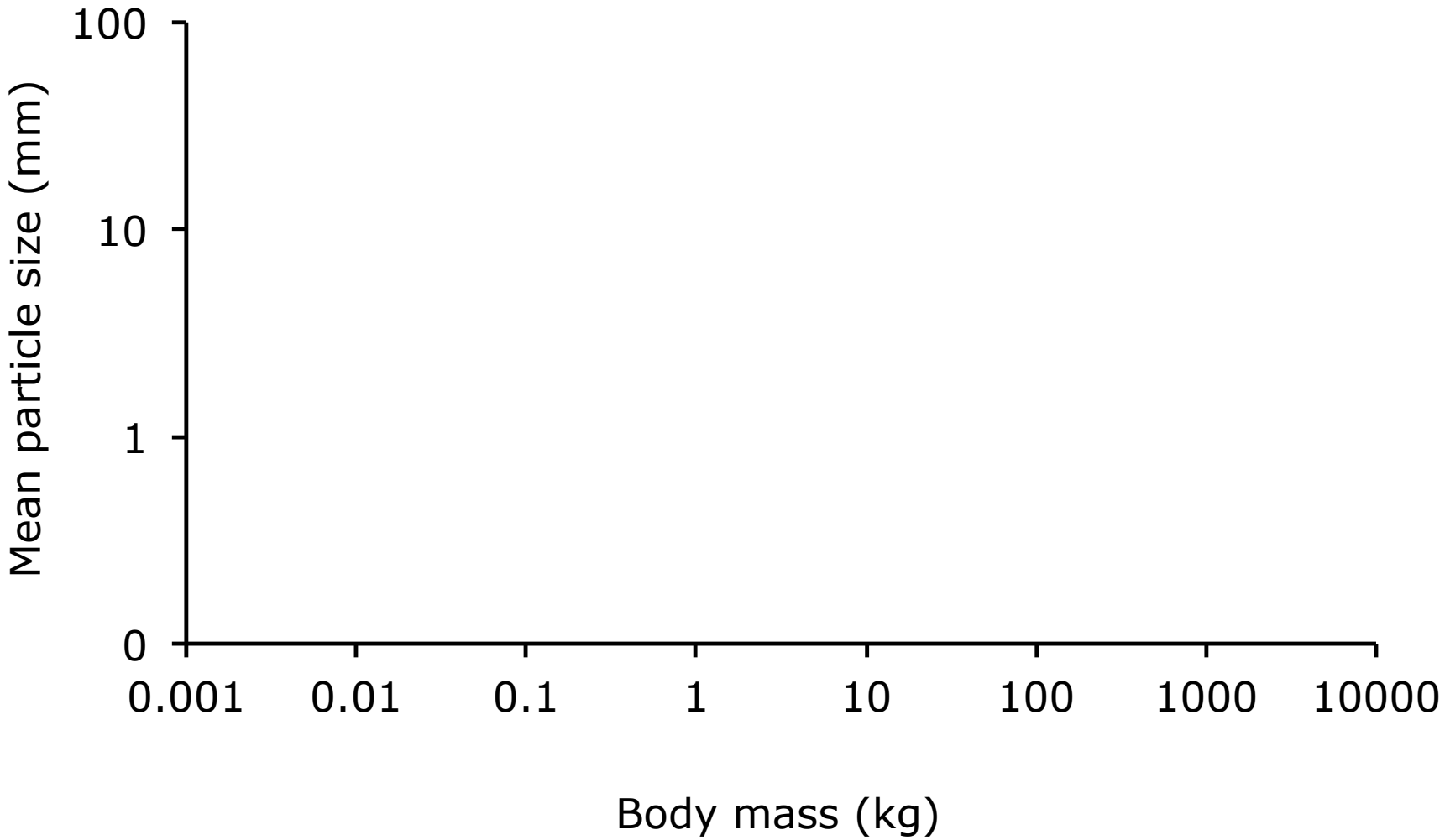
2. What about other, potential digestive disadvantages linked to larger body size – such as

   - digesta particle size

   - methane losses

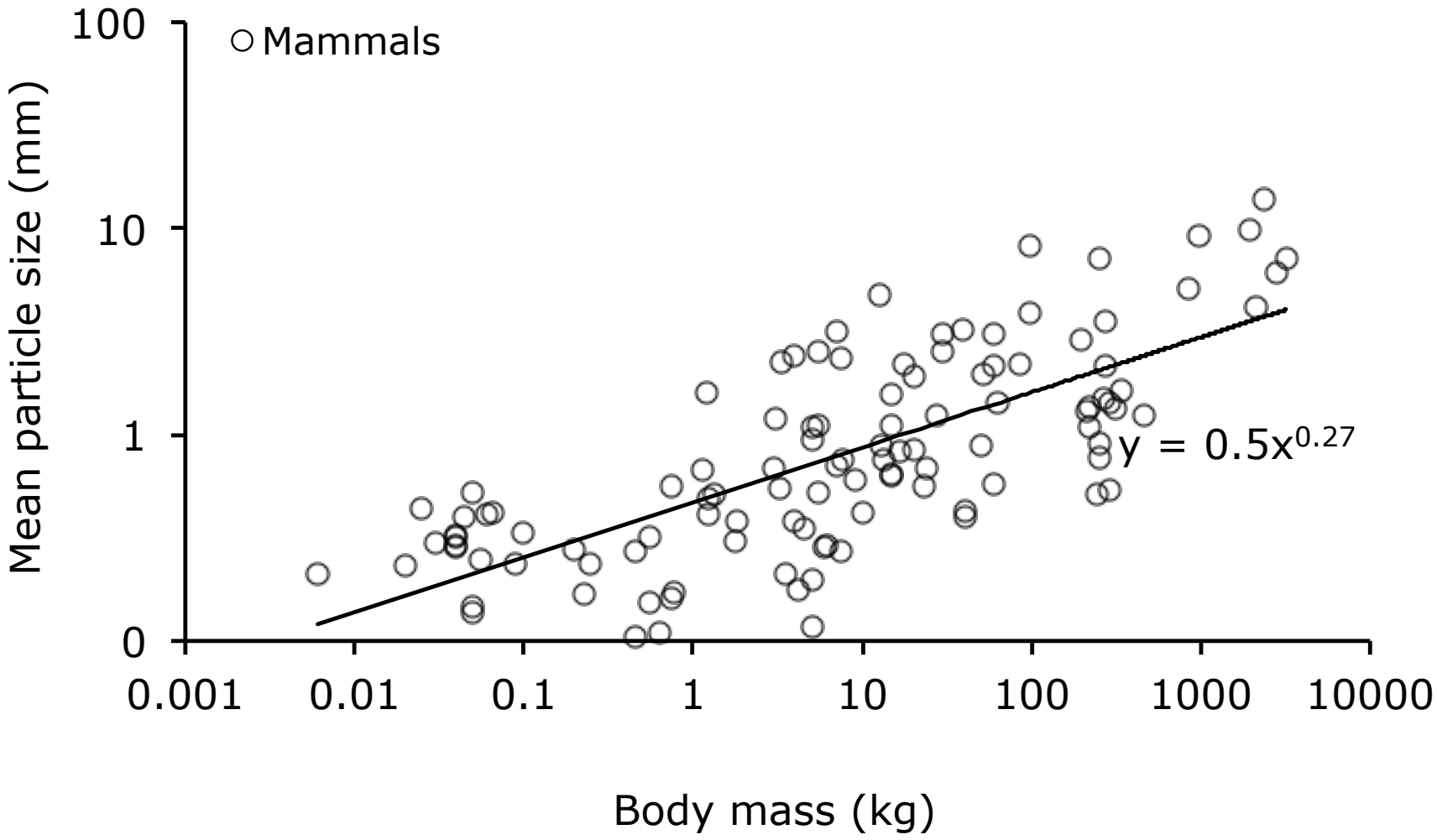
Particle size

Faecal particle size allometry in herbivores



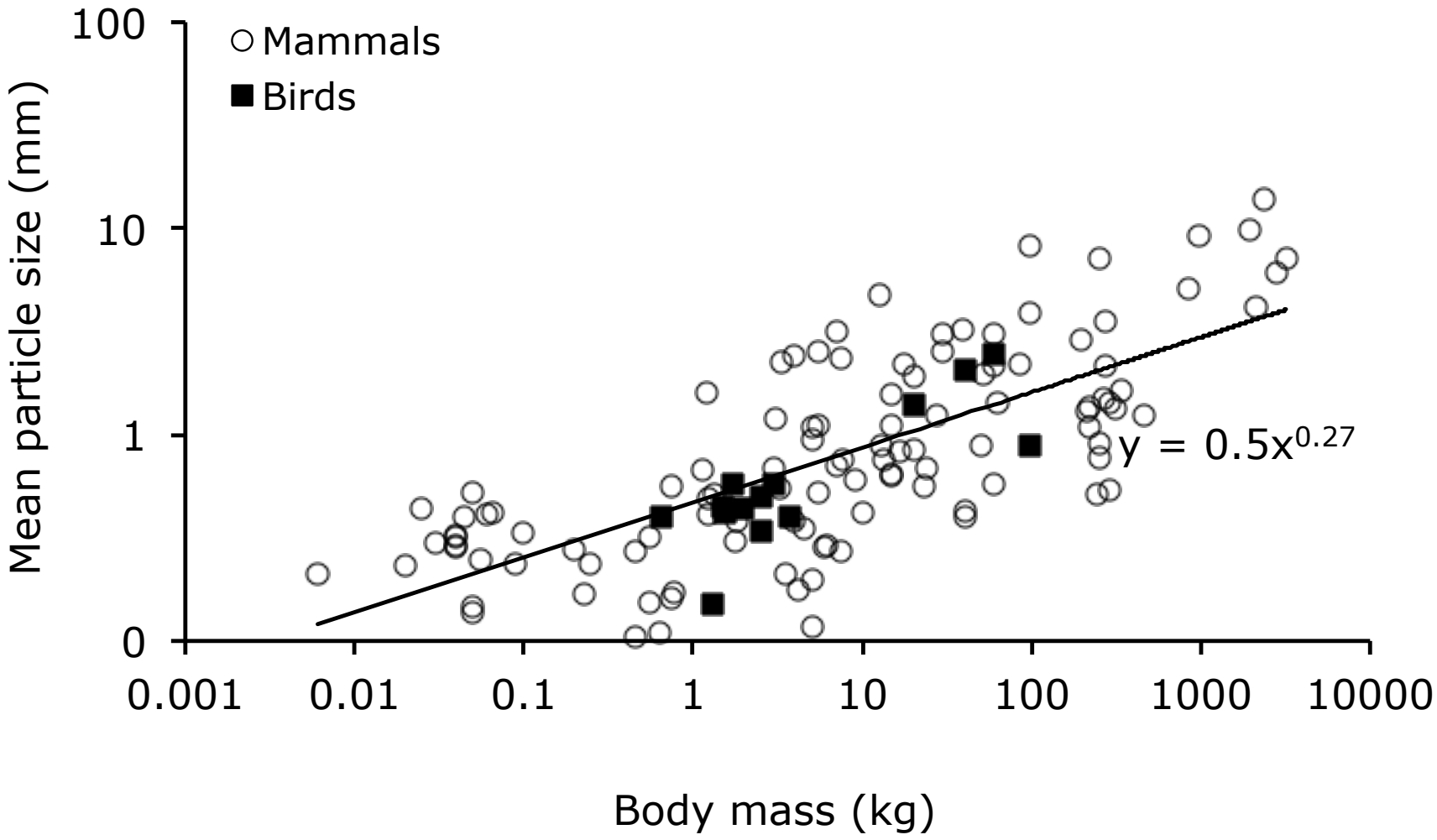
(Fritz et al. 209, 2010, 2011)

Faecal particle size allometry in herbivores



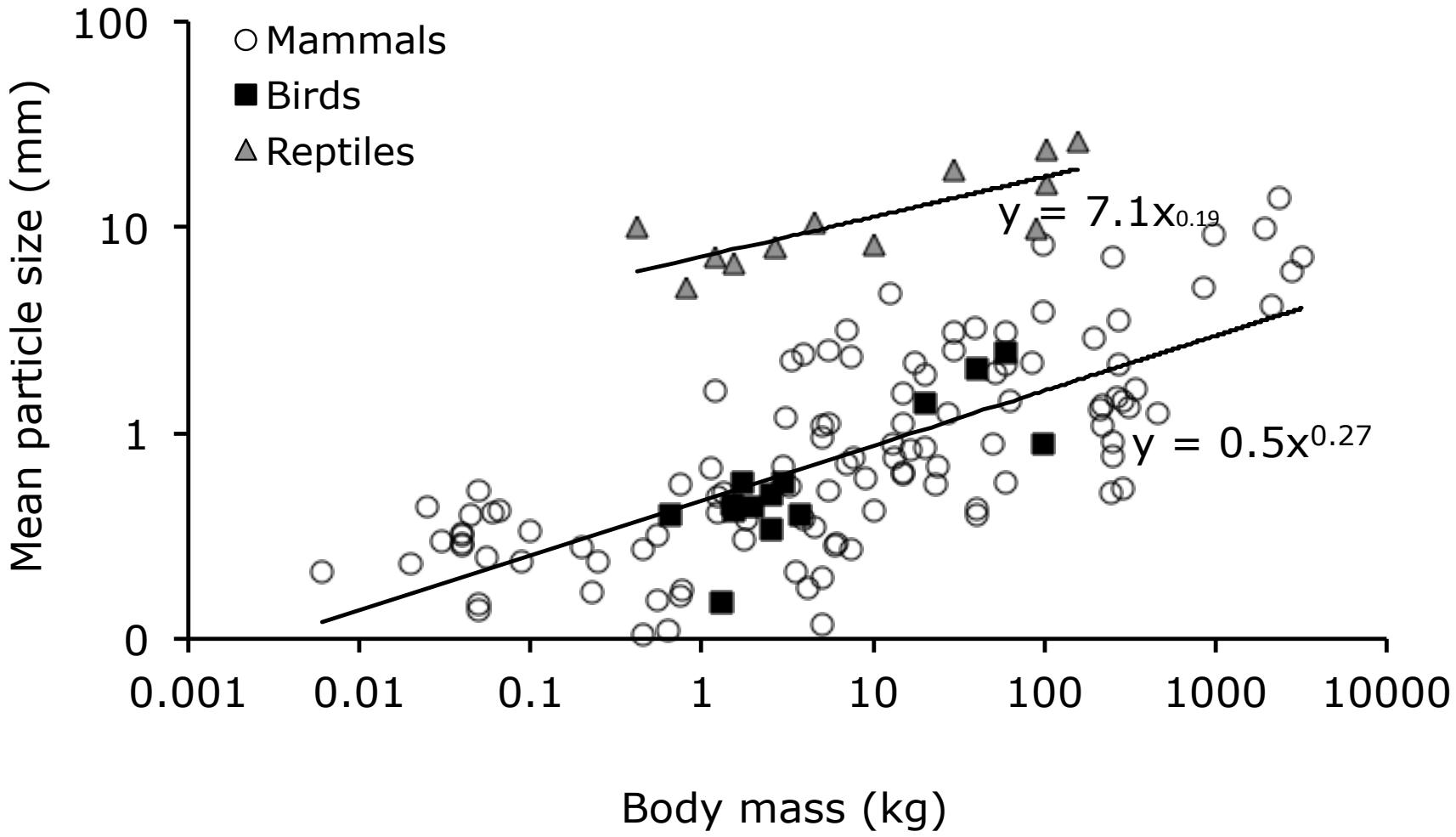
(Fritz et al. 209, 2010, 2011)

Faecal particle size allometry in herbivores



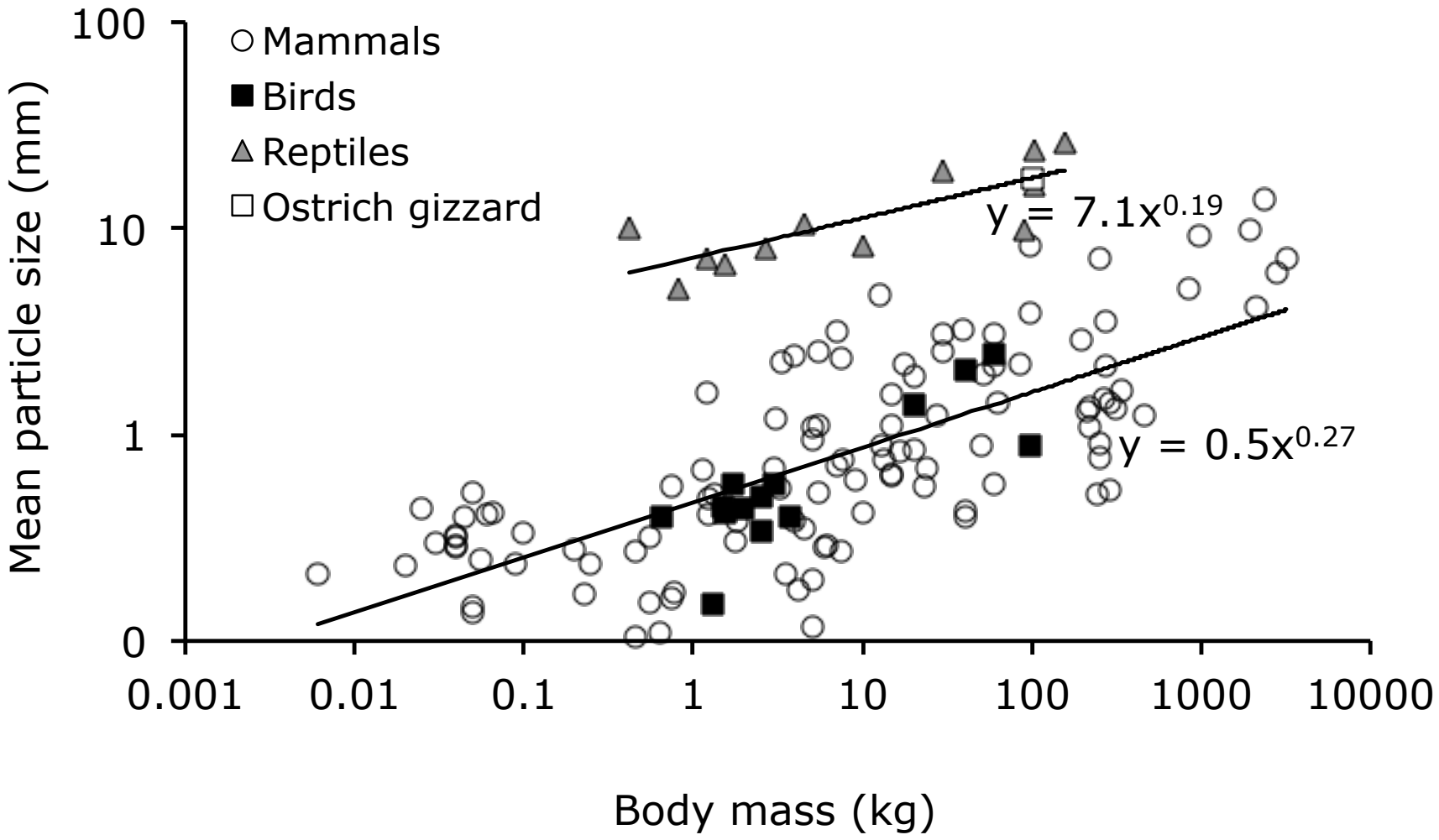
(Fritz et al. 209, 2010, 2011)

Faecal particle size allometry in herbivores



(Fritz et al. 209, 2010, 2011)

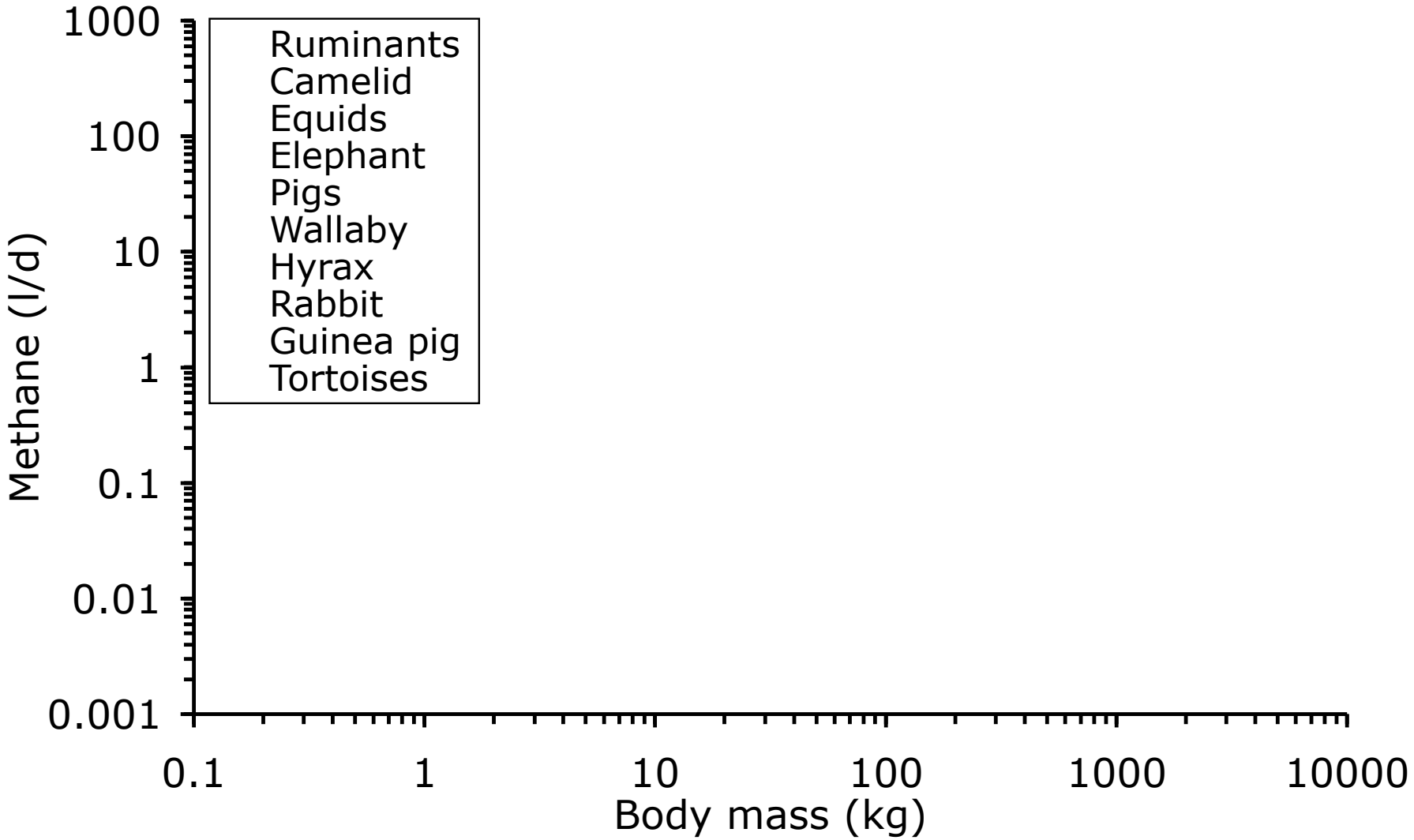
Faecal particle size allometry in herbivores



(Fritz et al. 209, 2010, 2011)

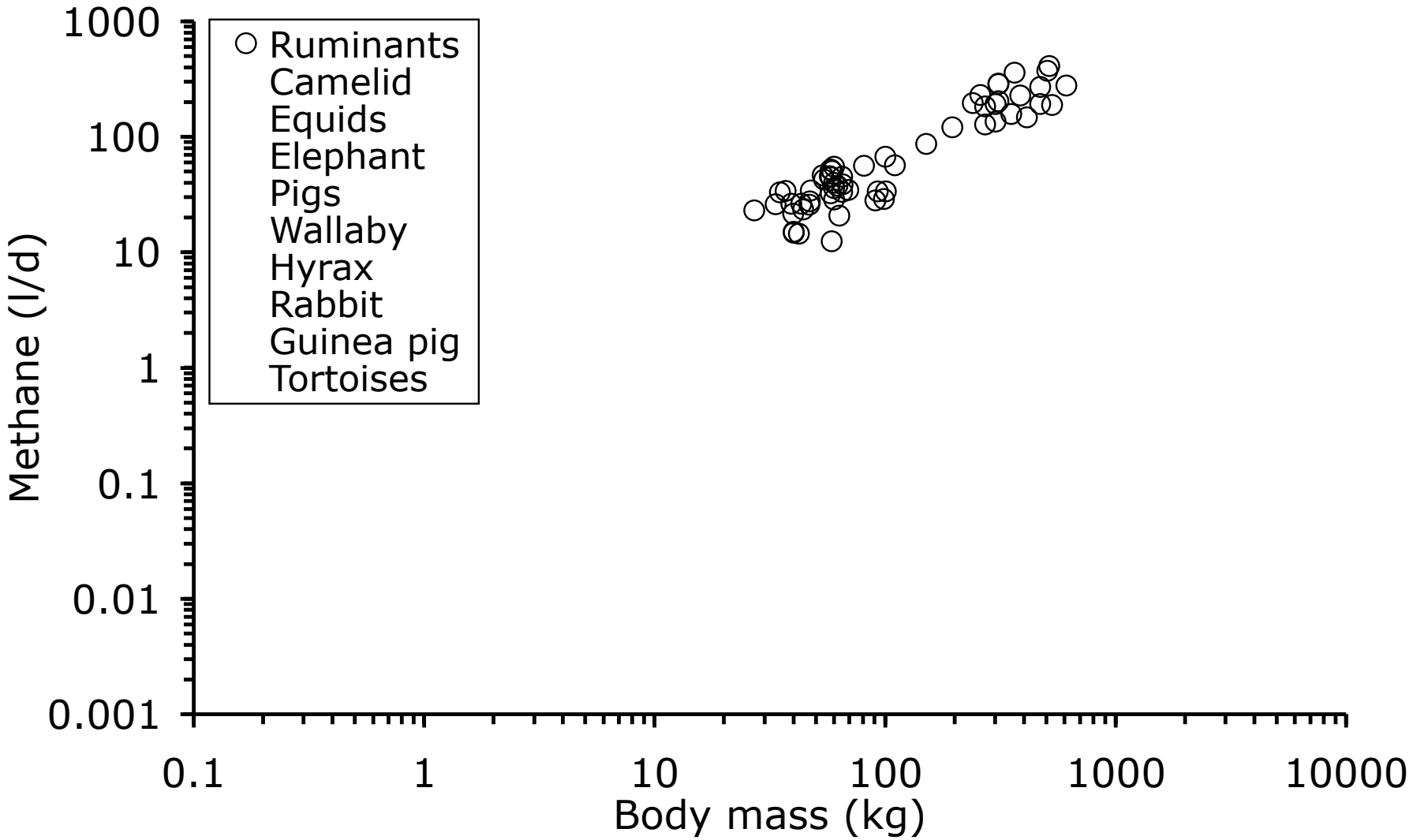
Methane

Methane allometry in herbivores



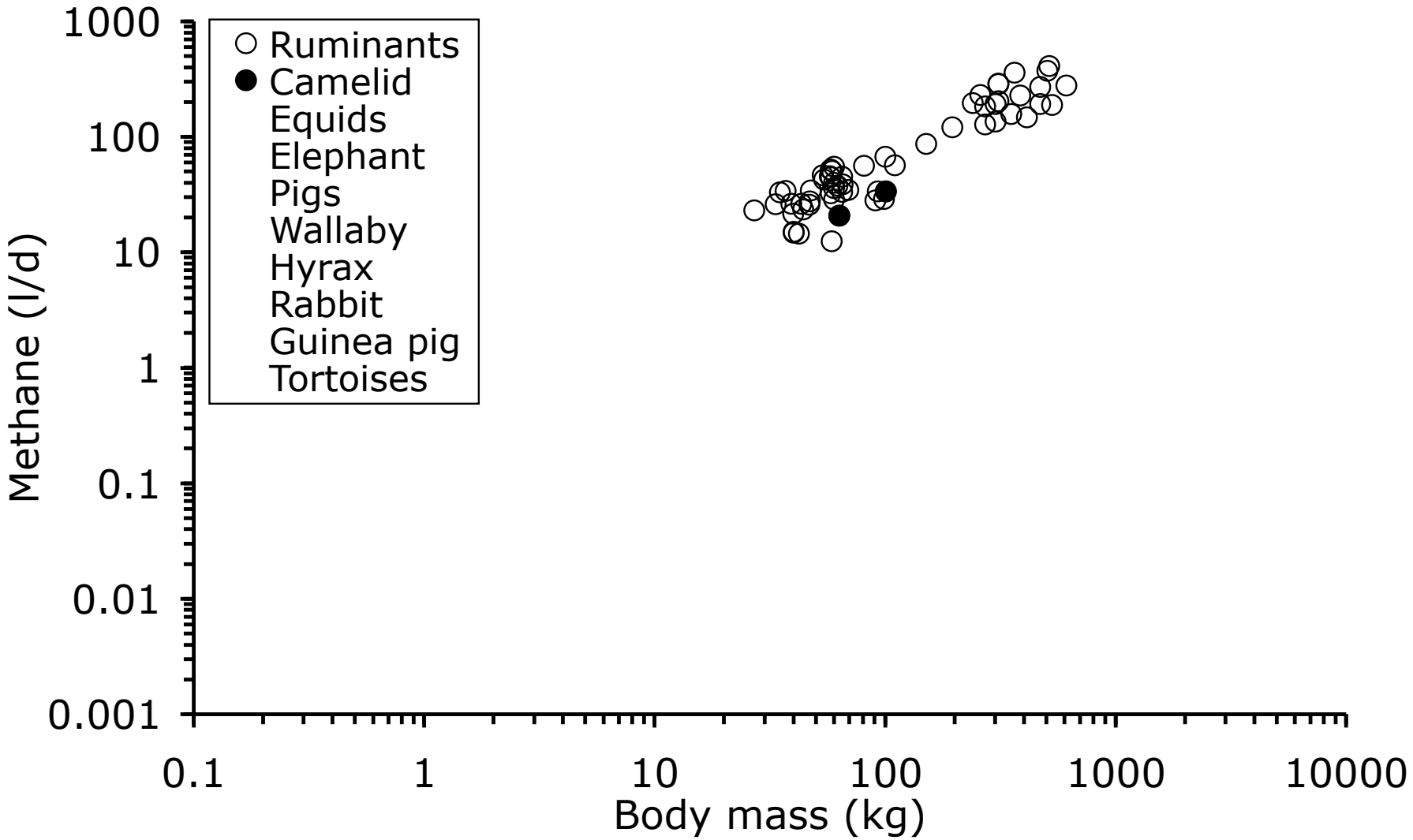
Literature collection and own data (Franz et al. 2010, 2011ab)

Methane allometry in herbivores



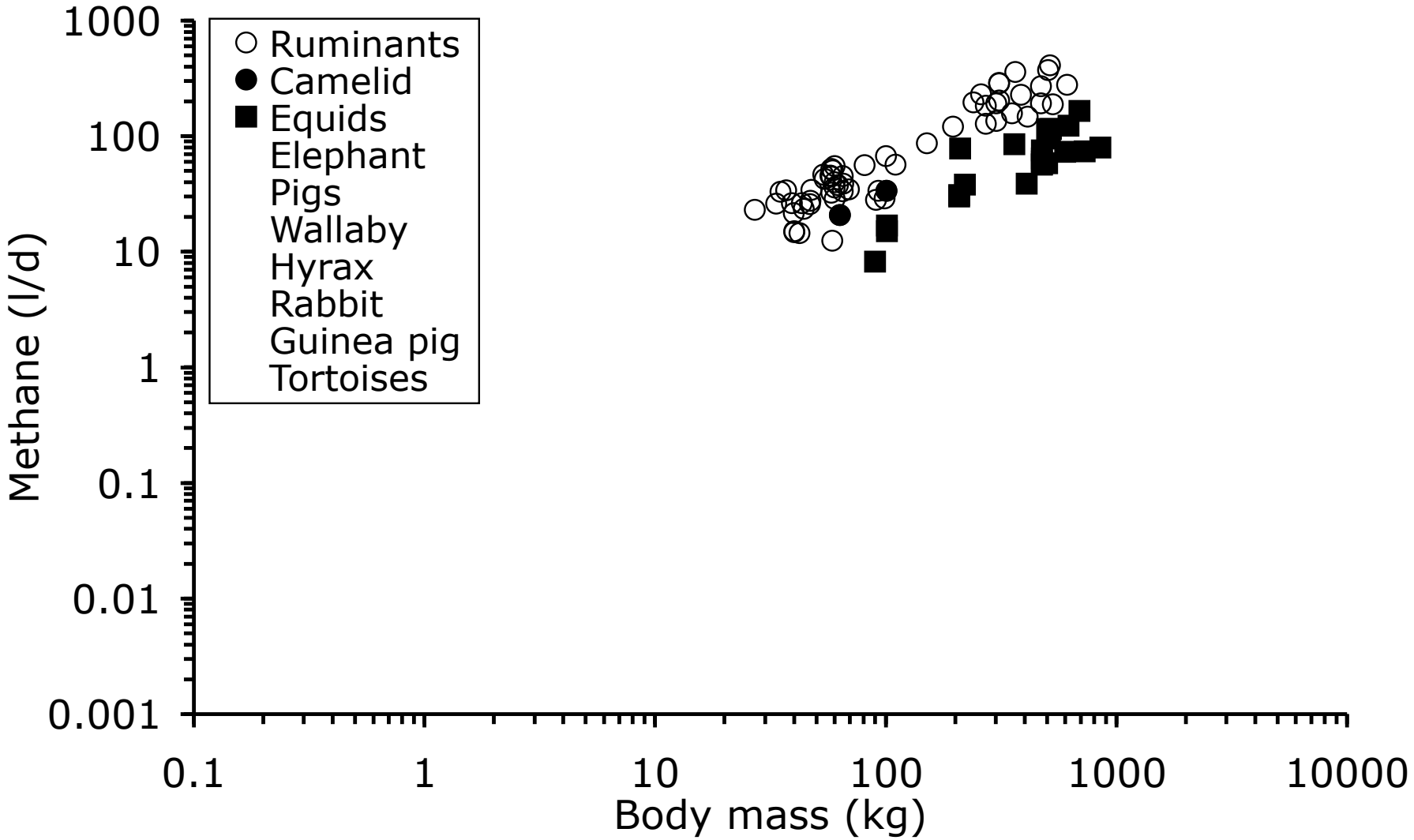
Literature collection and own data (Franz et al. 2010, 2011ab)

Methane allometry in herbivores



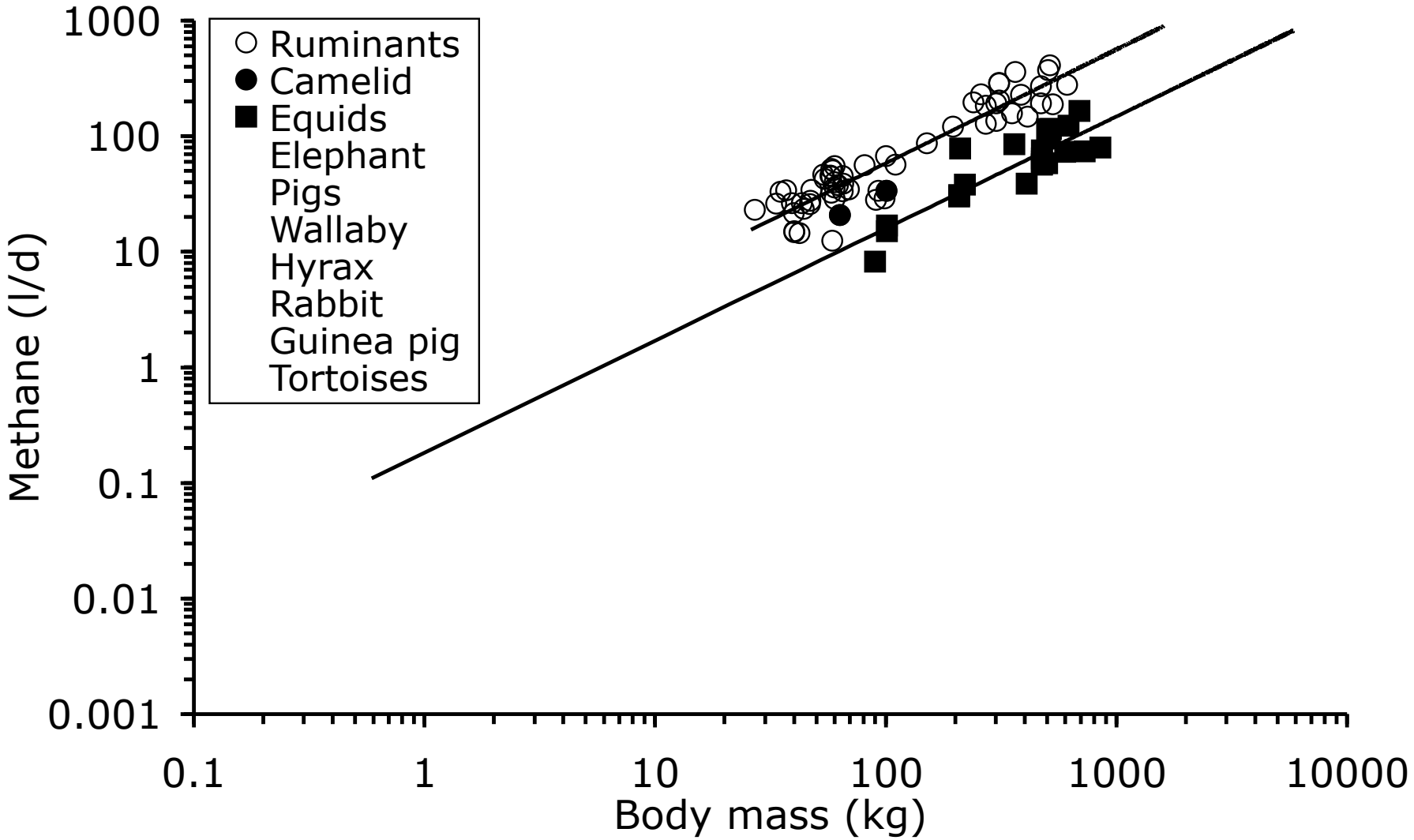
Literature collection and own data (Franz et al. 2010, 2011ab)

Methane allometry in herbivores



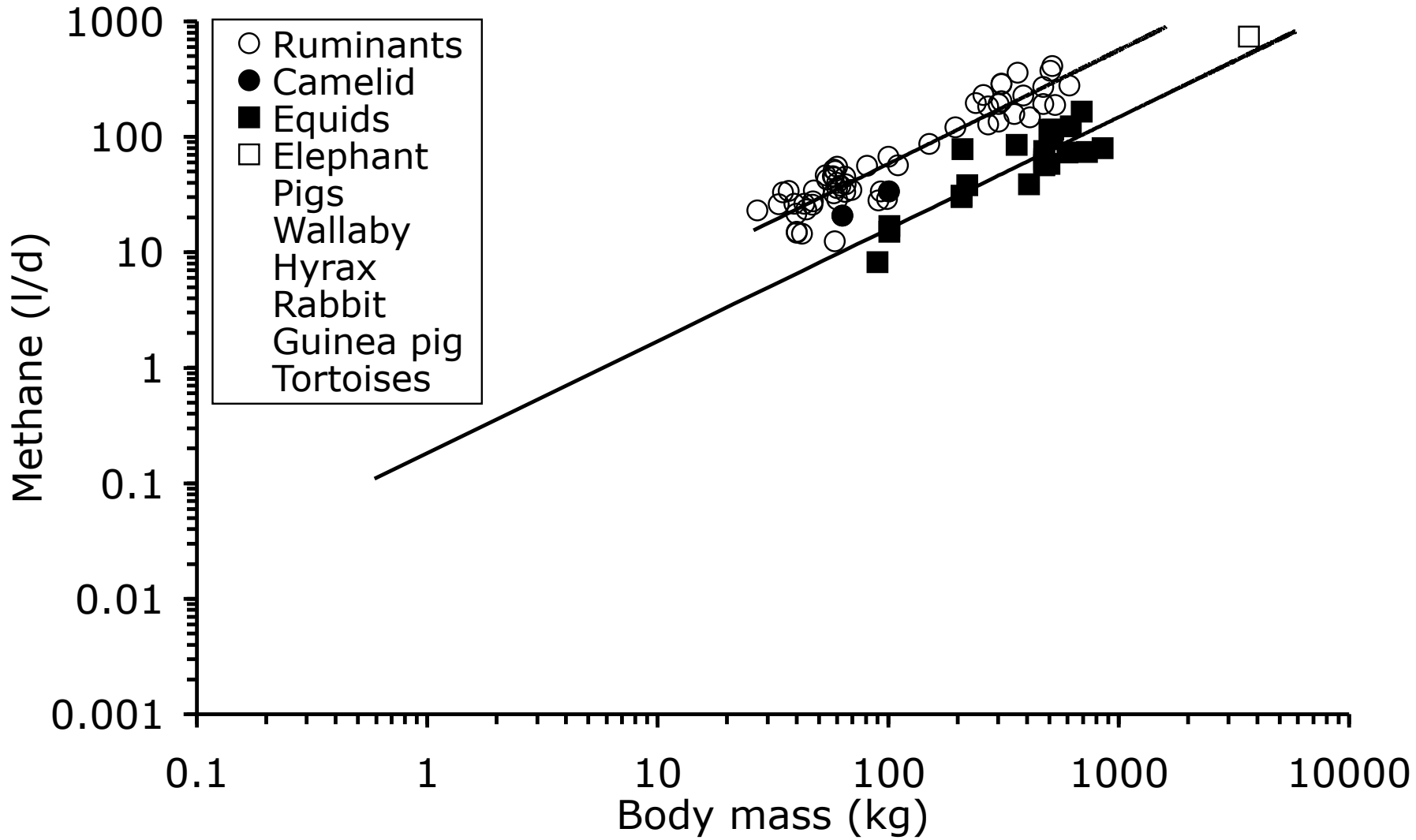
Literature collection and own data (Franz et al. 2010, 2011ab)

Methane allometry in herbivores



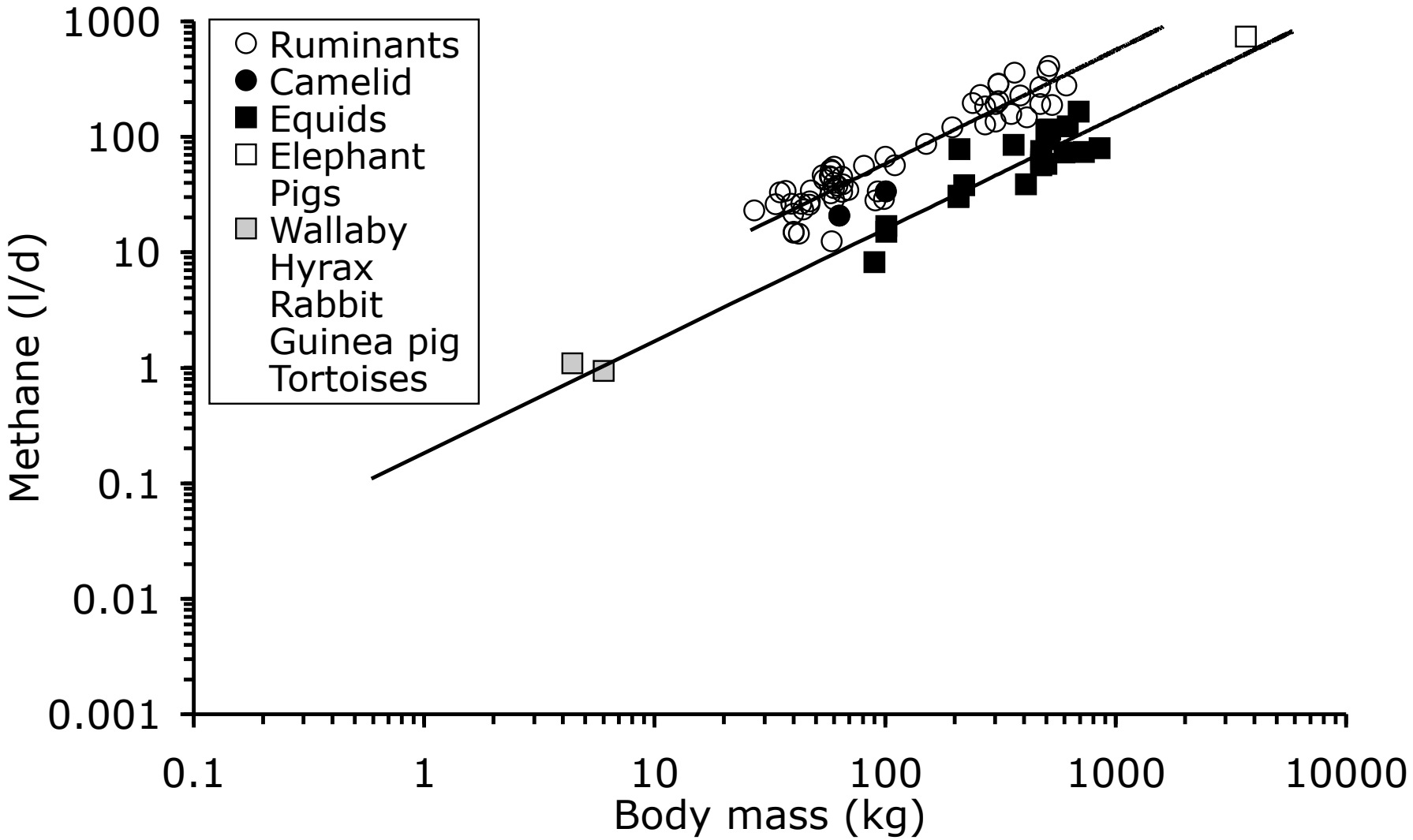
Literature collection and own data (Franz et al. 2010, 2011ab)

Methane allometry in herbivores



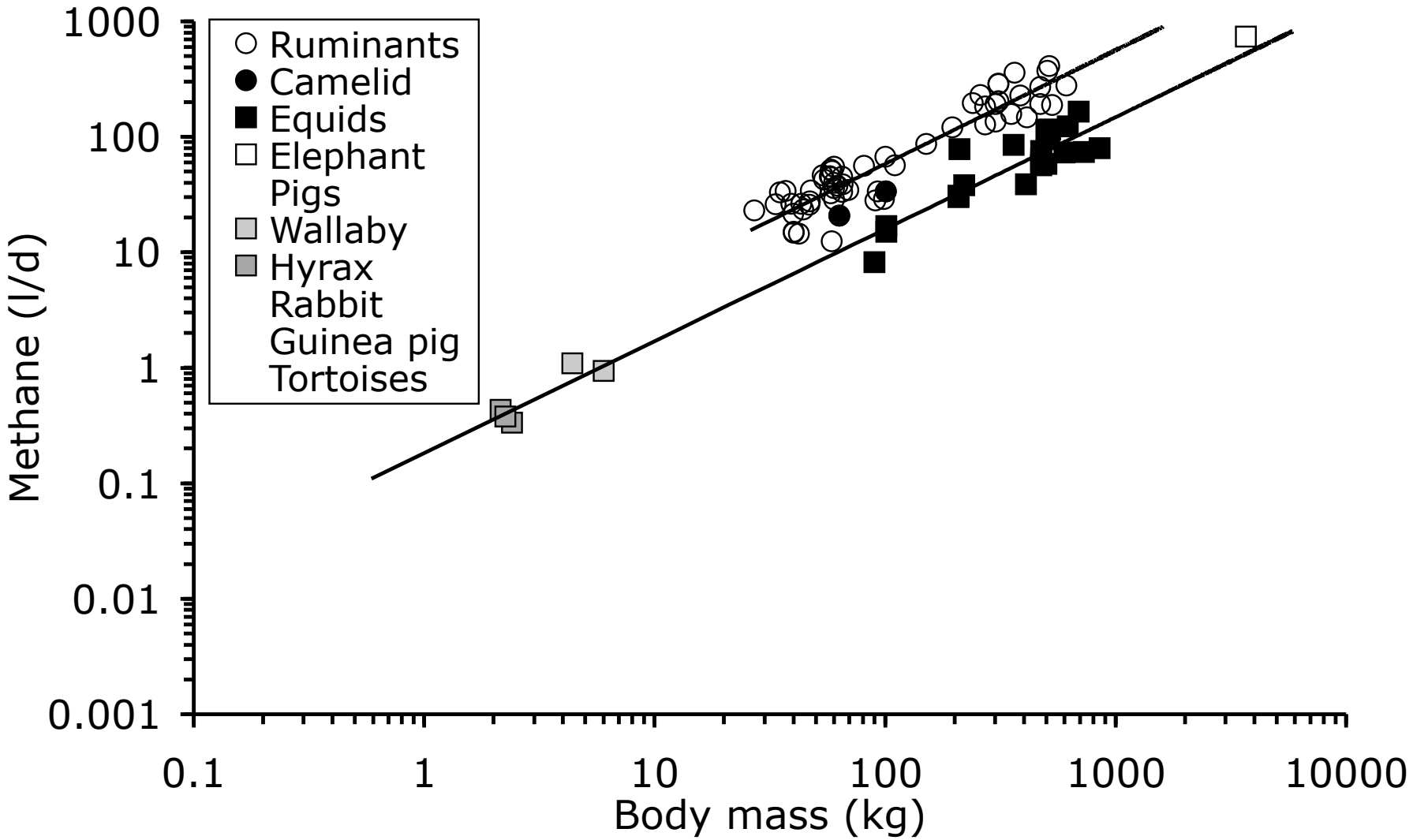
Literature collection and own data (Franz et al. 2010, 2011ab)

Methane allometry in herbivores



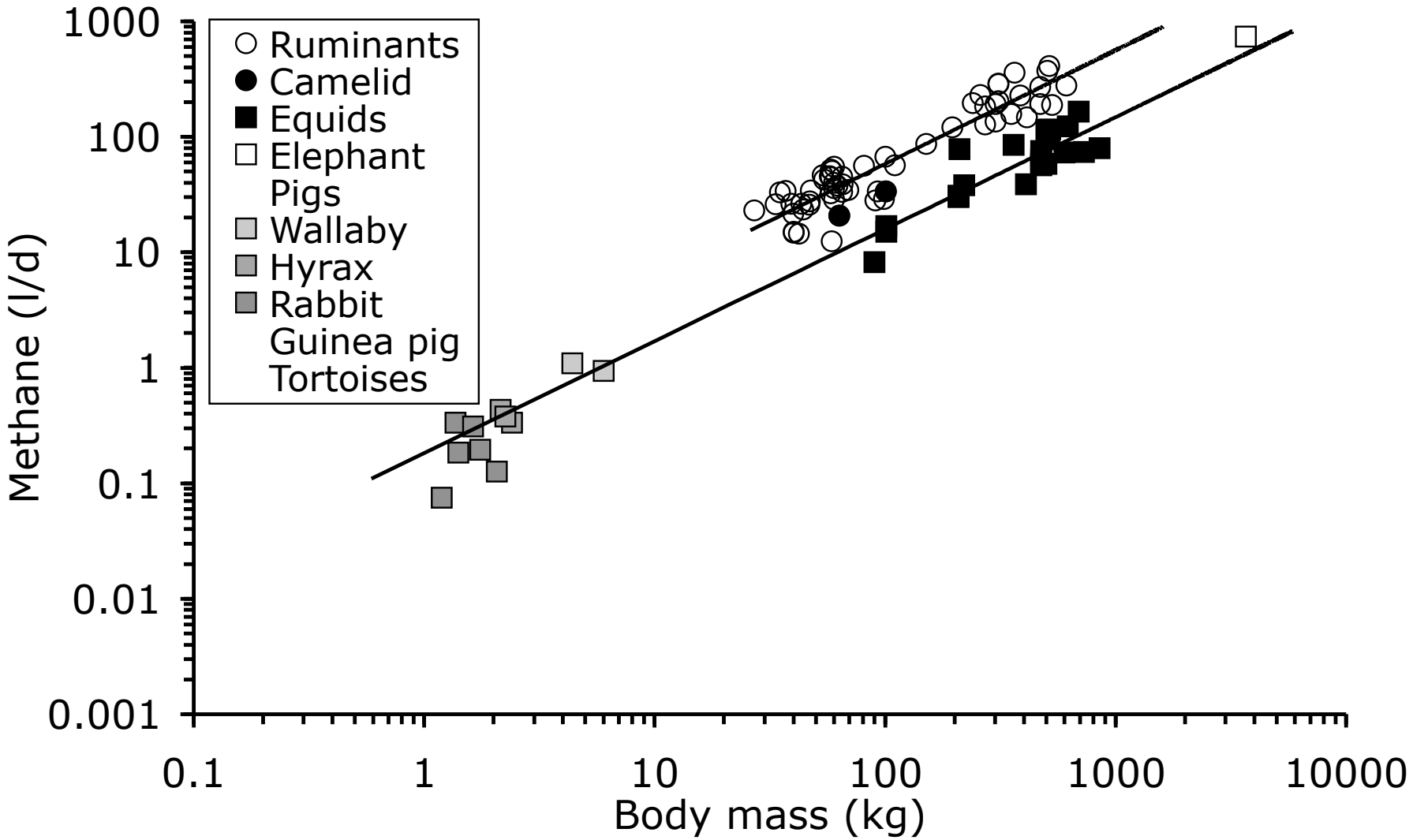
Literature collection and own data (Franz et al. 2010, 2011ab)

Methane allometry in herbivores



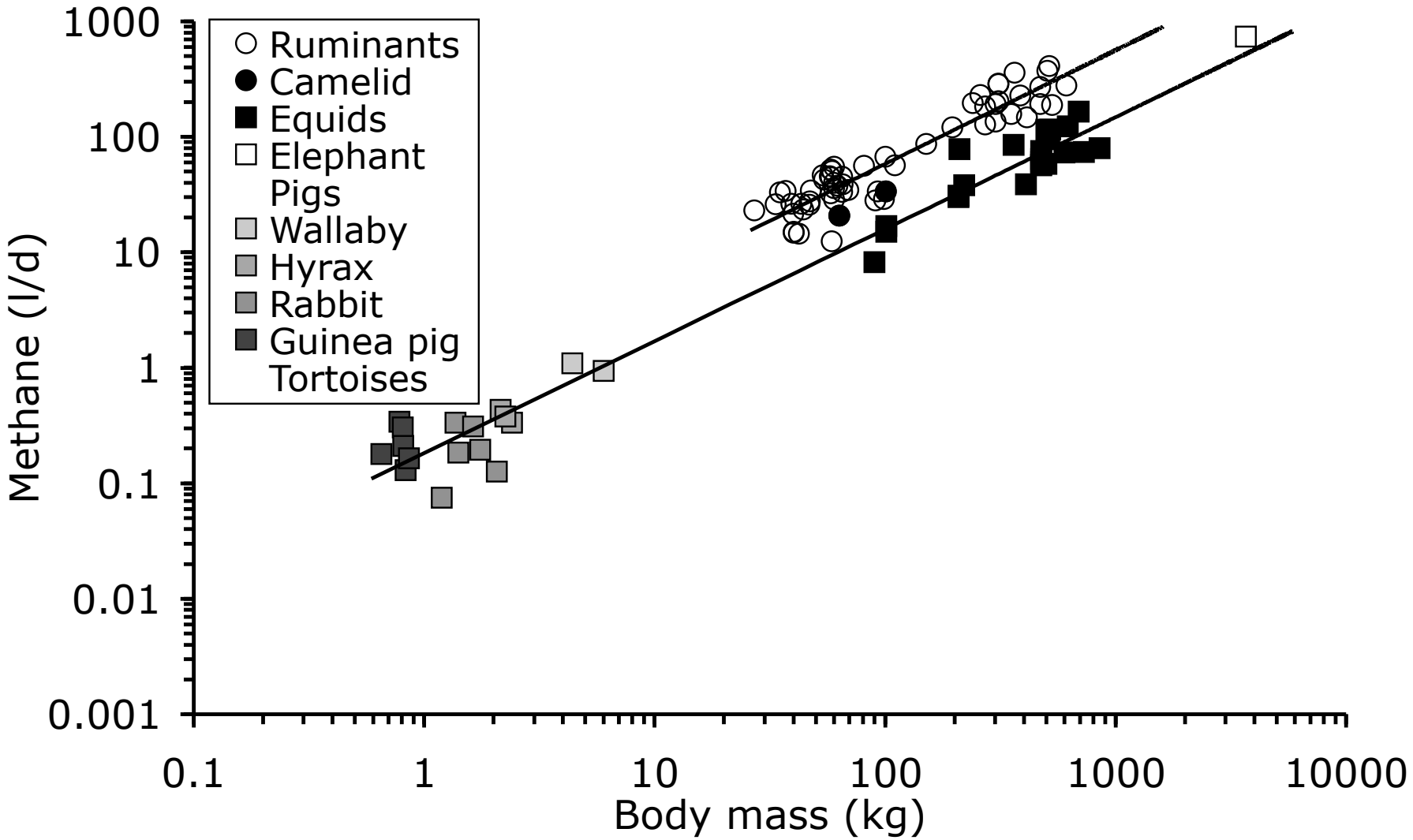
Literature collection and own data (Franz et al. 2010, 2011ab)

Methane allometry in herbivores



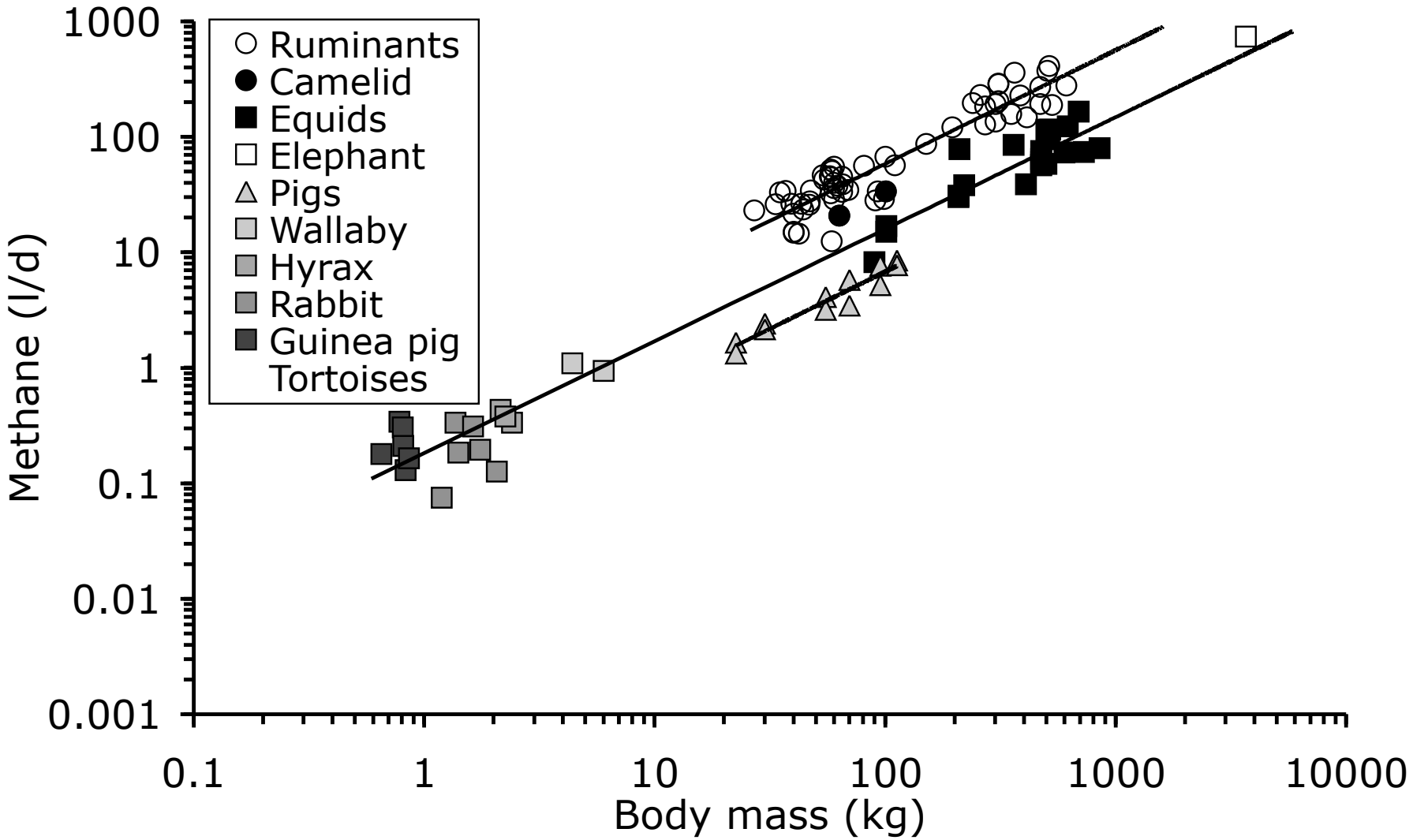
Literature collection and own data (Franz et al. 2010, 2011ab)

Methane allometry in herbivores



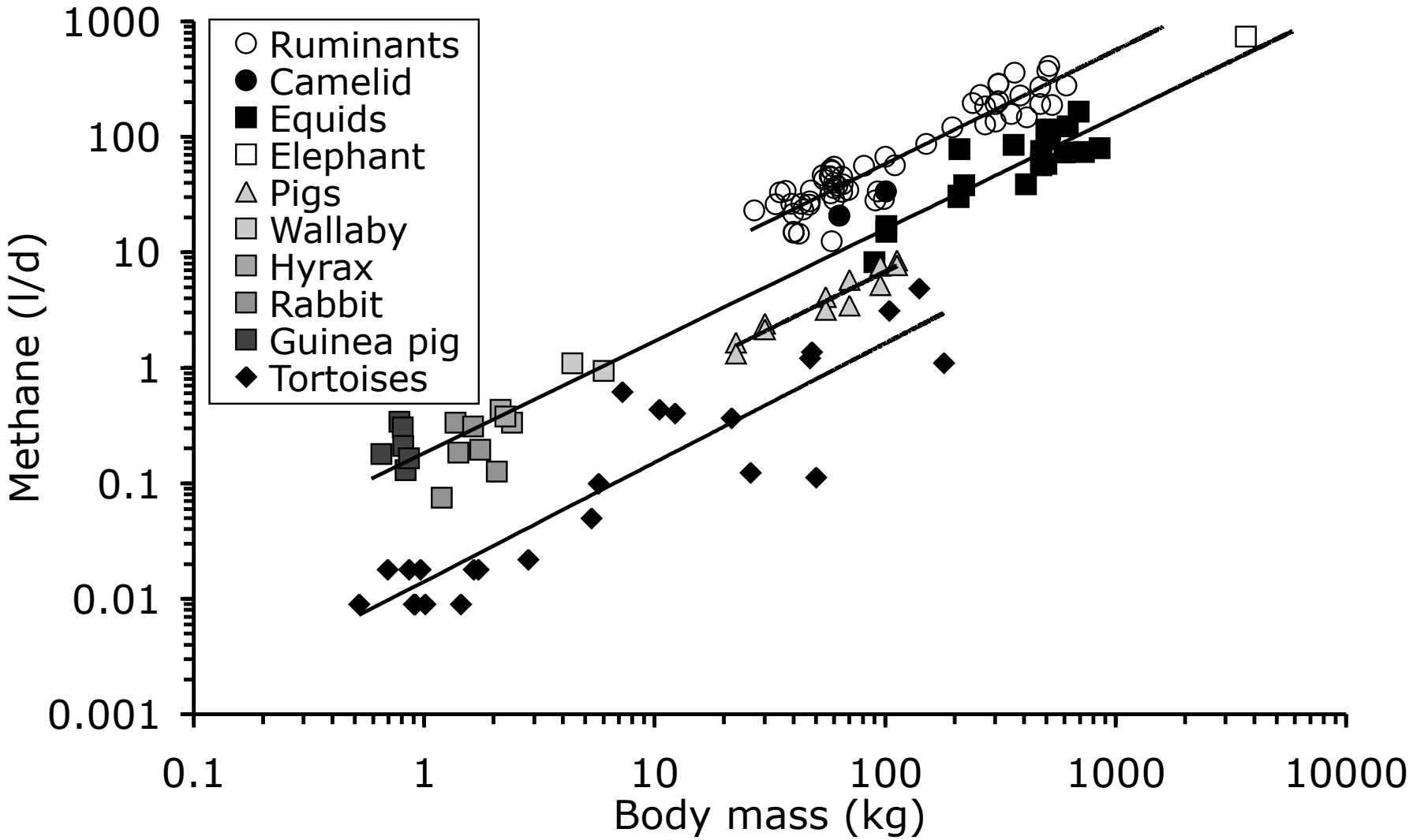
Literature collection and own data (Franz et al. 2010, 2011ab)

Methane allometry in herbivores



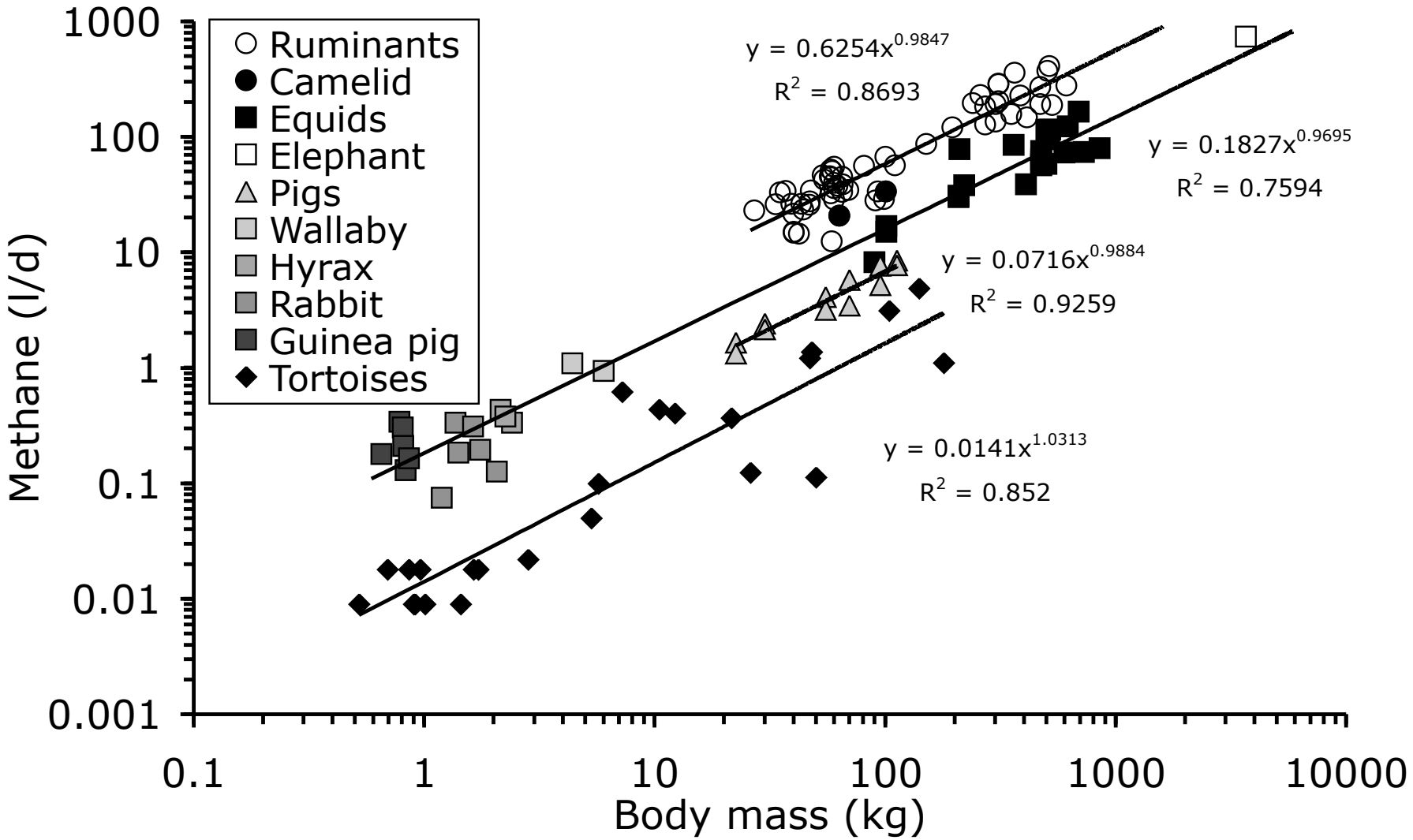
Literature collection and own data (Franz et al. 2010, 2011ab)

Methane allometry in herbivores



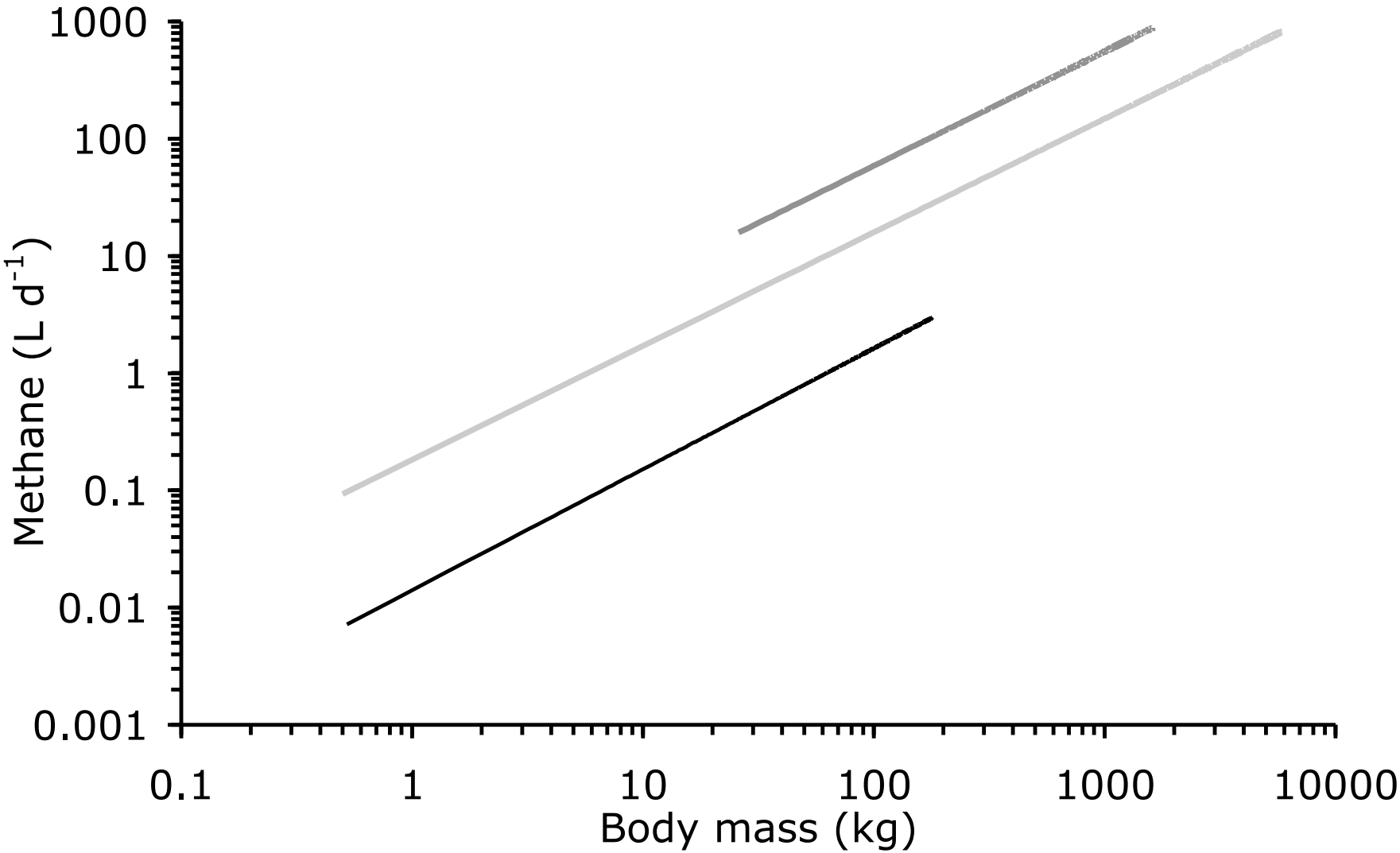
Literature collection and own data (Franz et al. 2010, 2011ab)

Methane allometry in herbivores



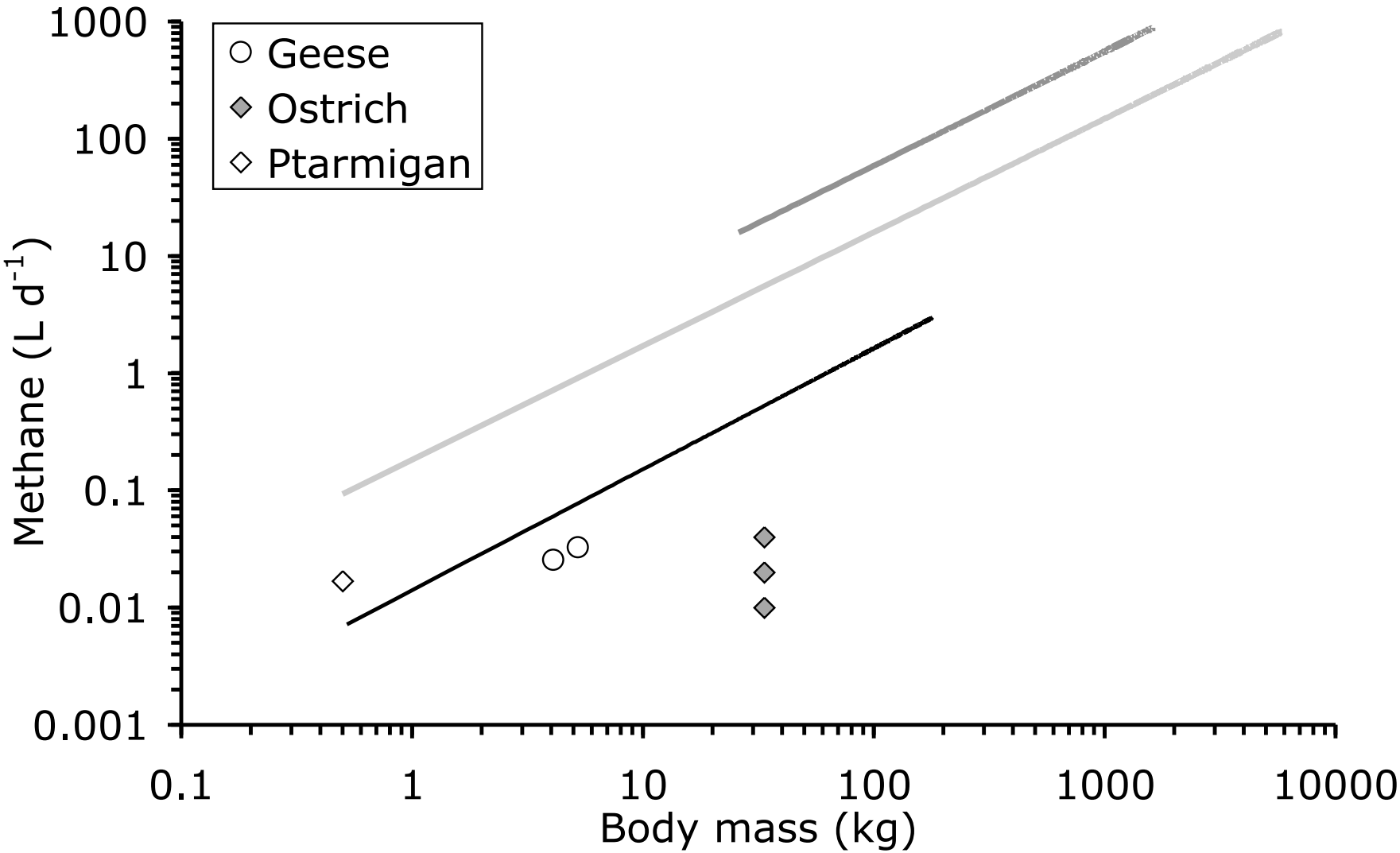
Literature collection and own data (Franz et al. 2010, 2011ab)

Methane allometry in herbivores



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

Methane allometry in herbivores



Literature collection (Fritz et al. 2012.) 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**

Conceptual problems

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

Conceptual problems

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

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

Conceptual problems

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!***

Conceptual problems

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

Conceptual problems – and a 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

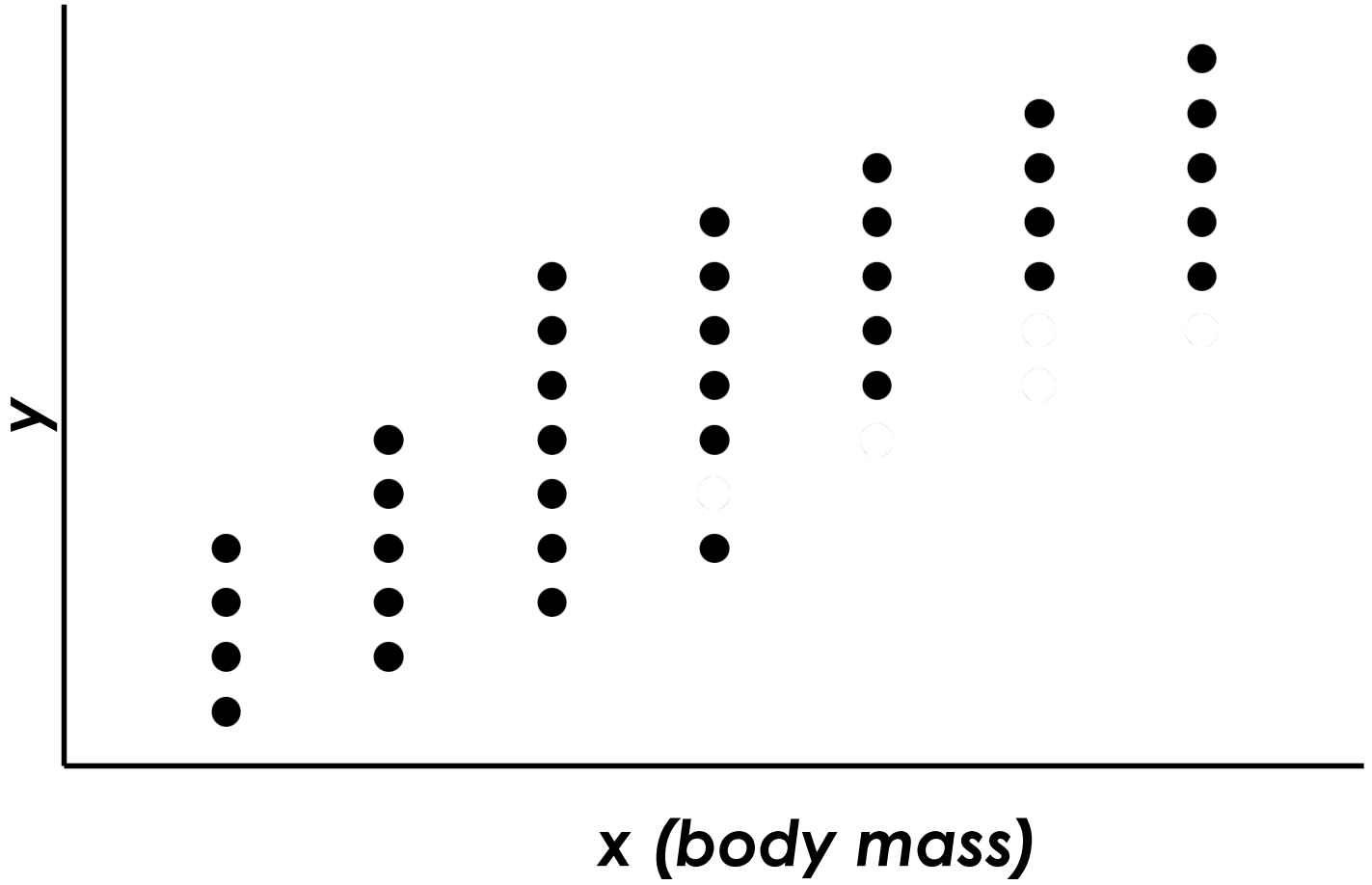
dry matter intake $BM^{0.89}$

requirements $BM^{0.75}$

Phylogenetic statistics

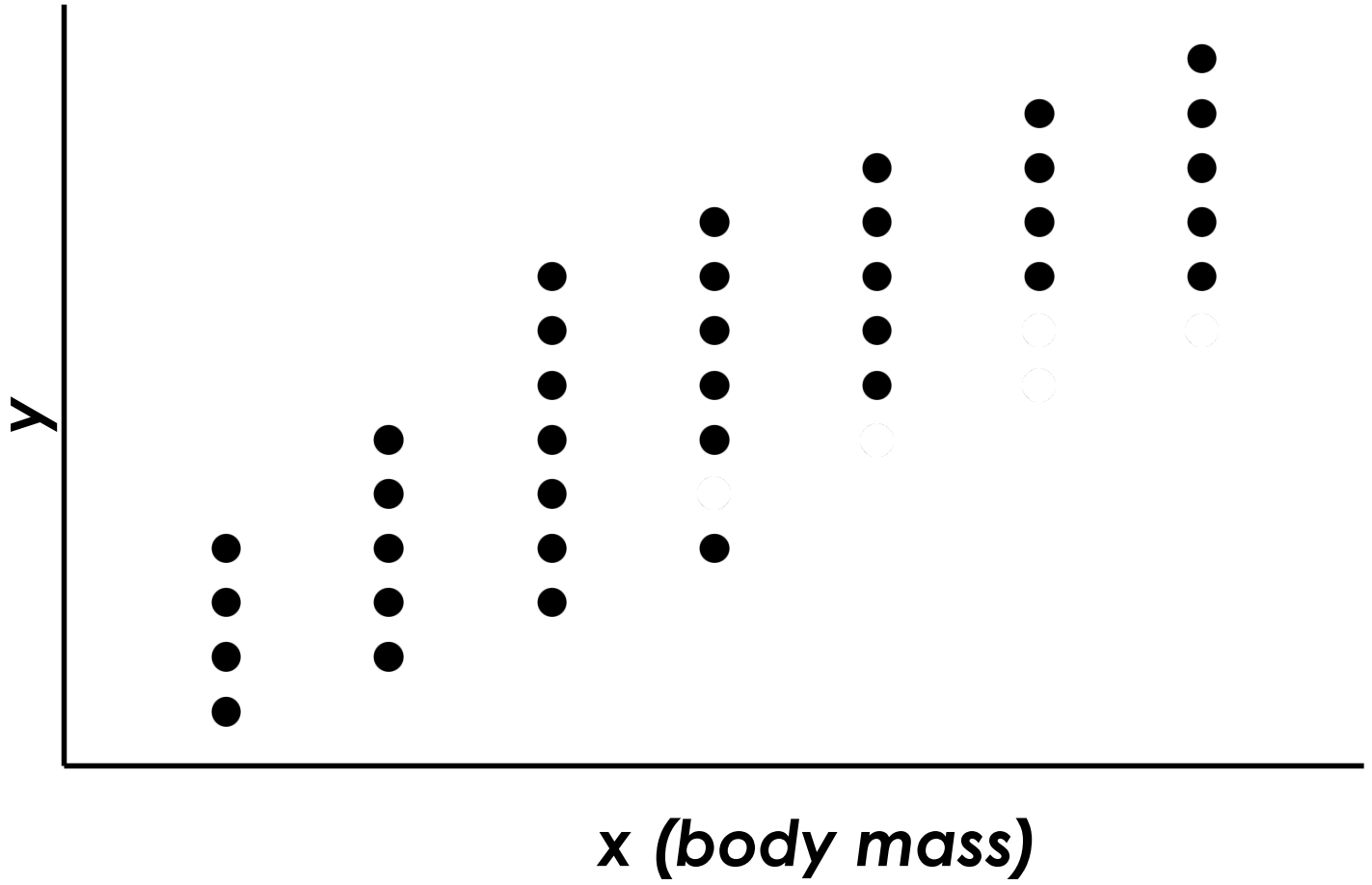
Comparative statistics

Conventional regression analysis assumes independence of data points.



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).

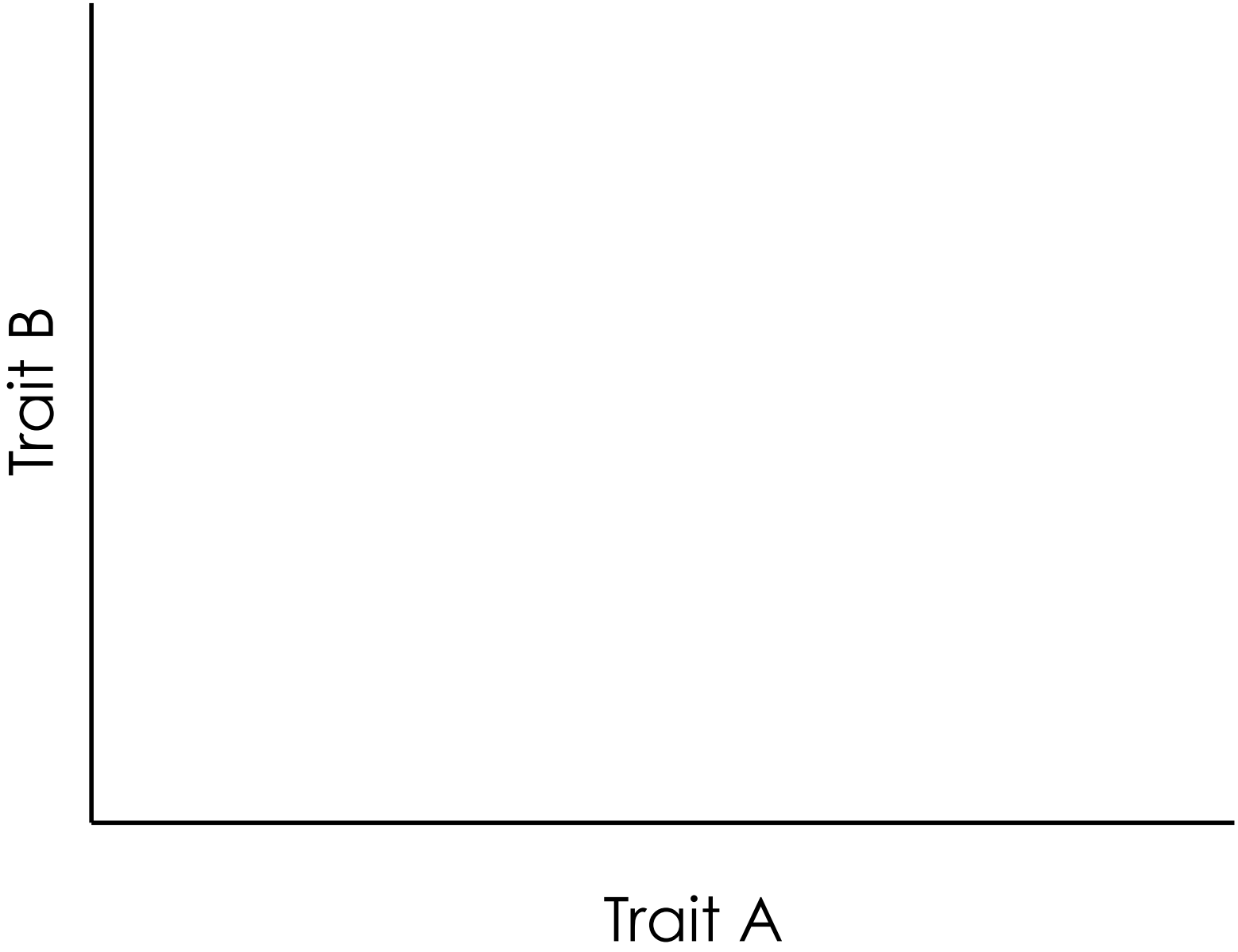
Comparative statistics

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

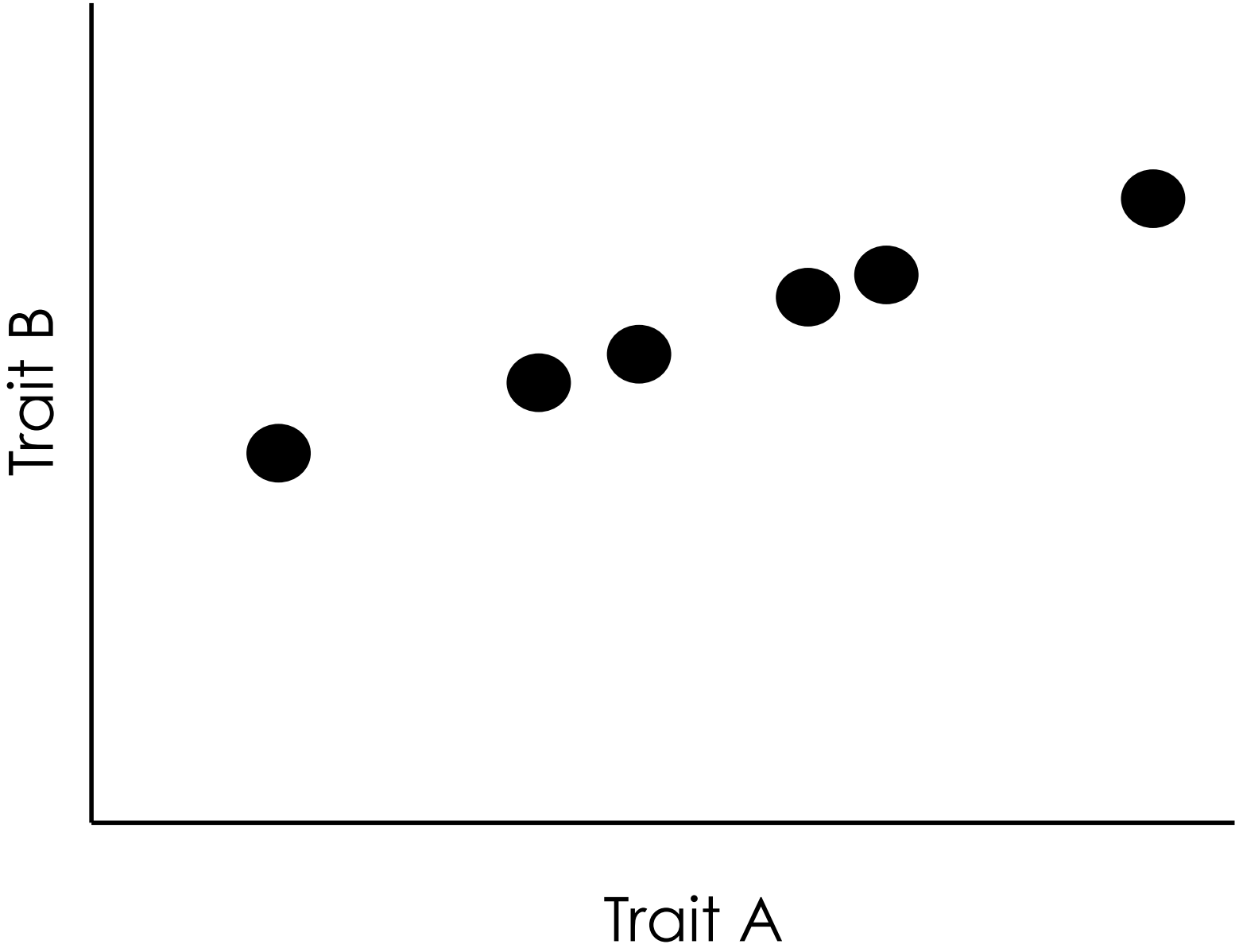
Therefore, we perform allometric analyses also with accounting for phylogeny, using PGLS (Phylogenetic Generalized Least Squares).

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.

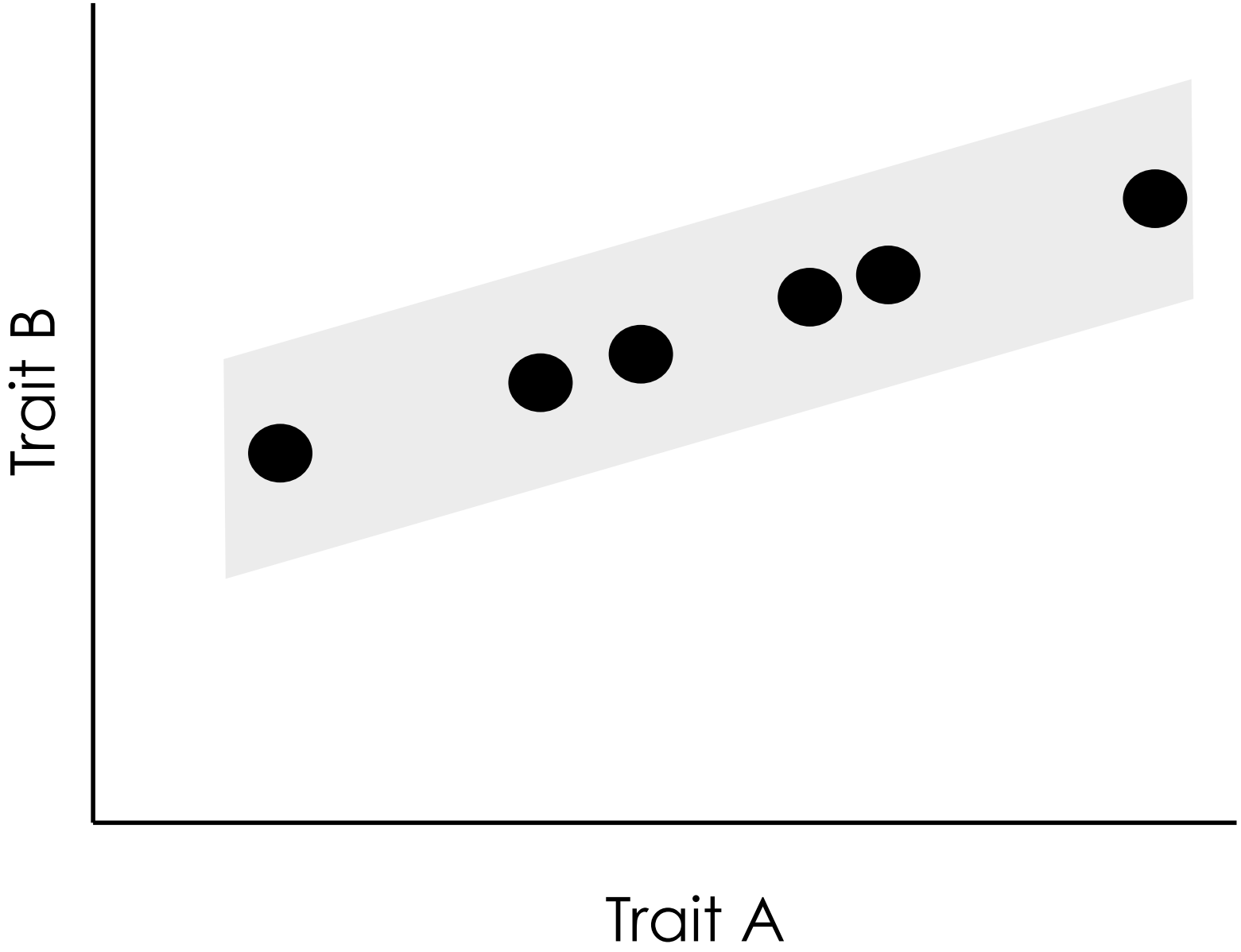
Accounting for phylogeny



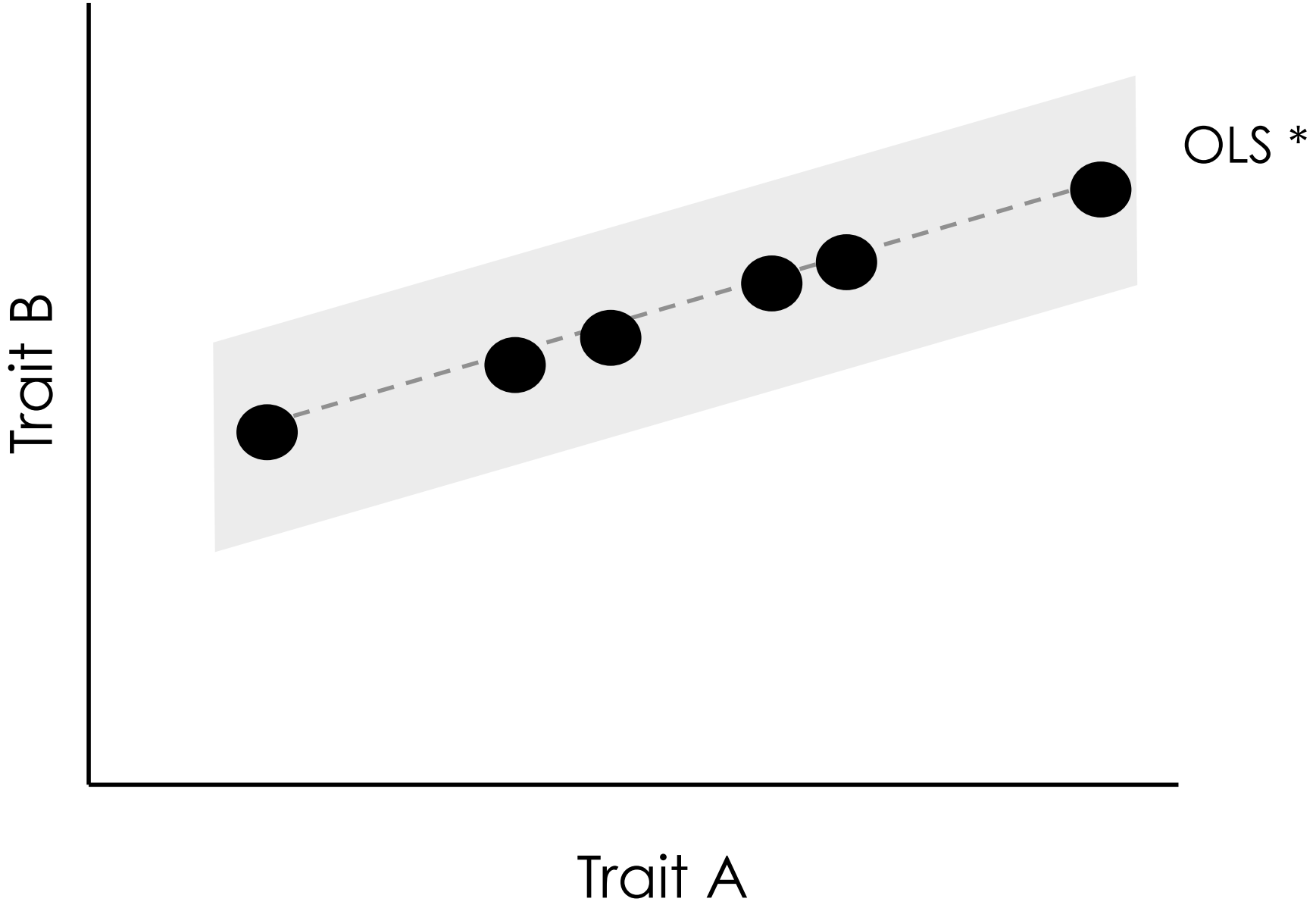
Accounting for phylogeny



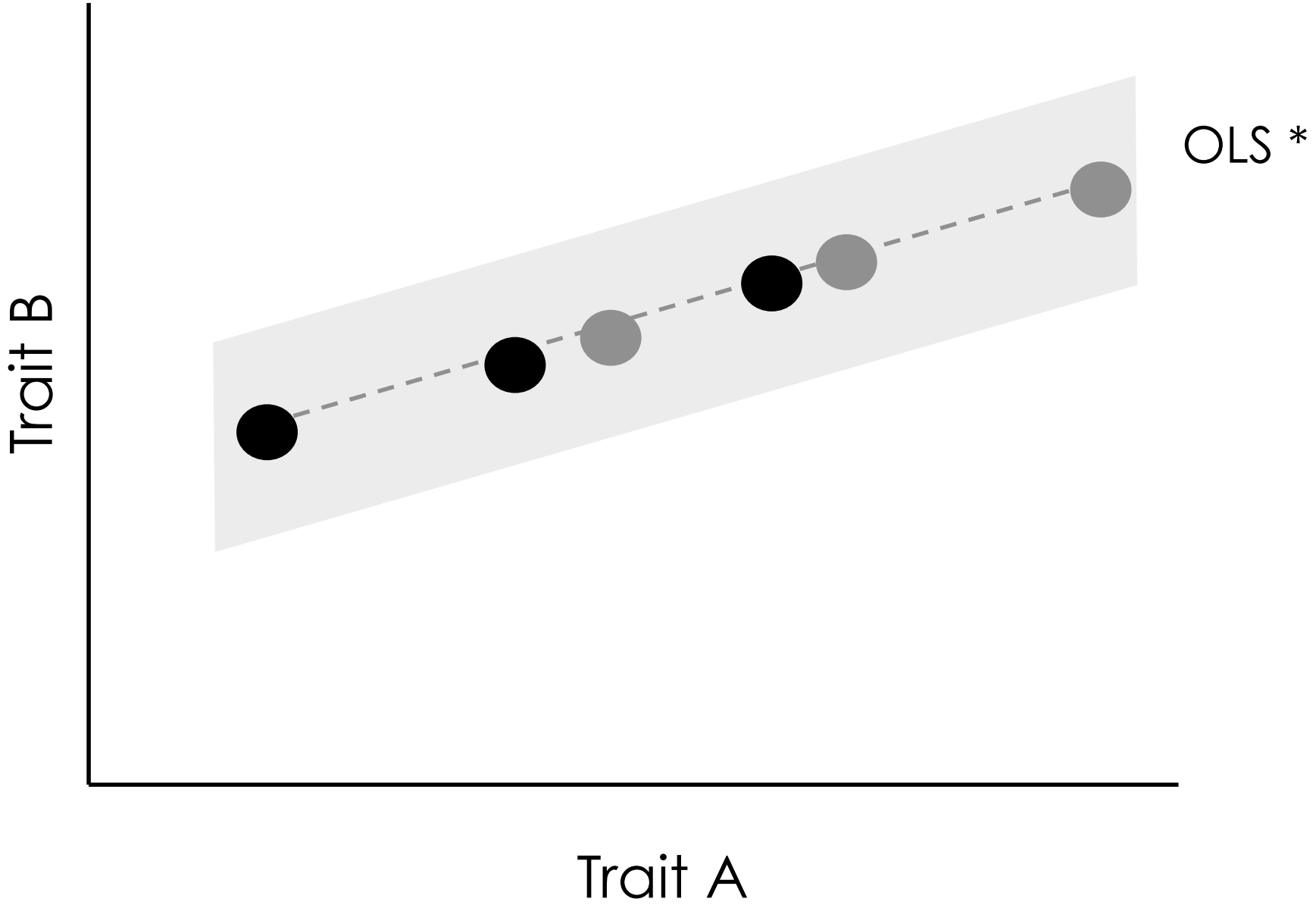
Accounting for phylogeny



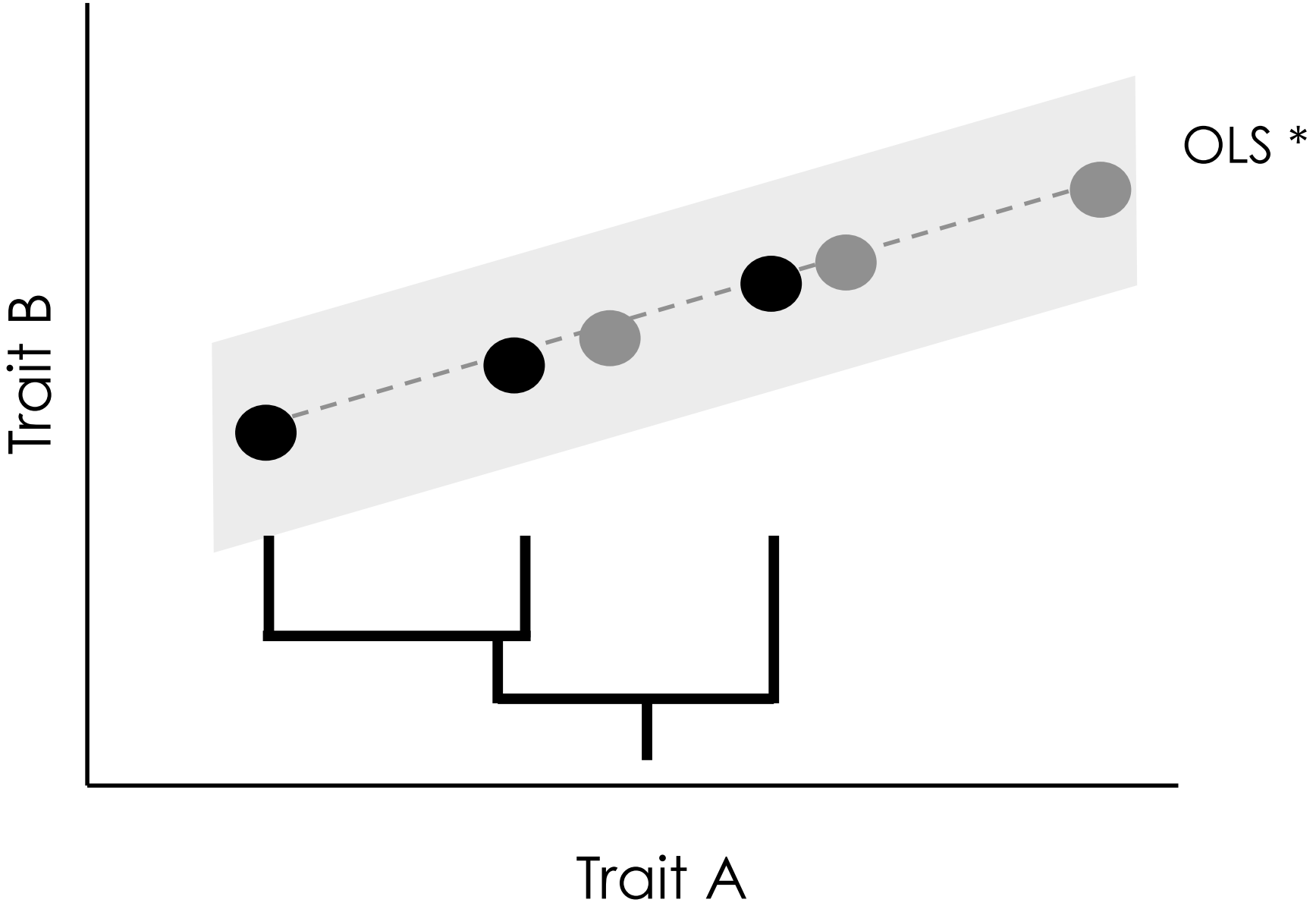
Accounting for phylogeny



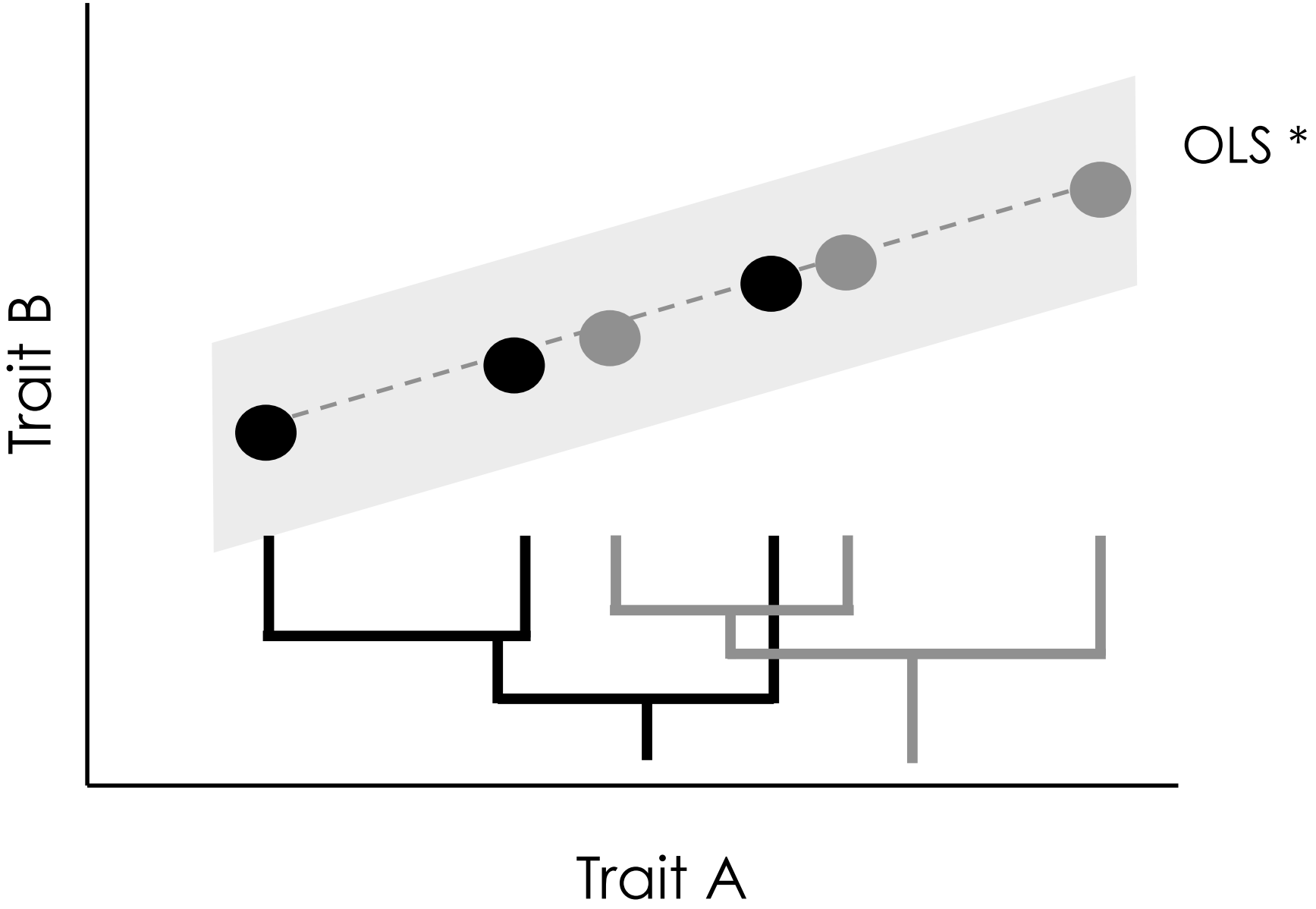
Accounting for phylogeny



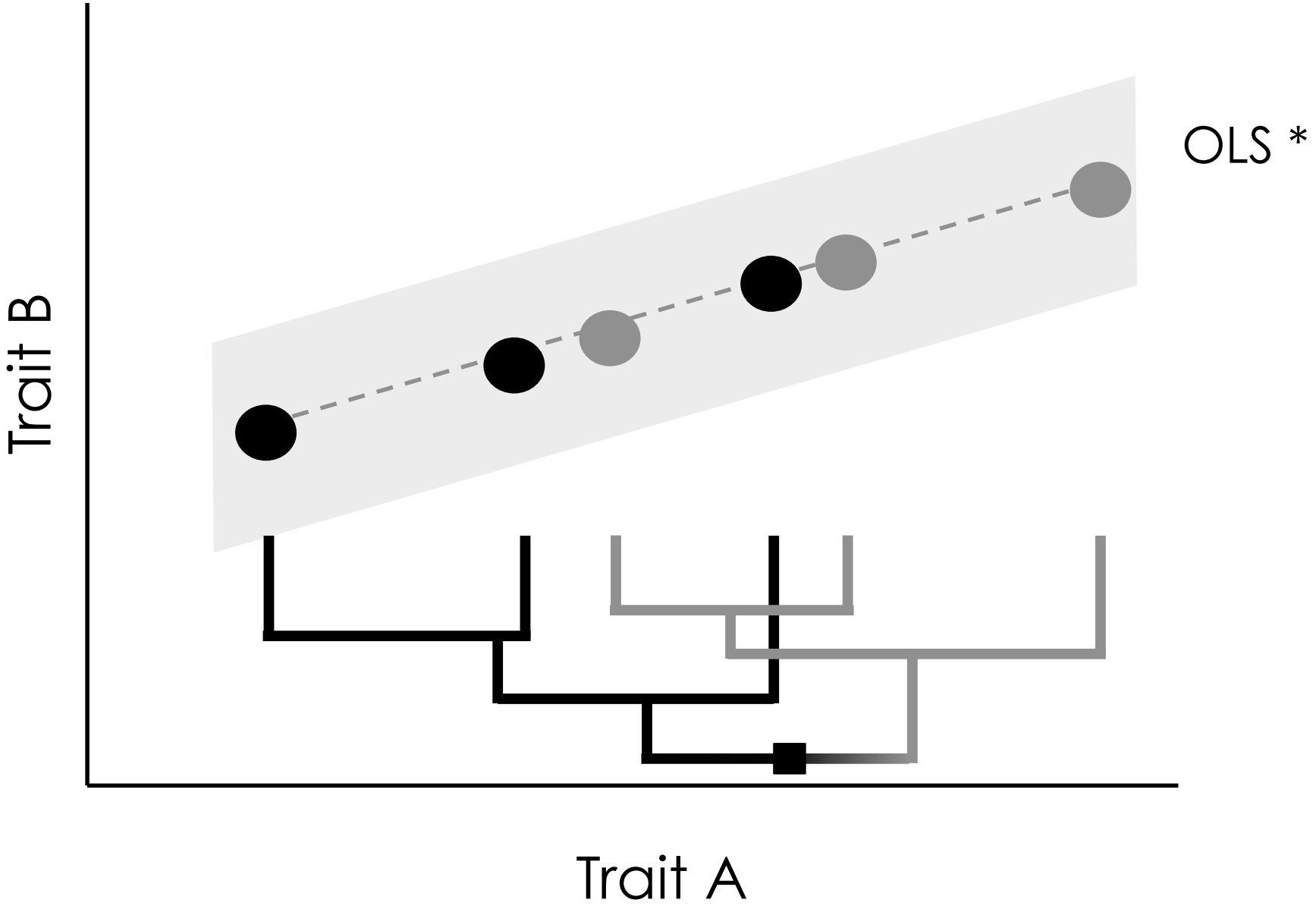
Accounting for phylogeny



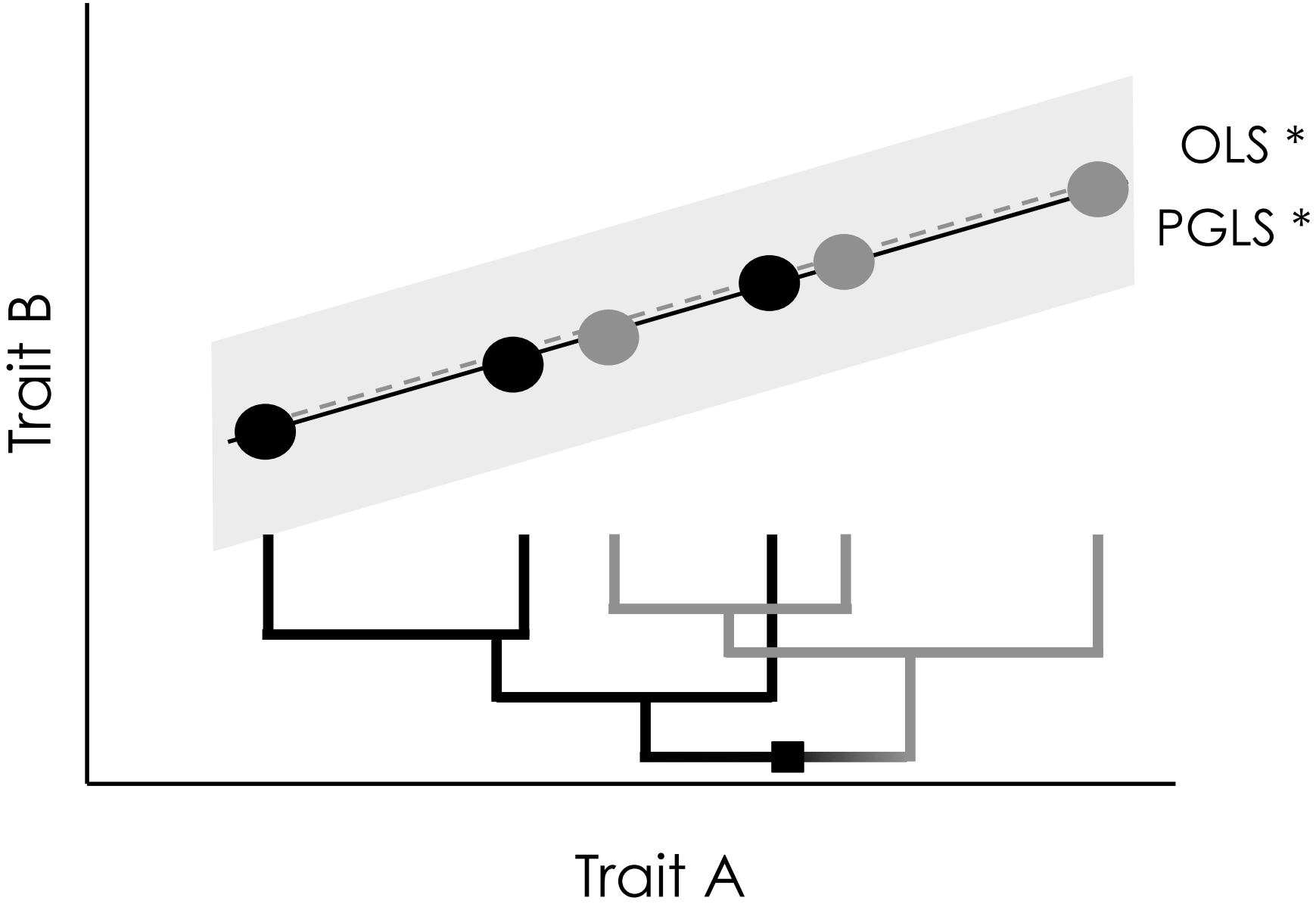
Accounting for phylogeny



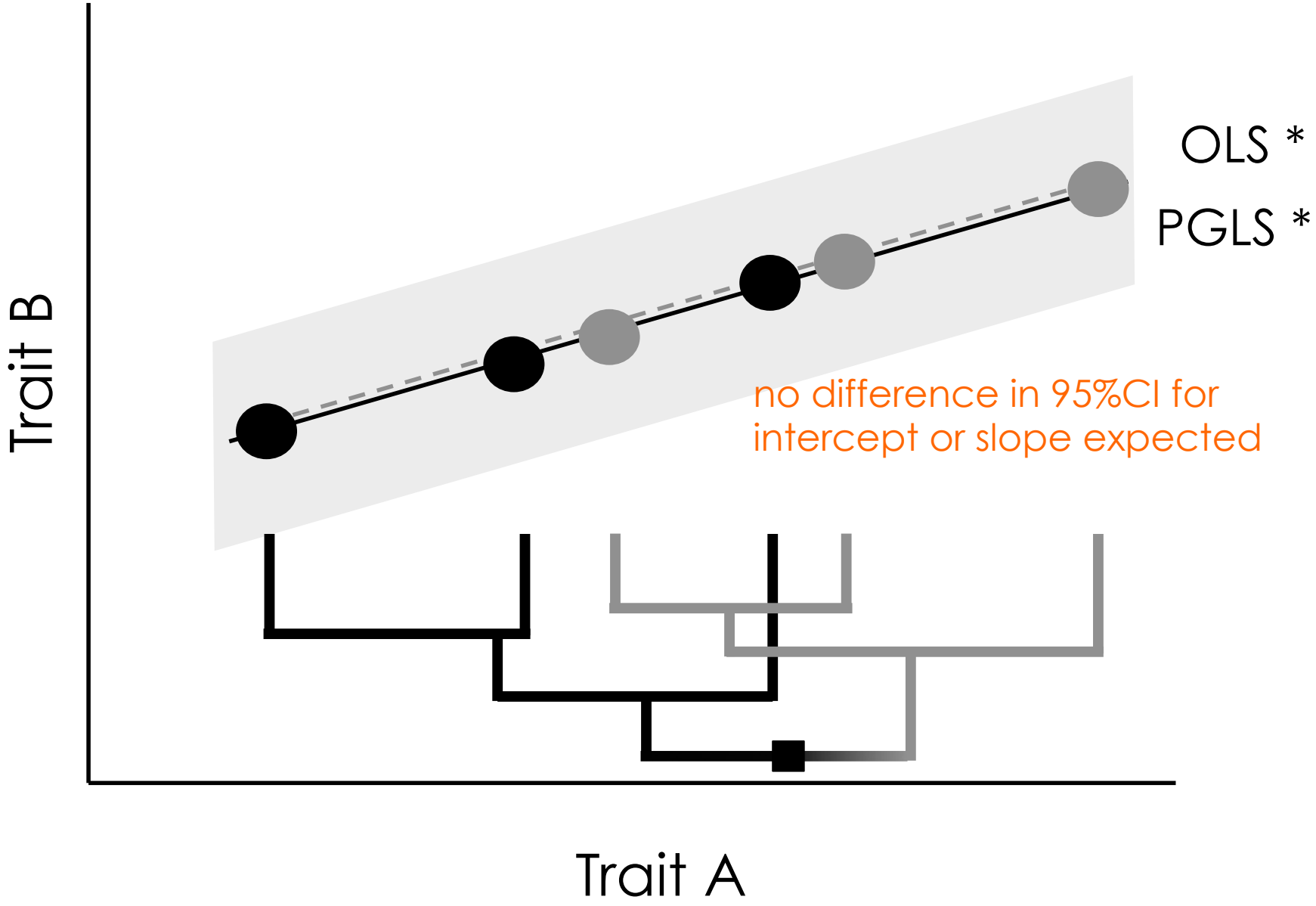
Accounting for phylogeny



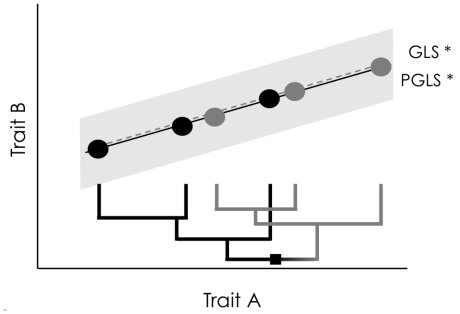
Accounting for phylogeny



Accounting for phylogeny

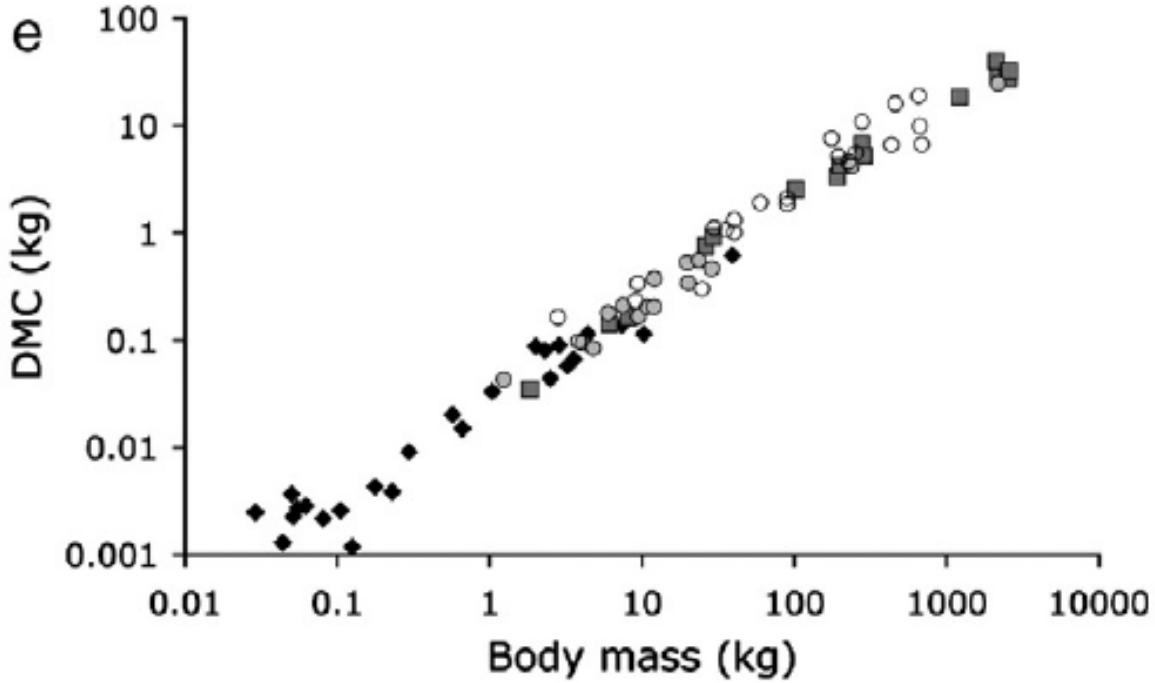


Example I: gut contents



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

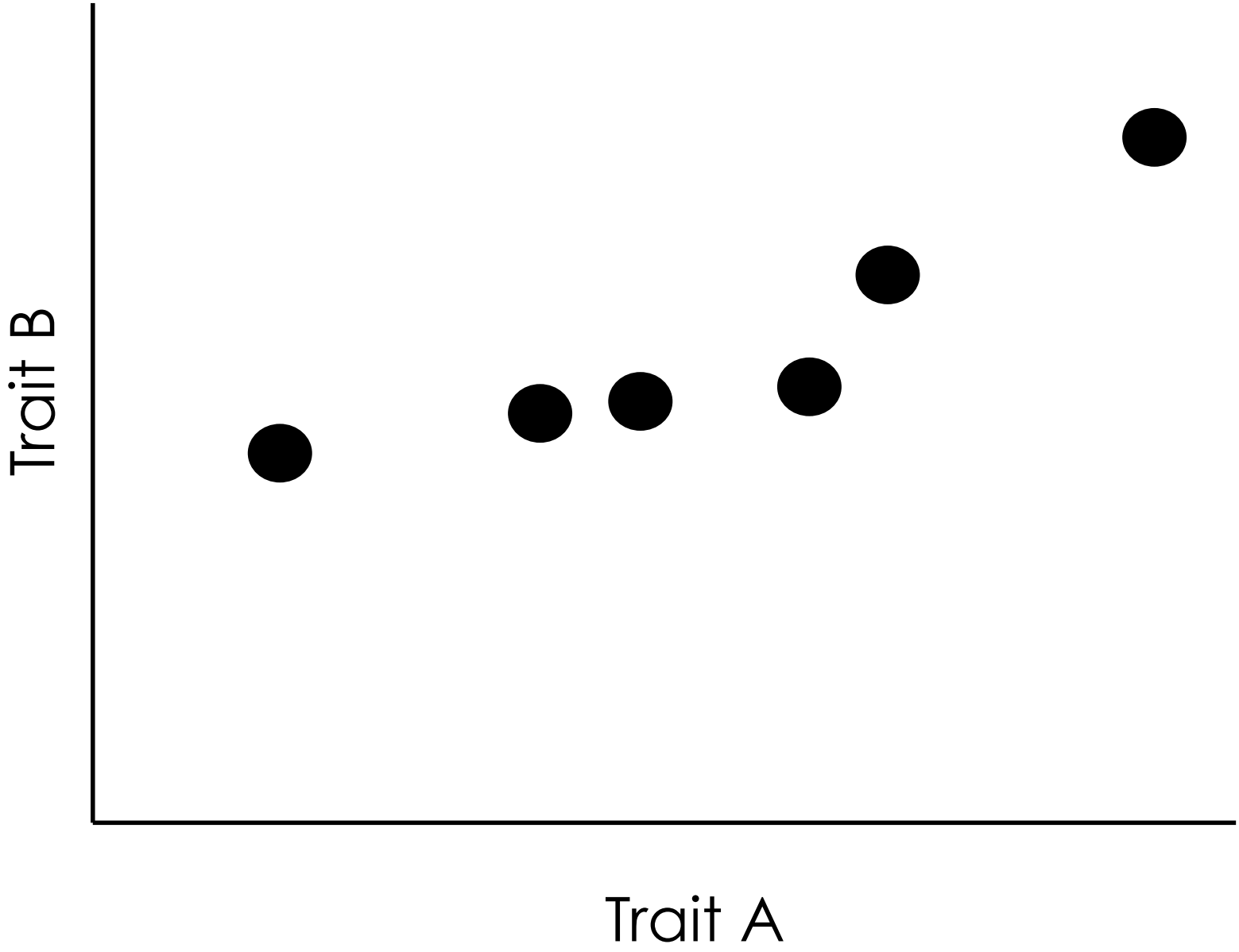
PGLS: 0.03 (0.010-0.075) $BM^{0.92\ (0.85\text{-}0.98)}$



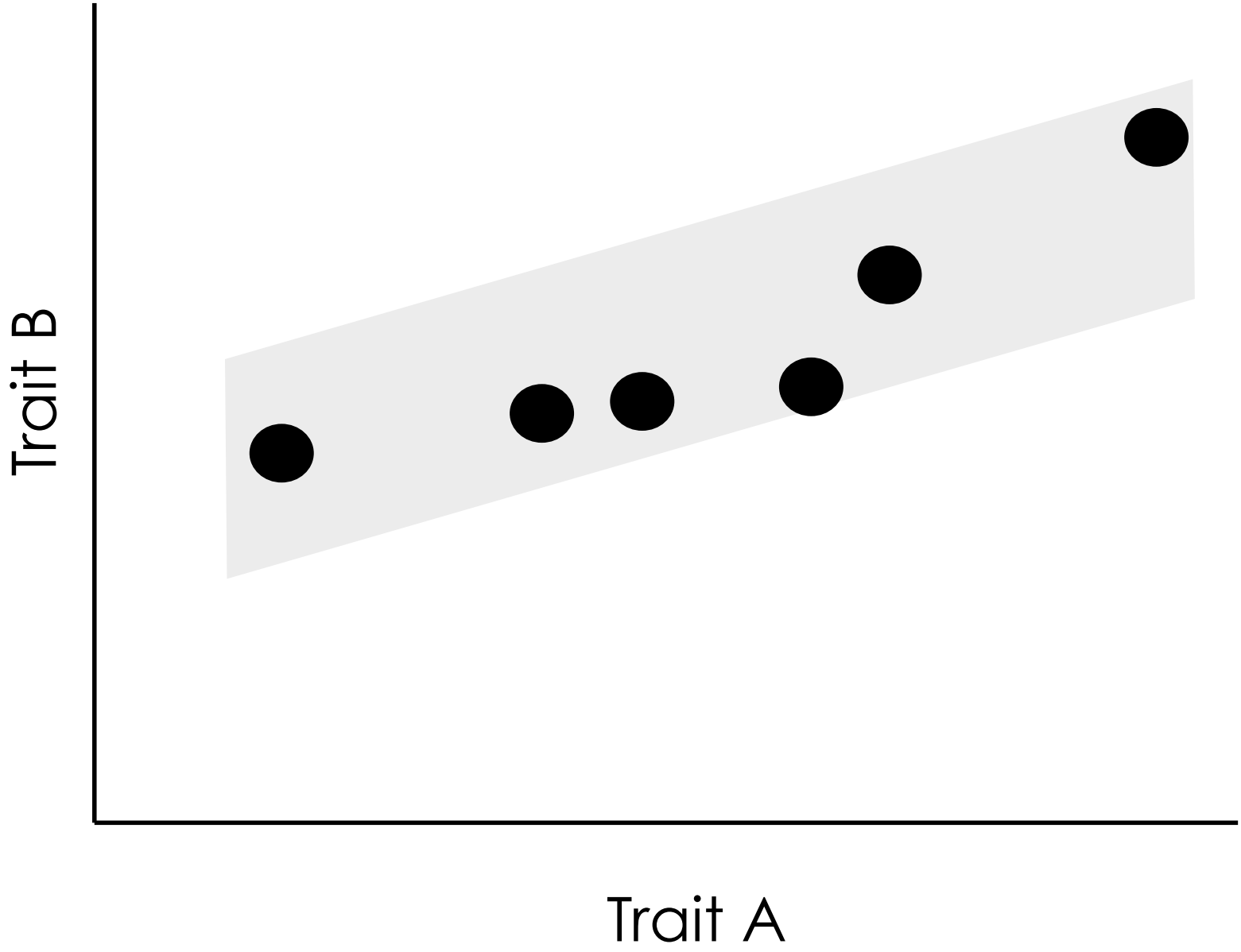
from Müller et al. (2013) CBP A

Accounting for phylogeny

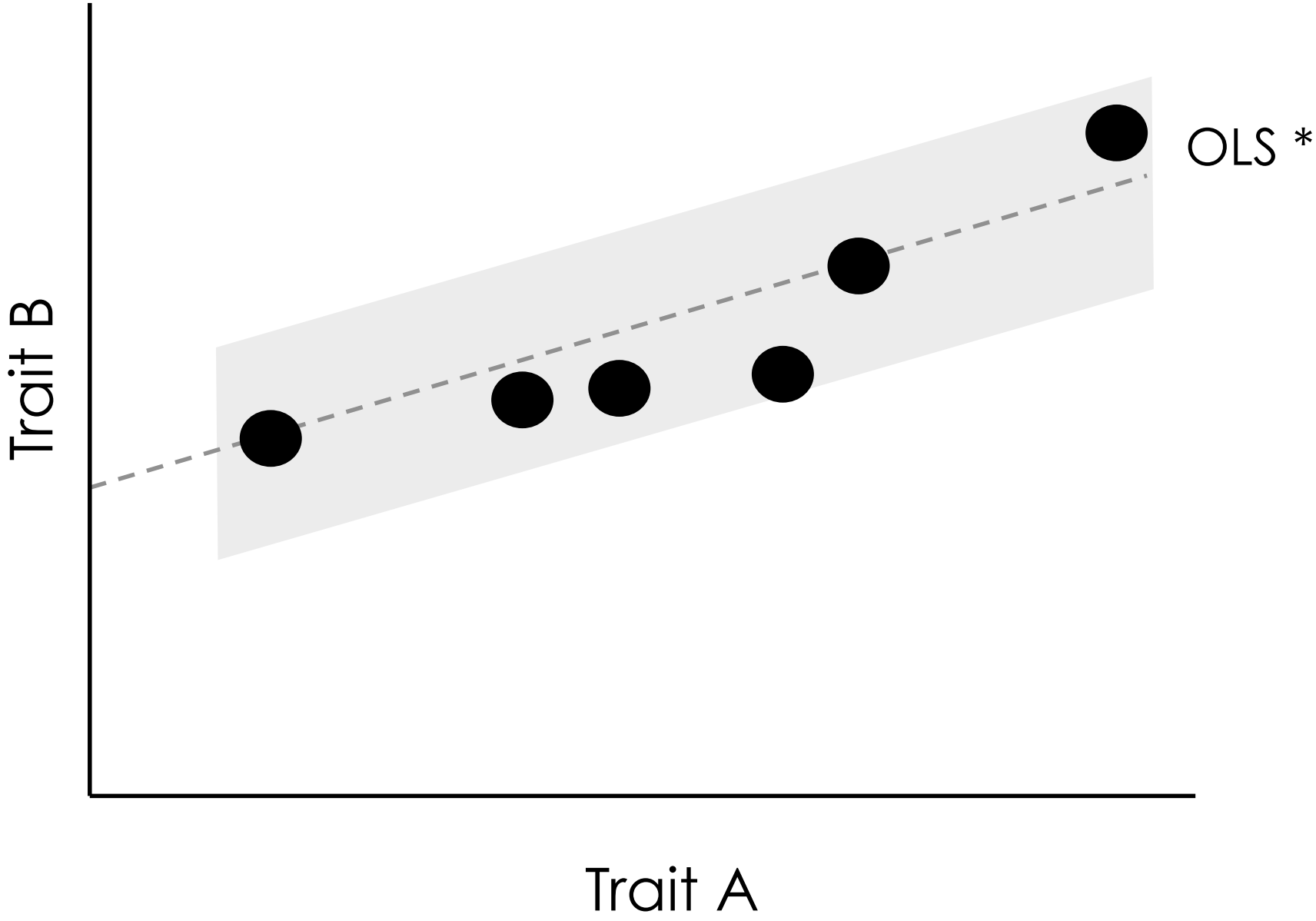
Accounting for phylogeny



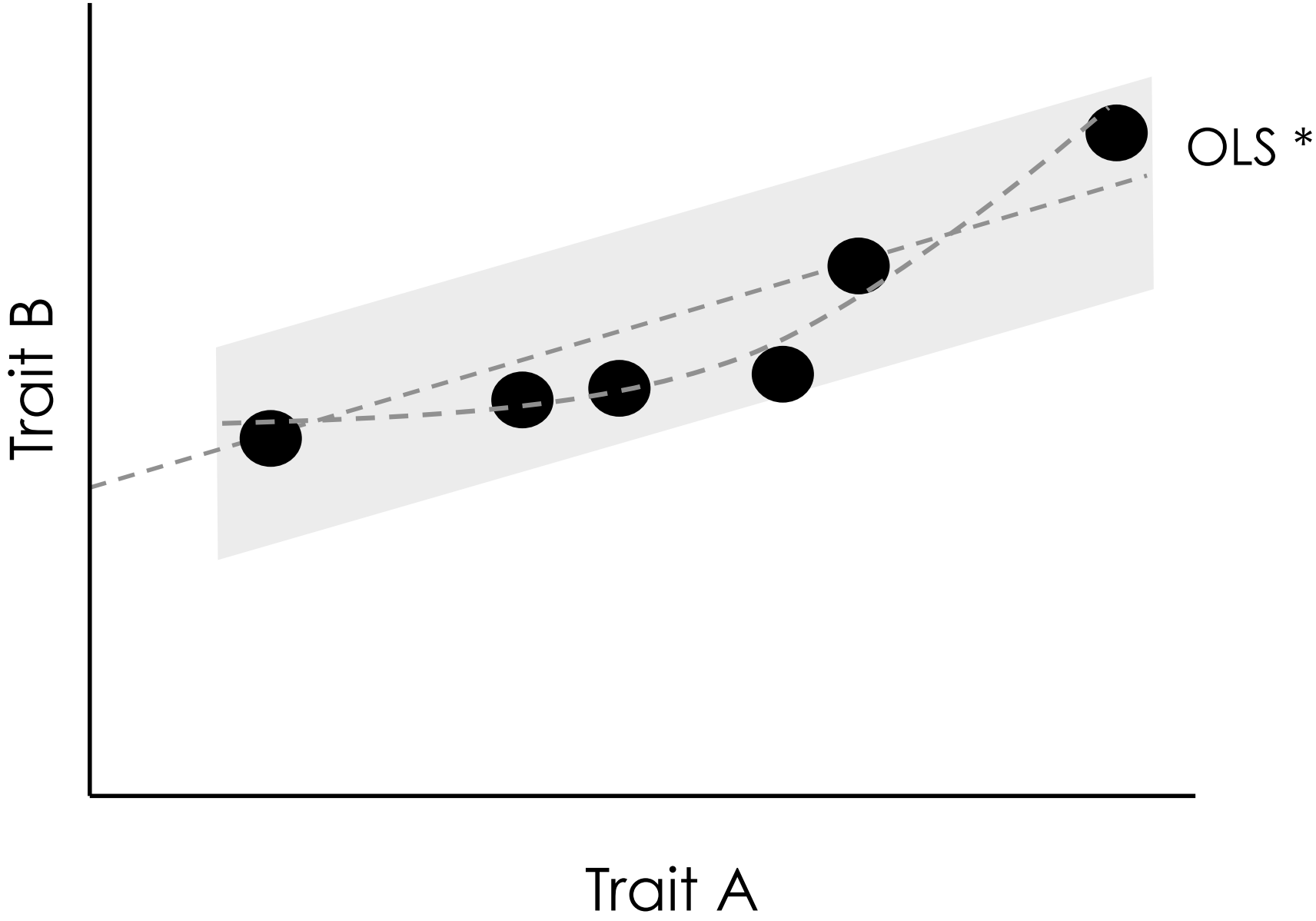
Accounting for phylogeny



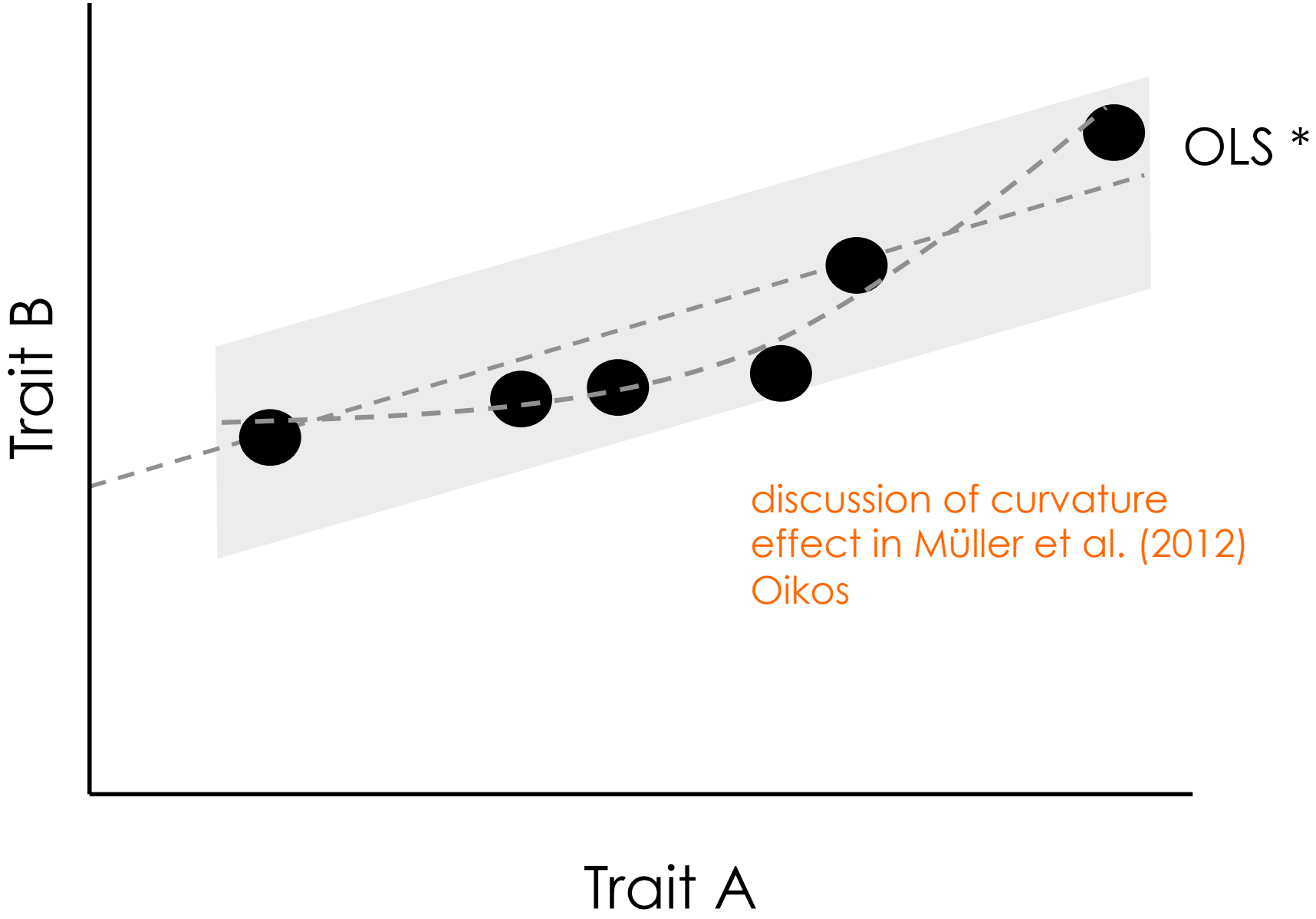
Accounting for phylogeny



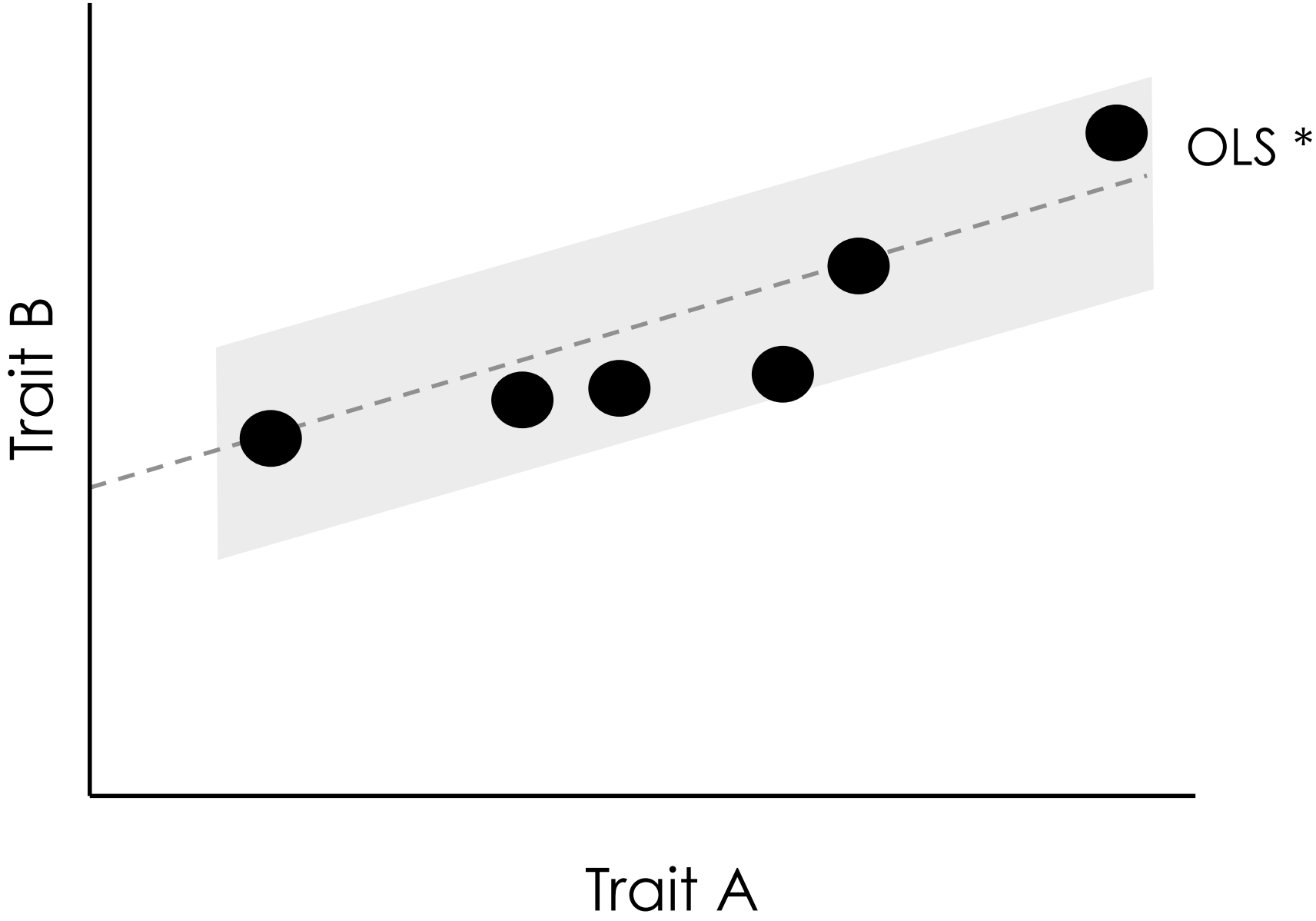
Accounting for phylogeny



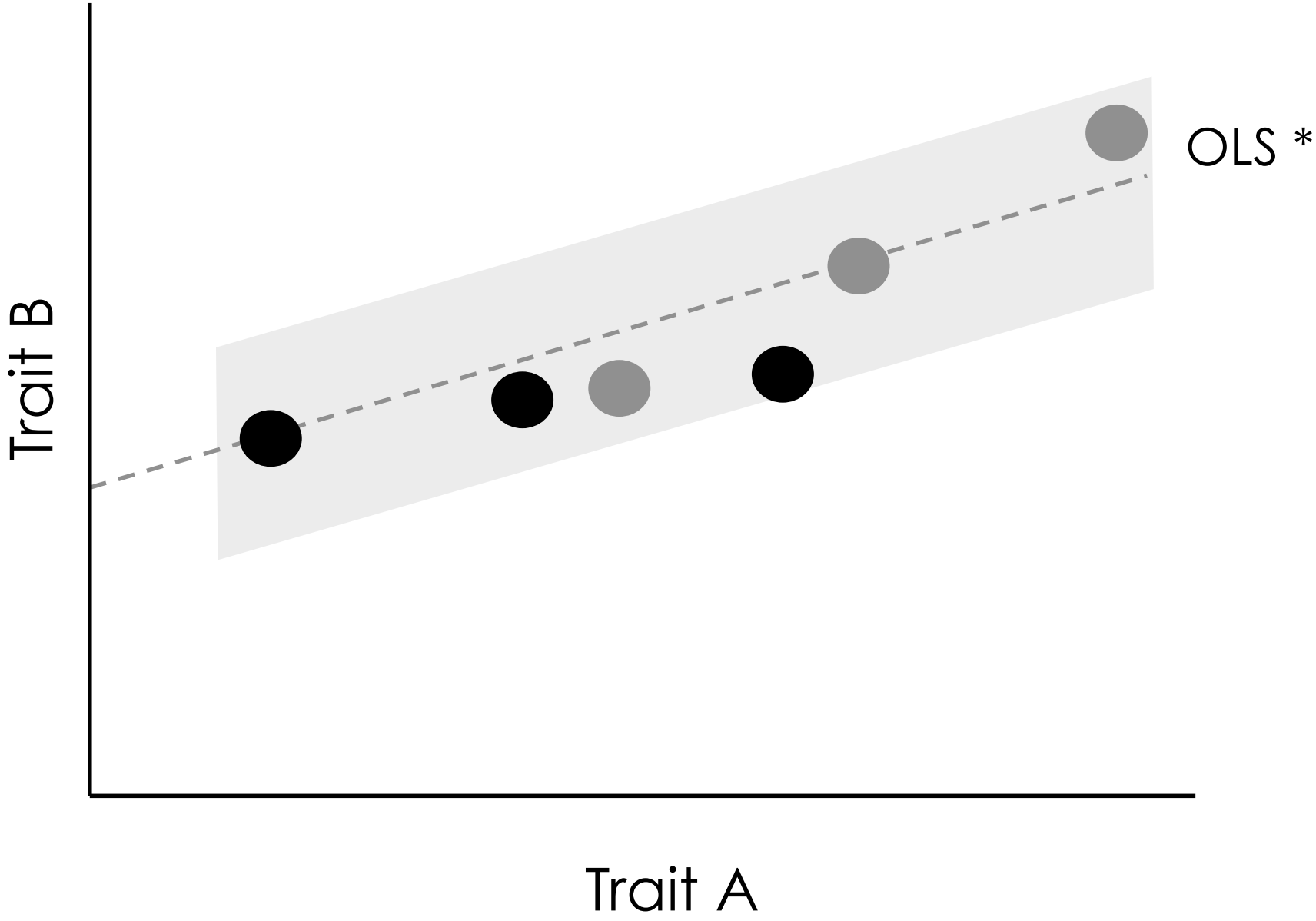
Accounting for phylogeny



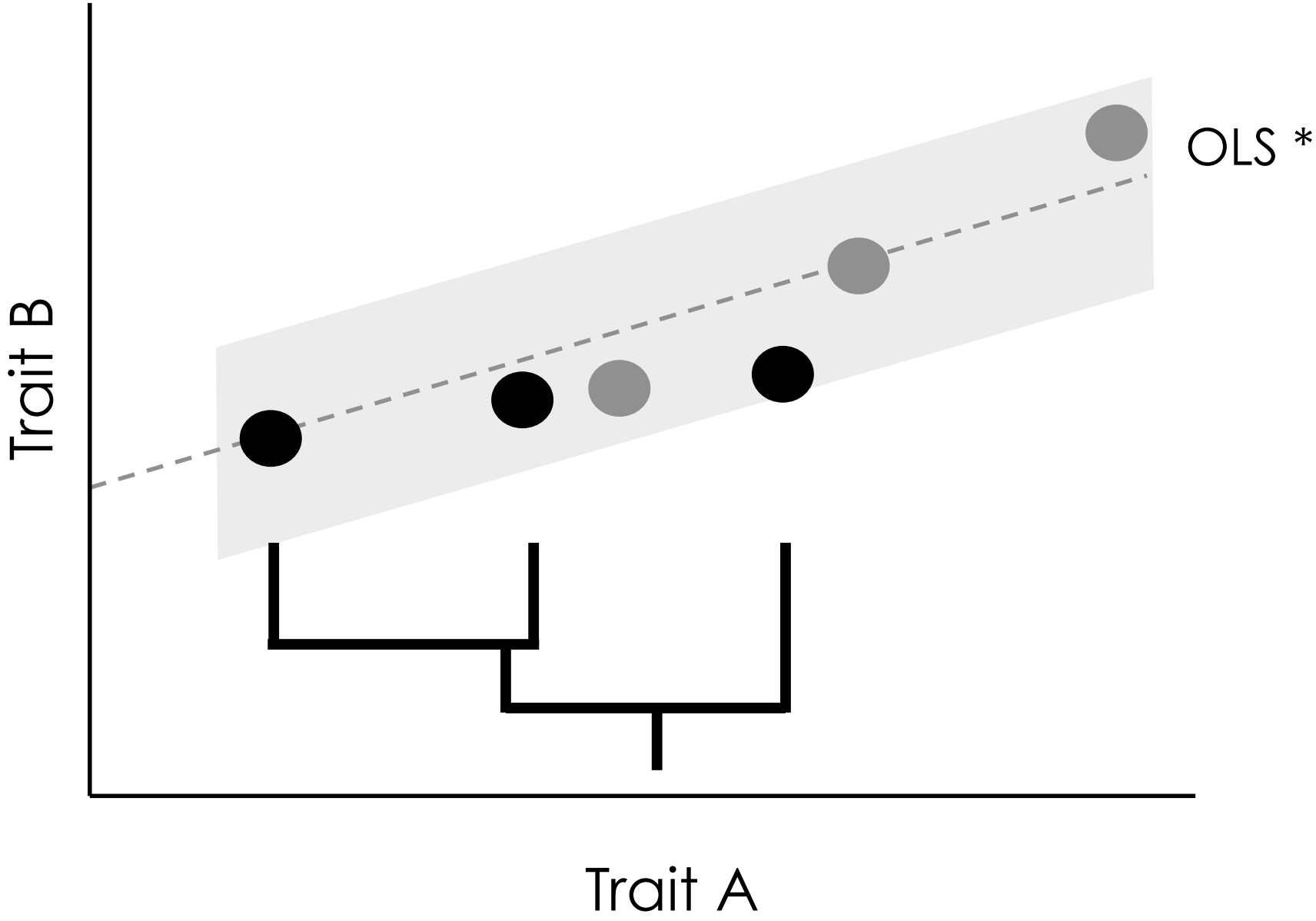
Accounting for phylogeny



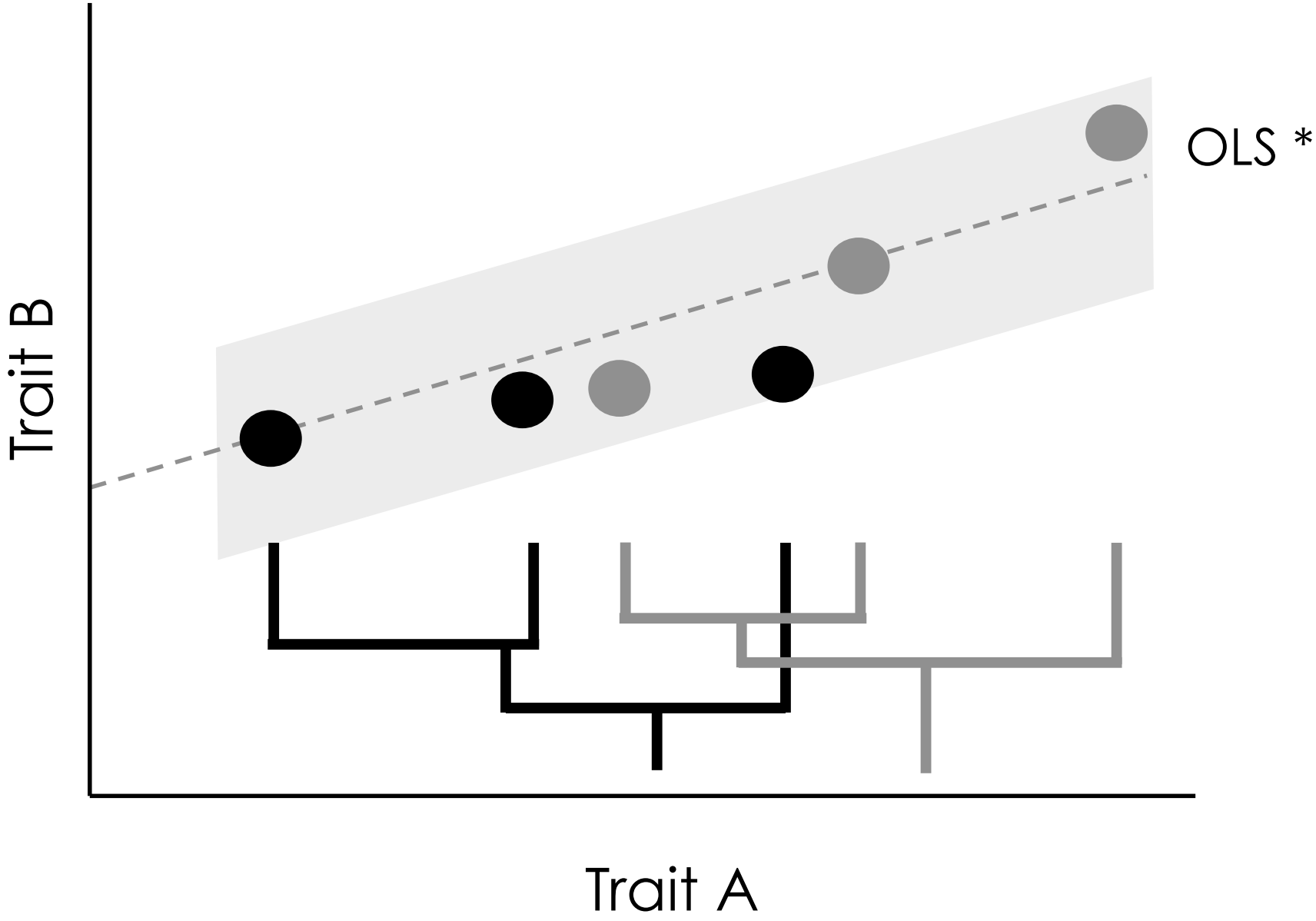
Accounting for phylogeny



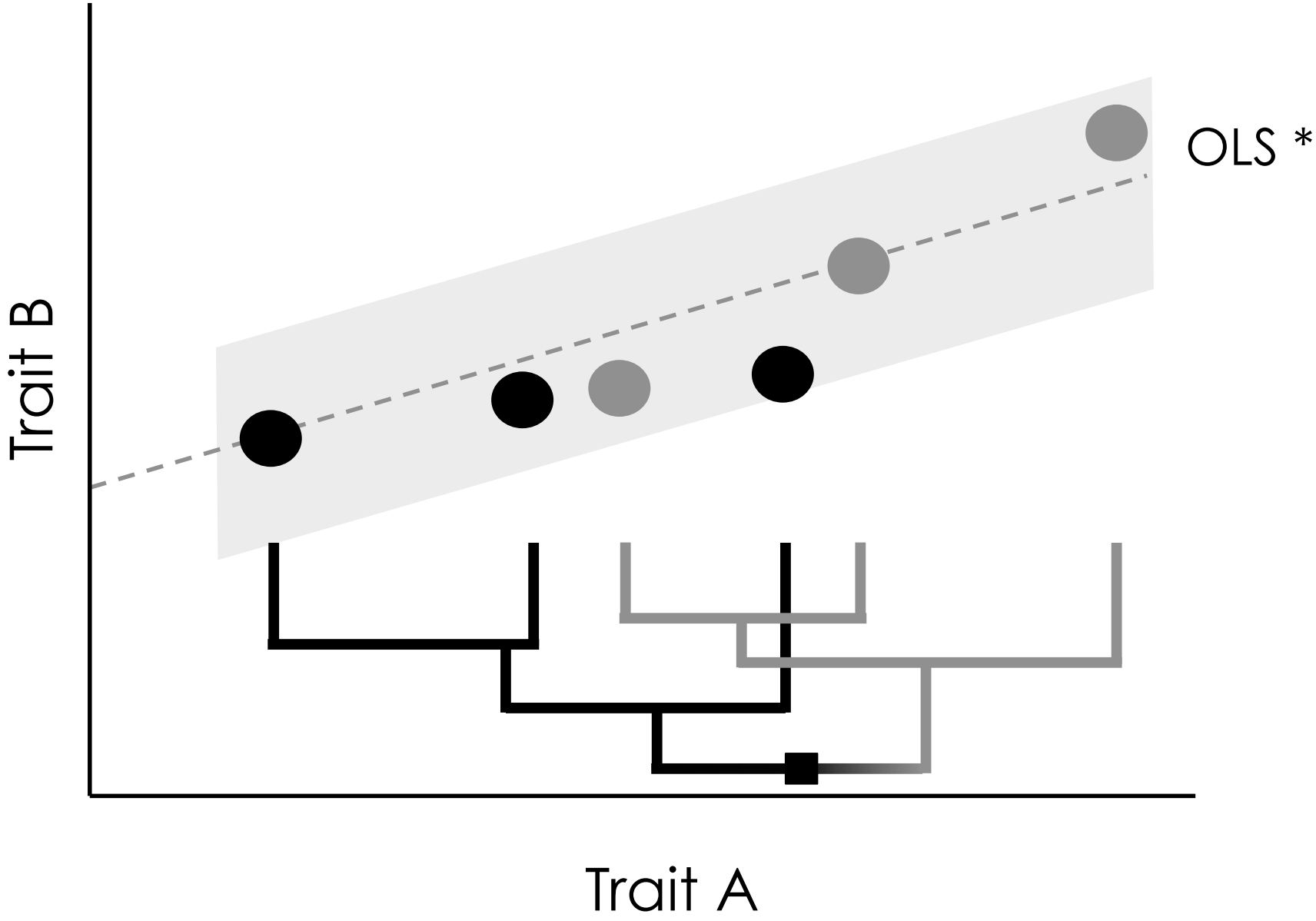
Accounting for phylogeny



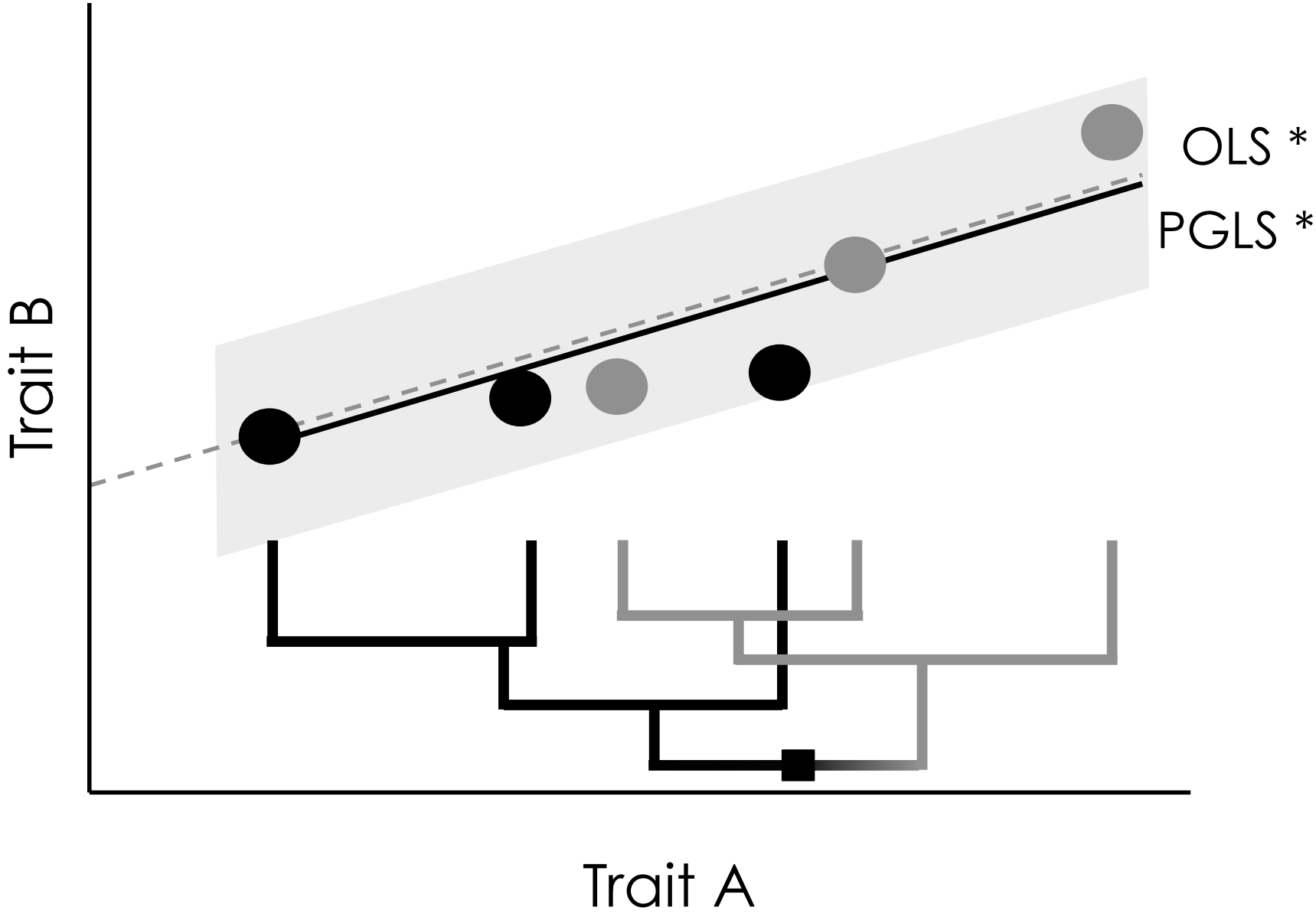
Accounting for phylogeny



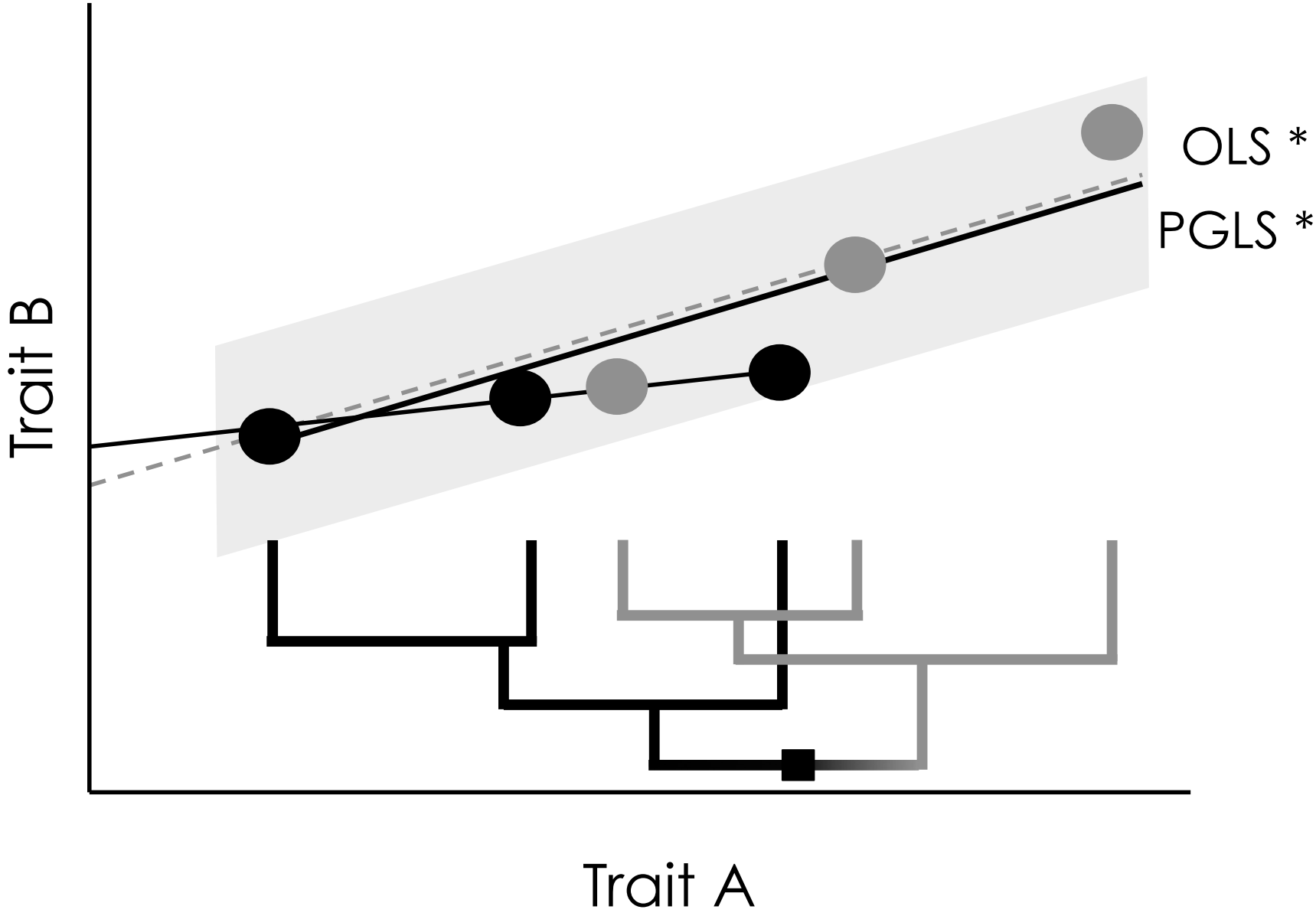
Accounting for phylogeny



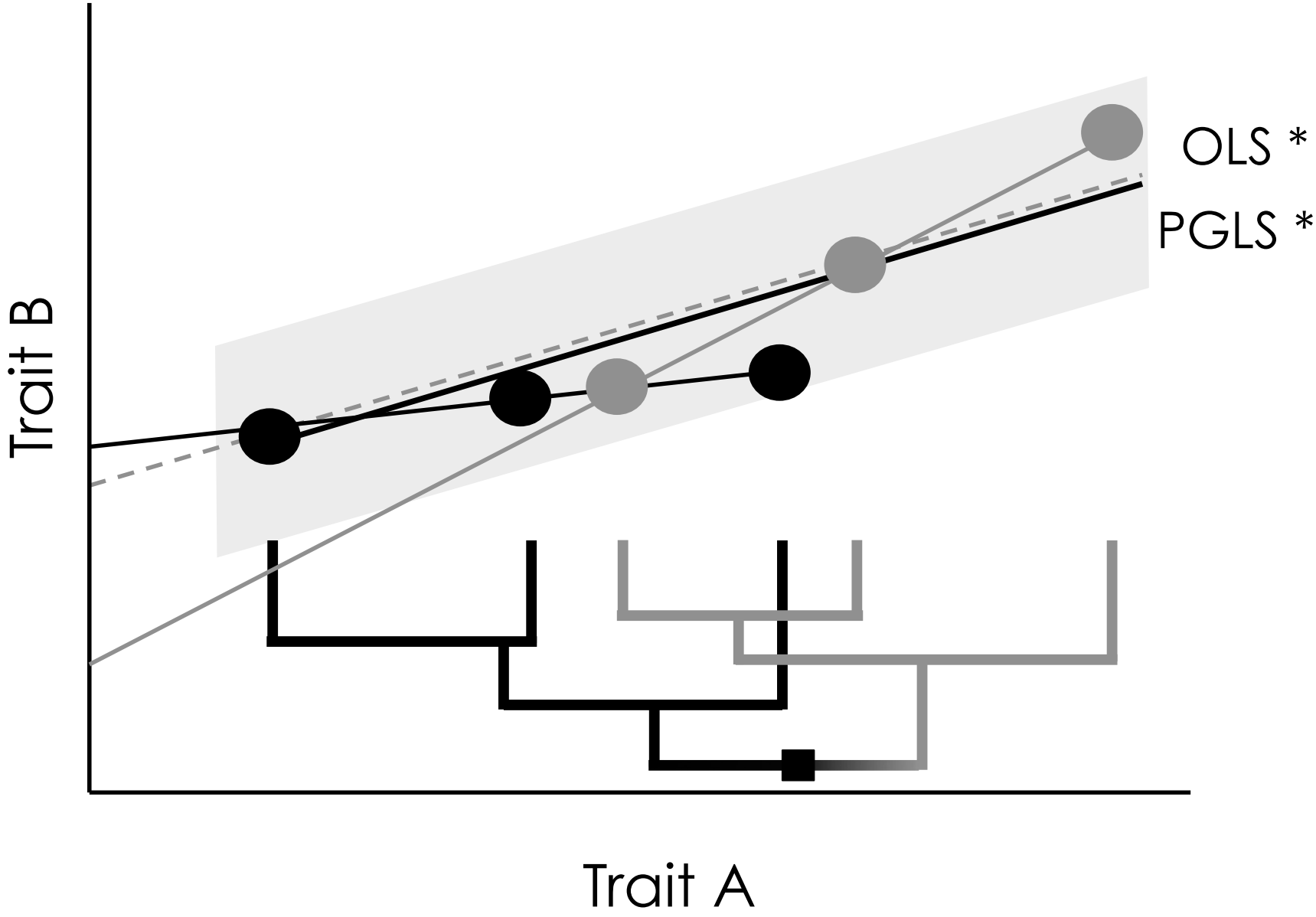
Accounting for phylogeny



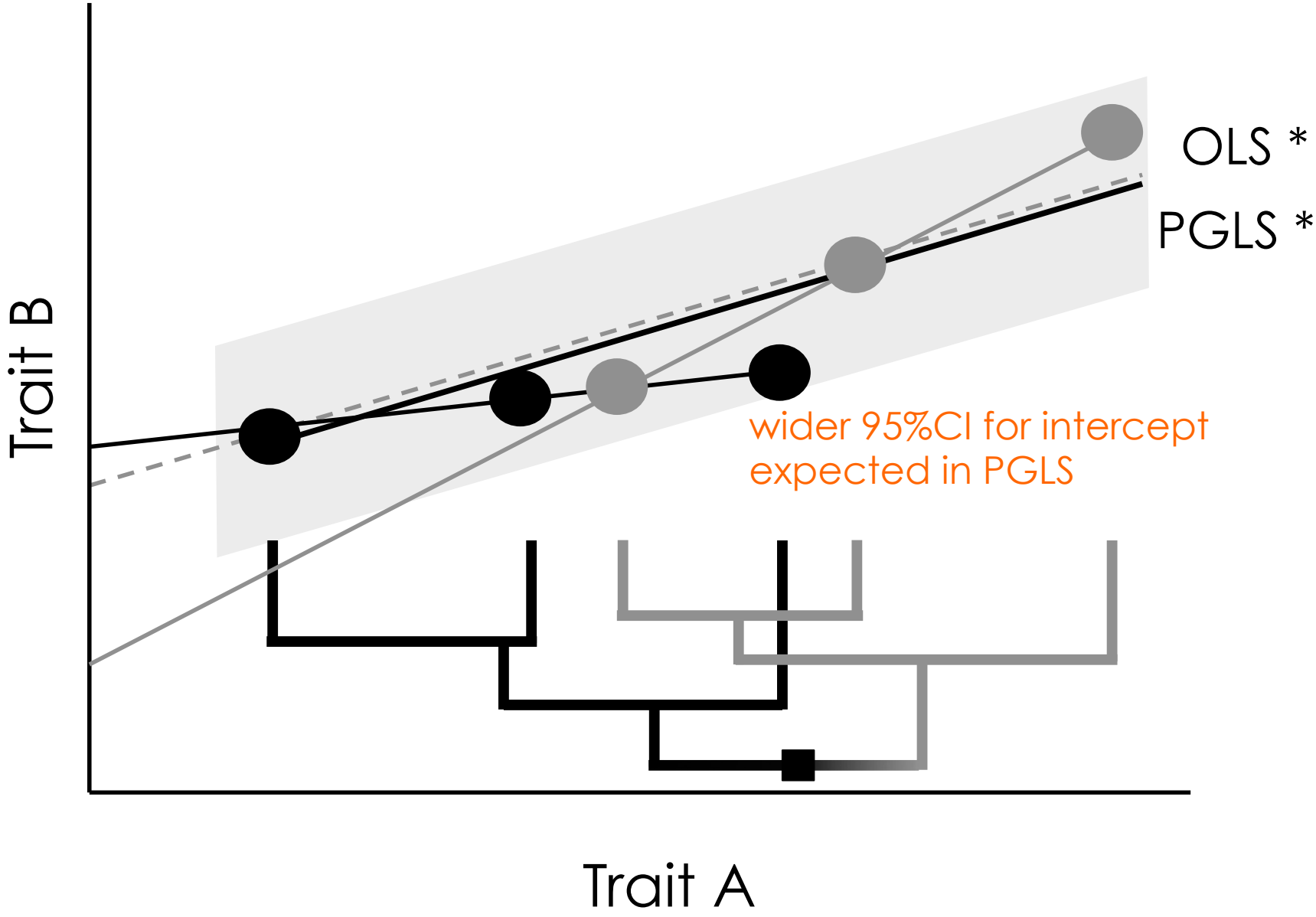
Accounting for phylogeny



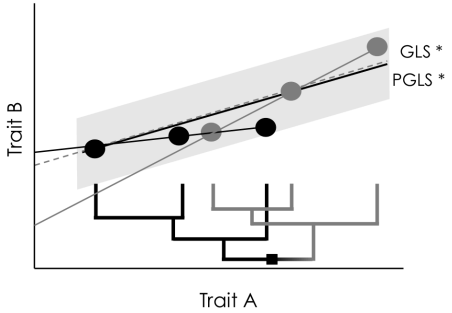
Accounting for phylogeny



Accounting for phylogeny

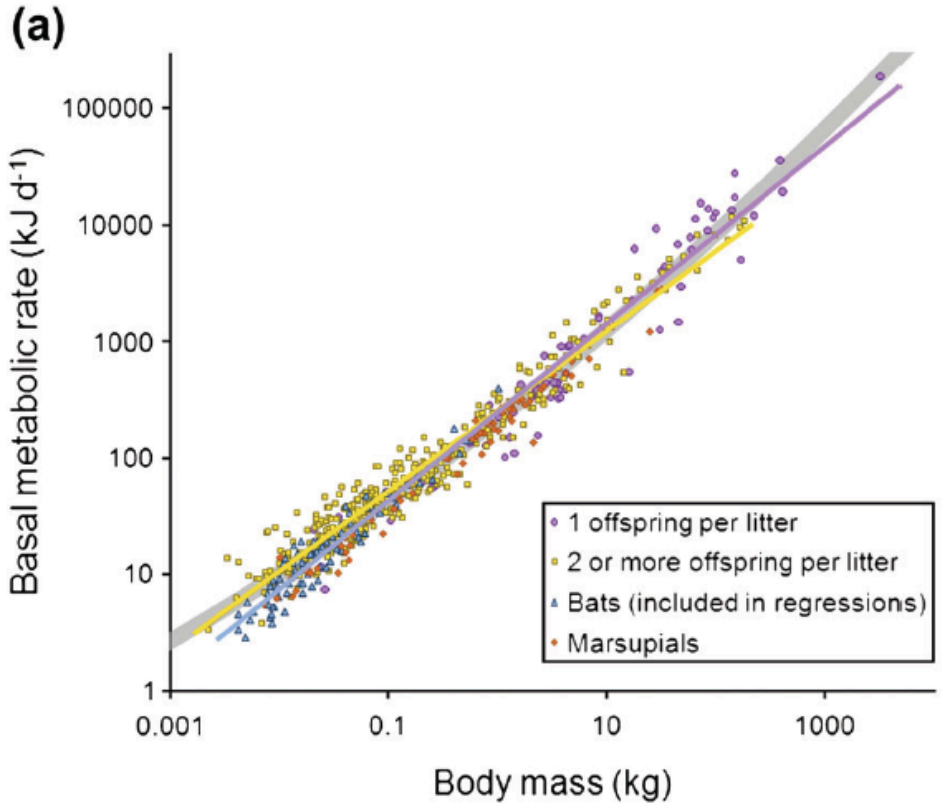


Example II: basal metabolic rate



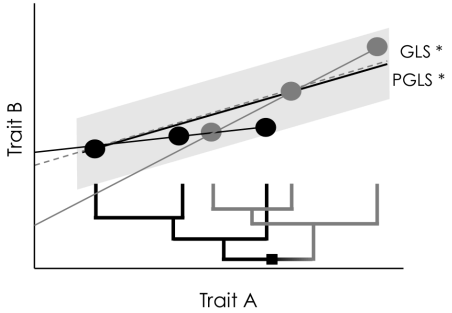
OLS: 2.38 (2.37-2.40) $BM^{0.72\ (0.71\text{-}0.73)}$

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



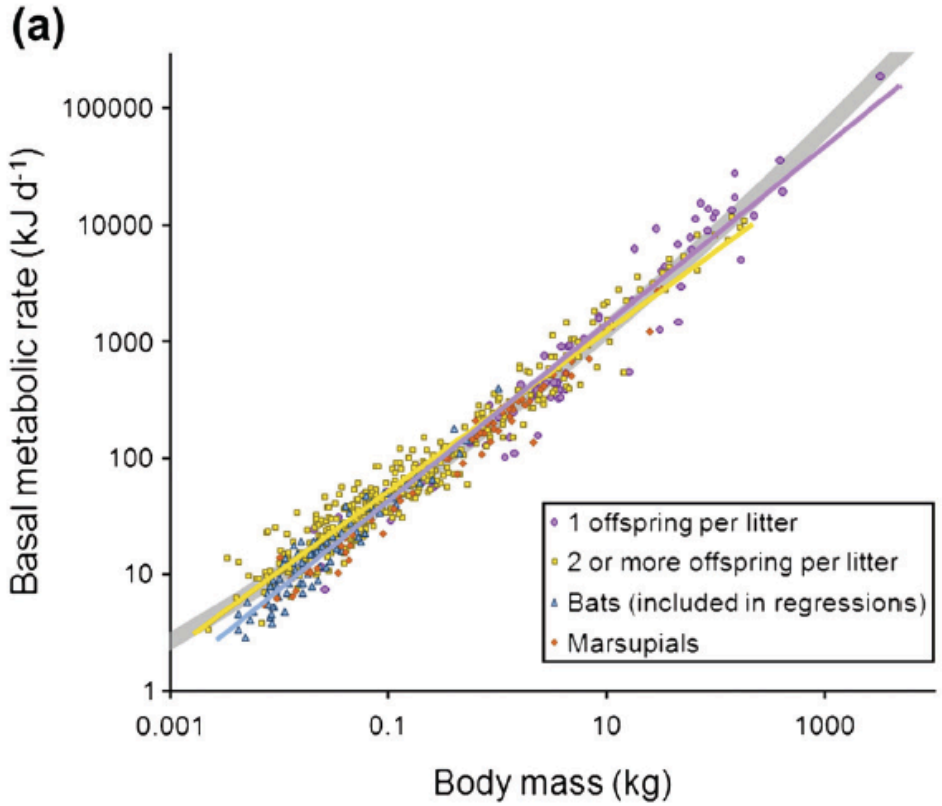
from Müller et al. (2012) Oikos

Example II: basal metabolic rate



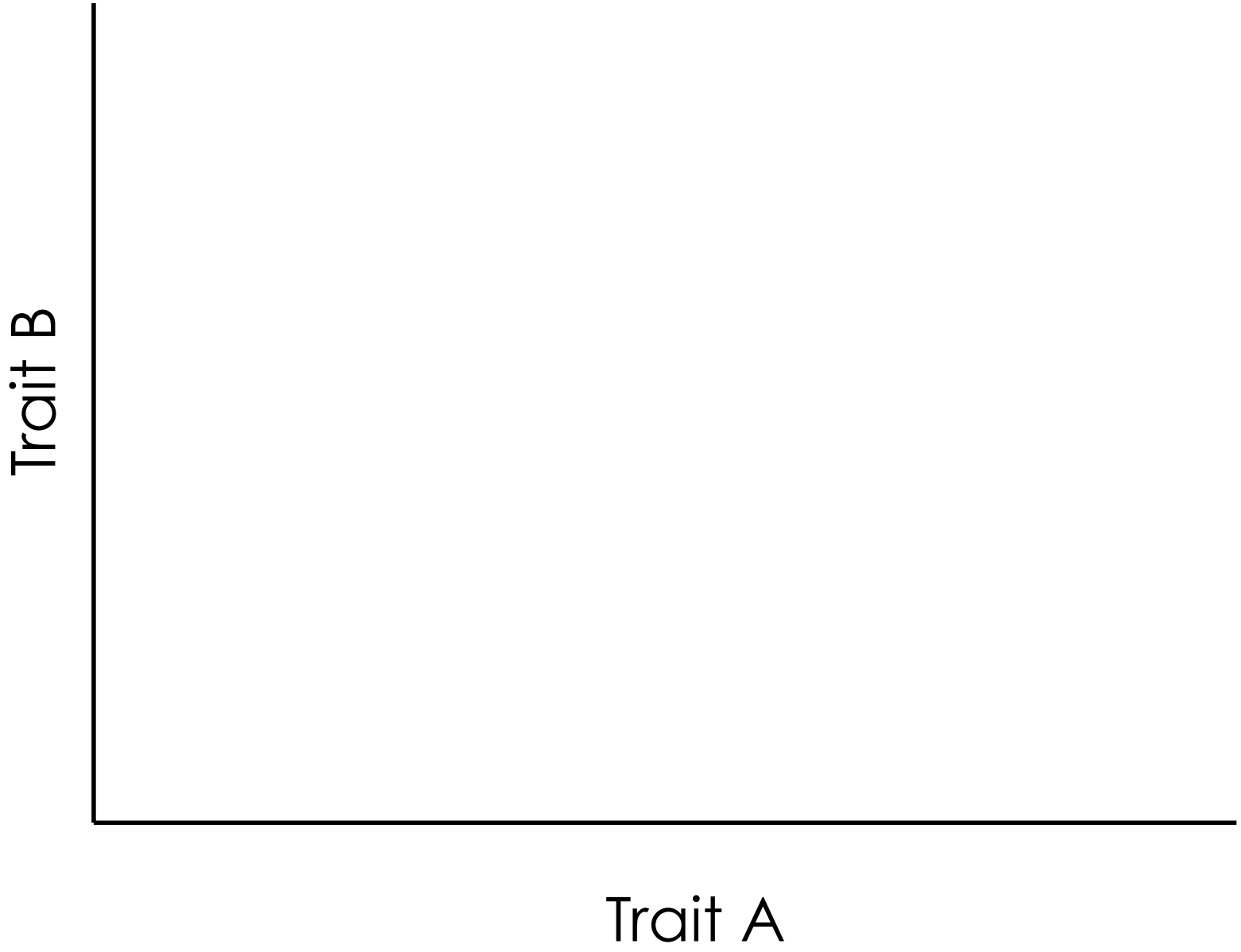
OLS: 2.38 (2.37-2.40) $BM^{0.72\ (0.71\text{-}0.73)}$

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

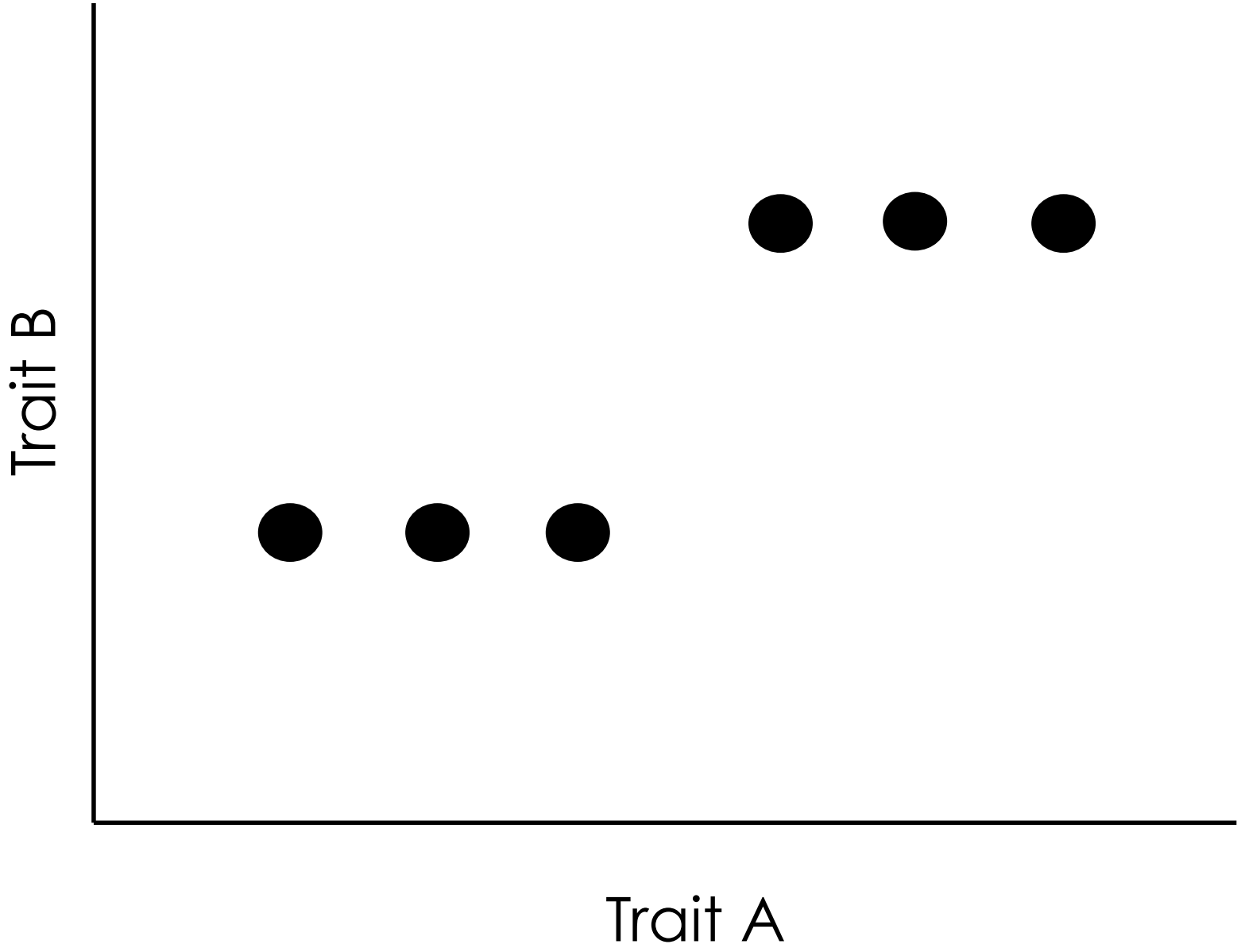


from Müller et al. (2012) Oikos

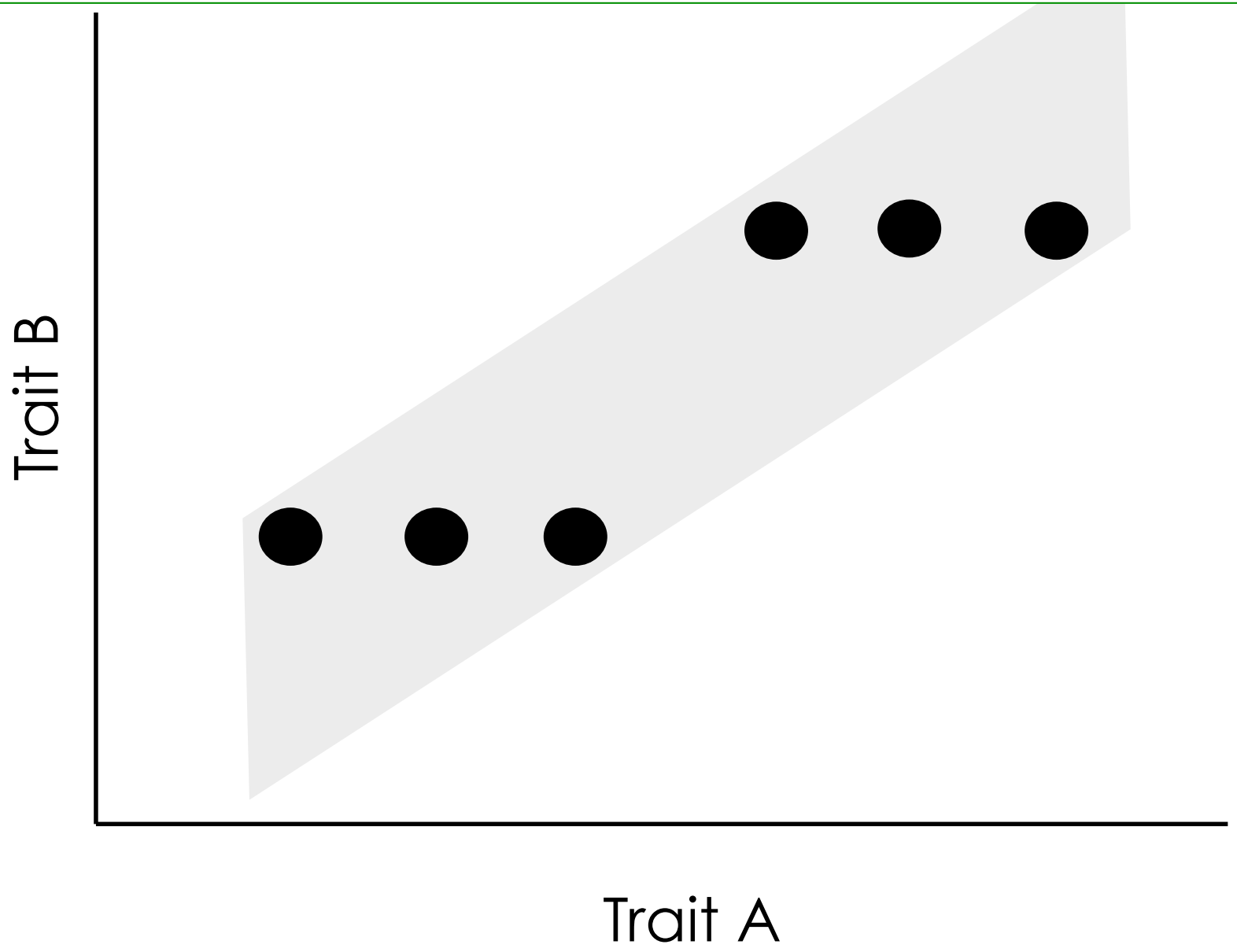
Accounting for phylogeny



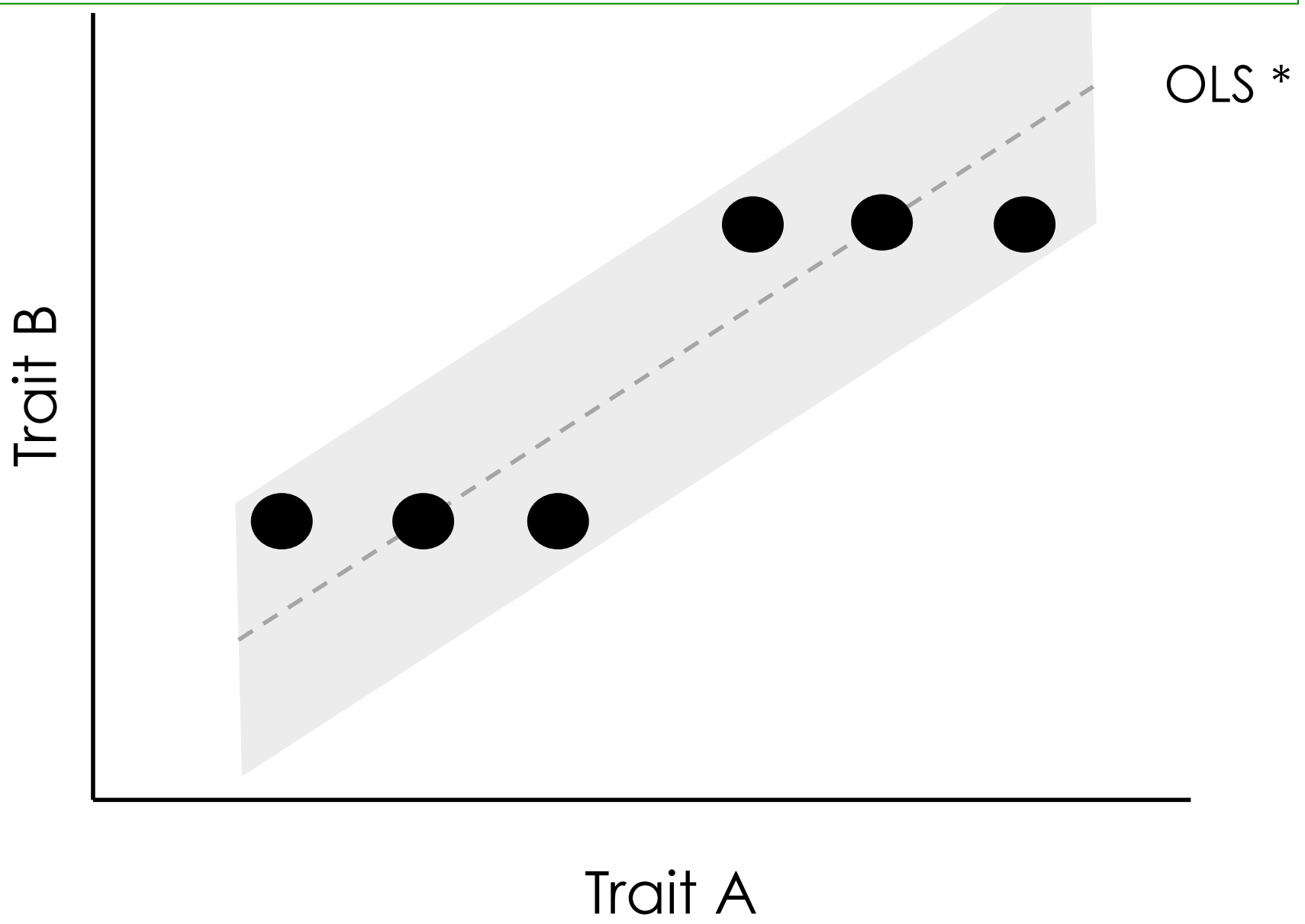
Accounting for phylogeny



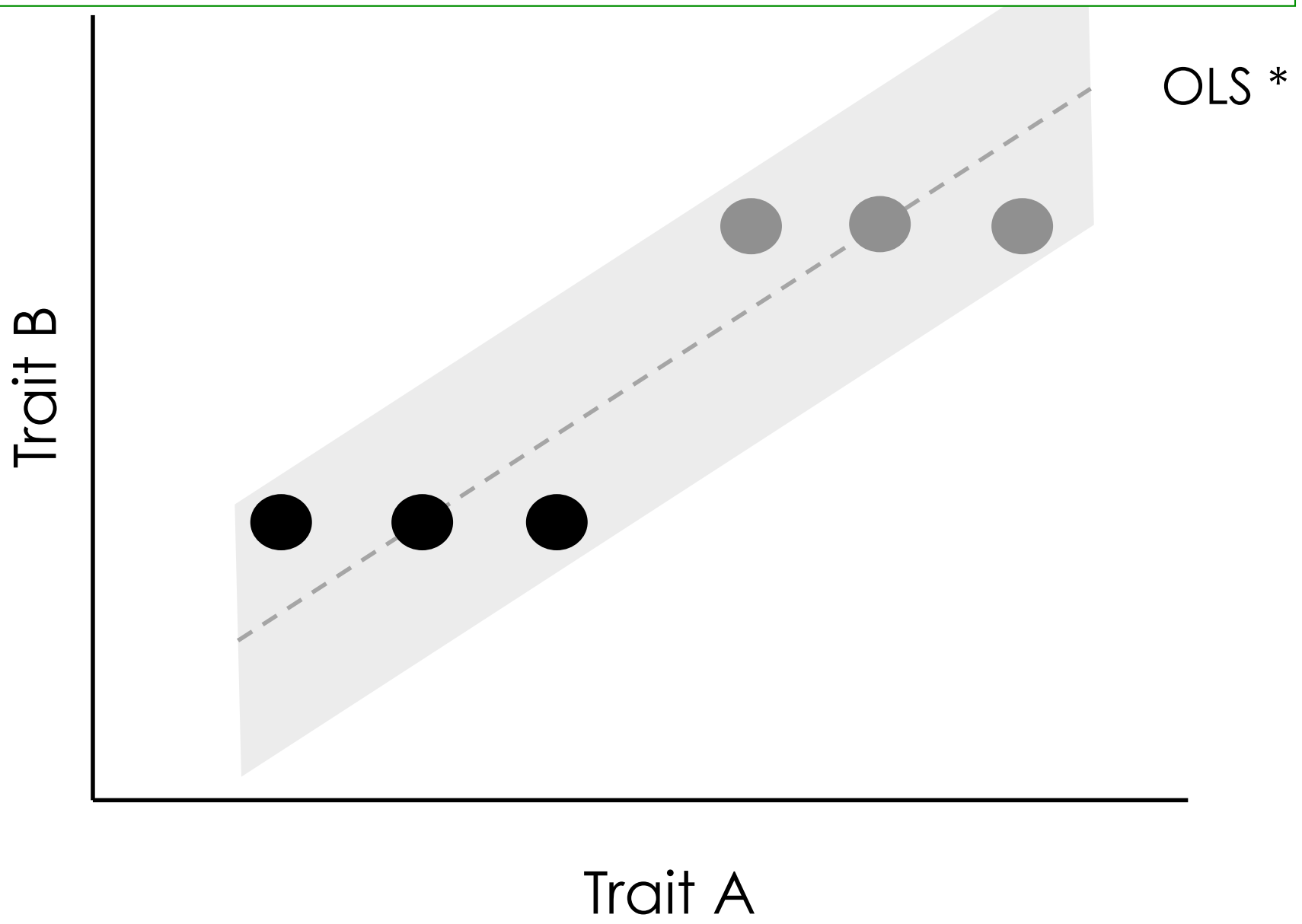
Accounting for phylogeny



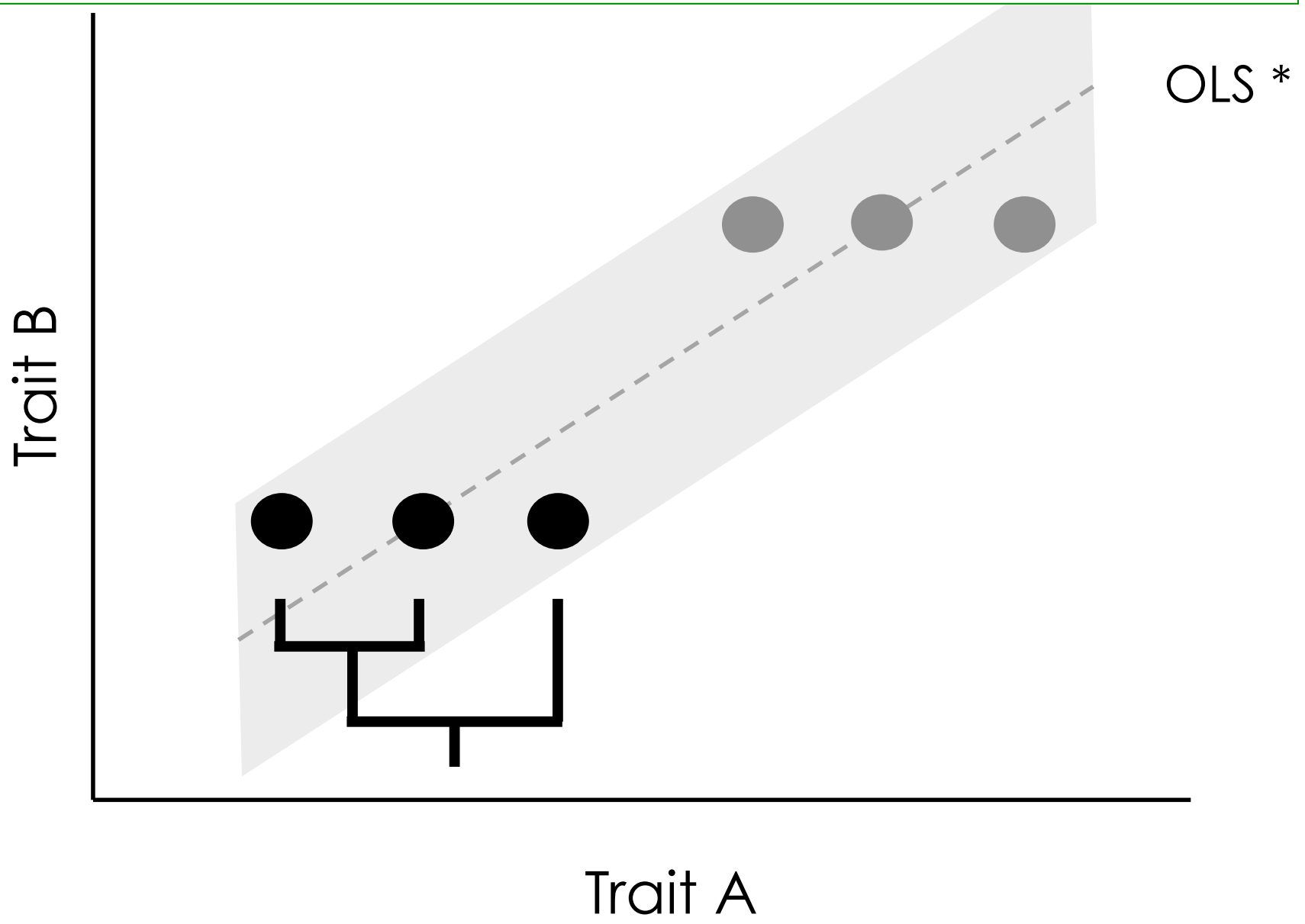
Accounting for phylogeny



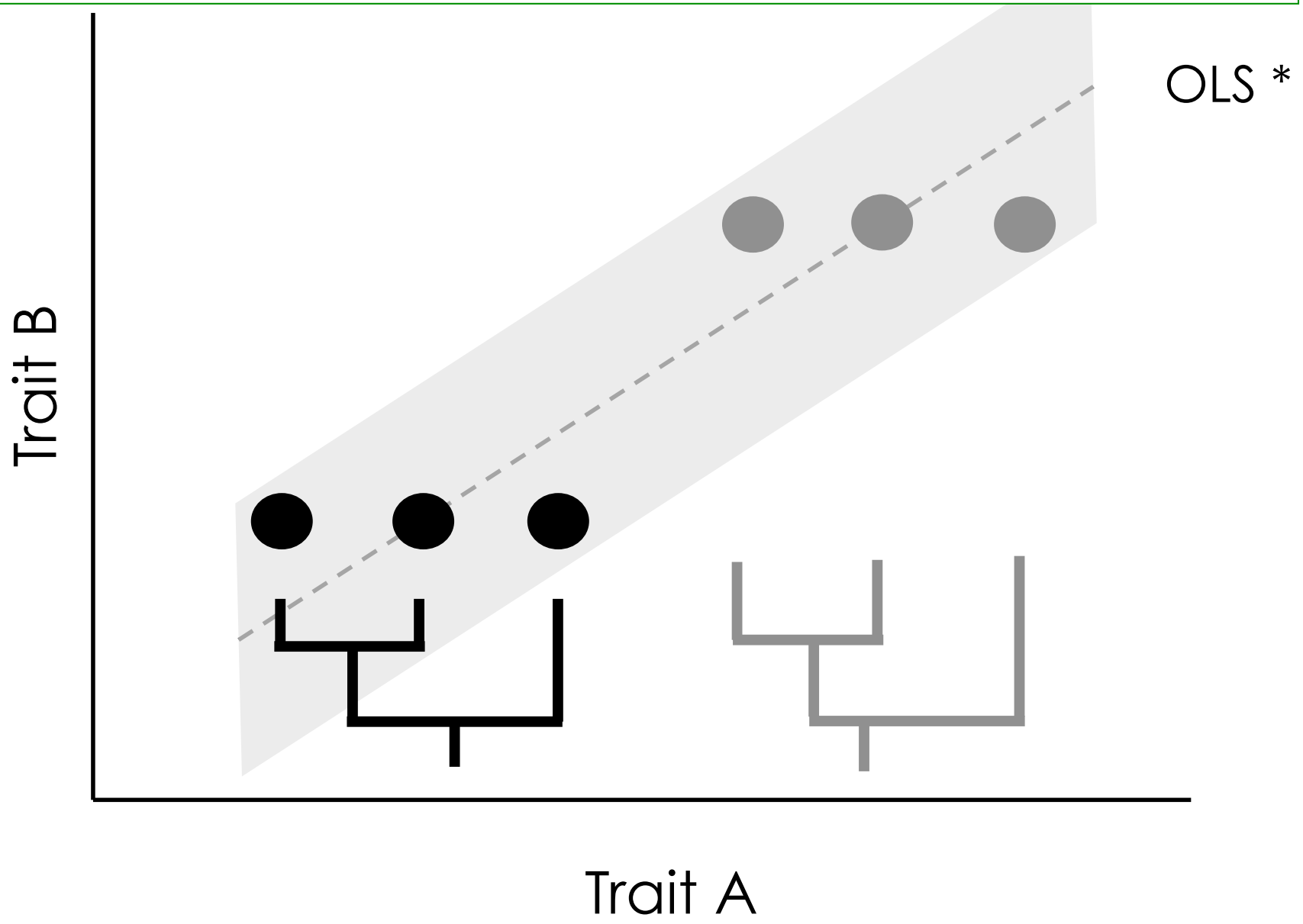
Accounting for phylogeny



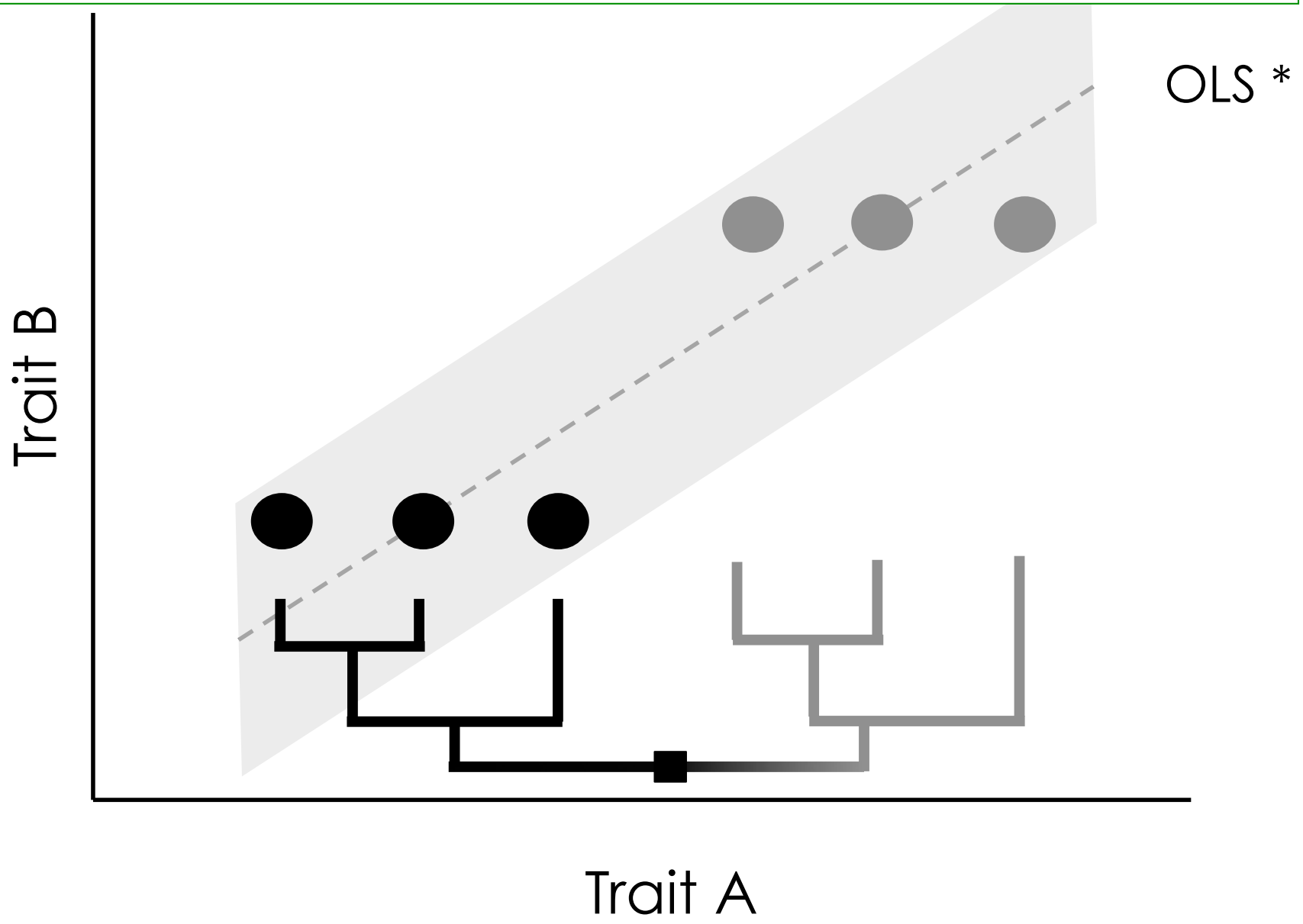
Accounting for phylogeny



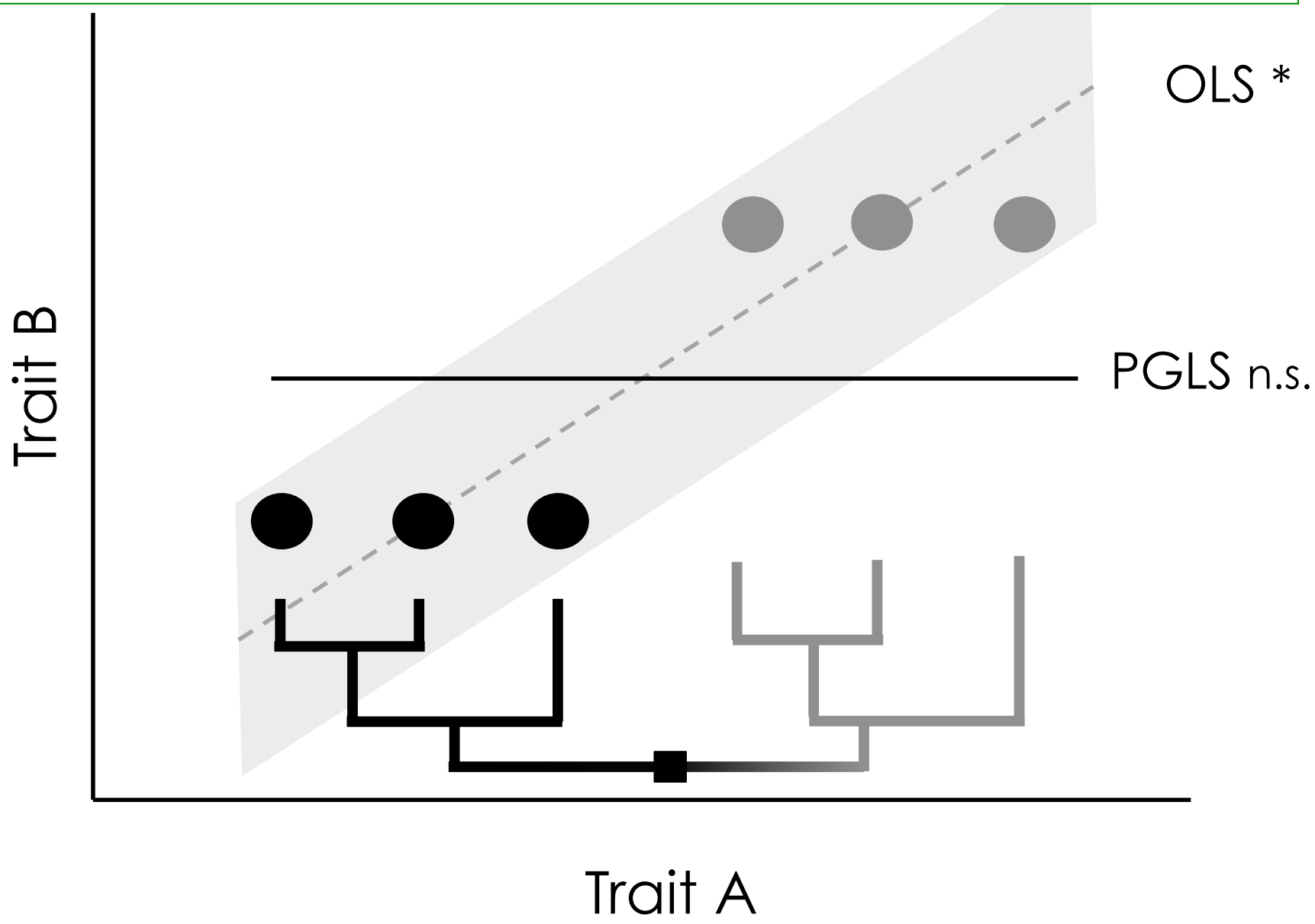
Accounting for phylogeny



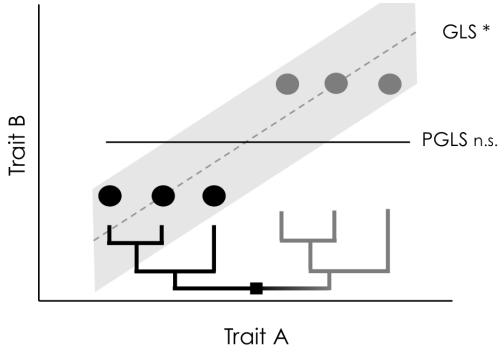
Accounting for phylogeny



Accounting for phylogeny

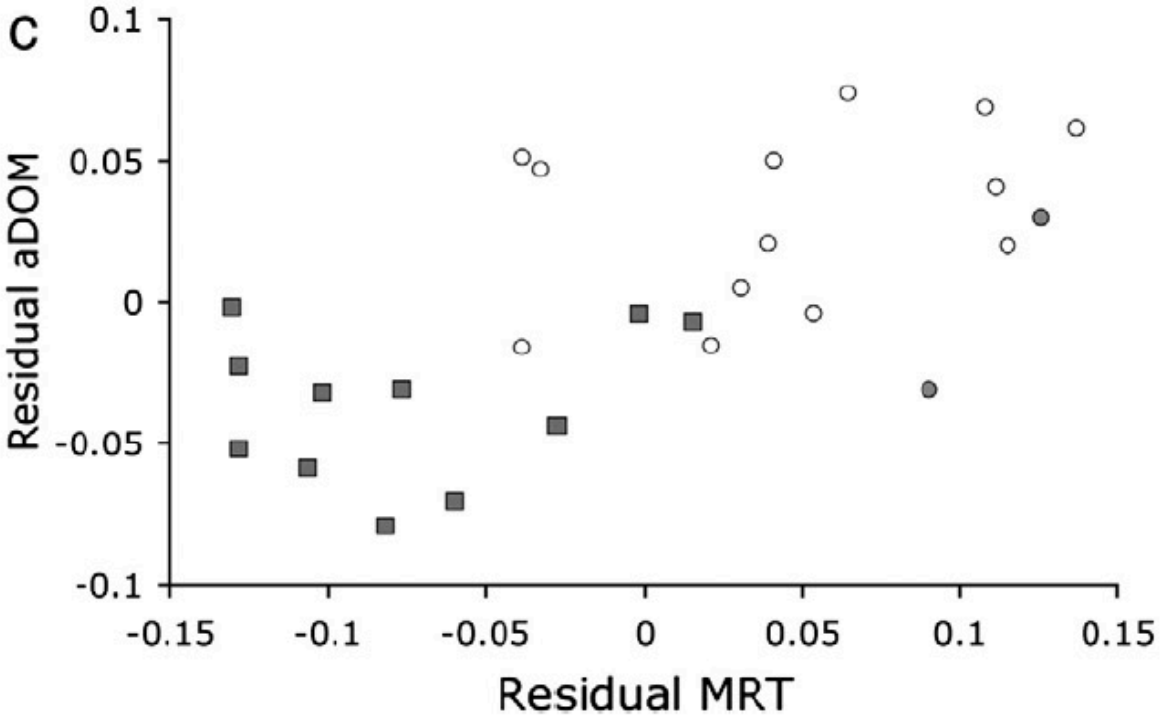


Example III: retention/digestibility



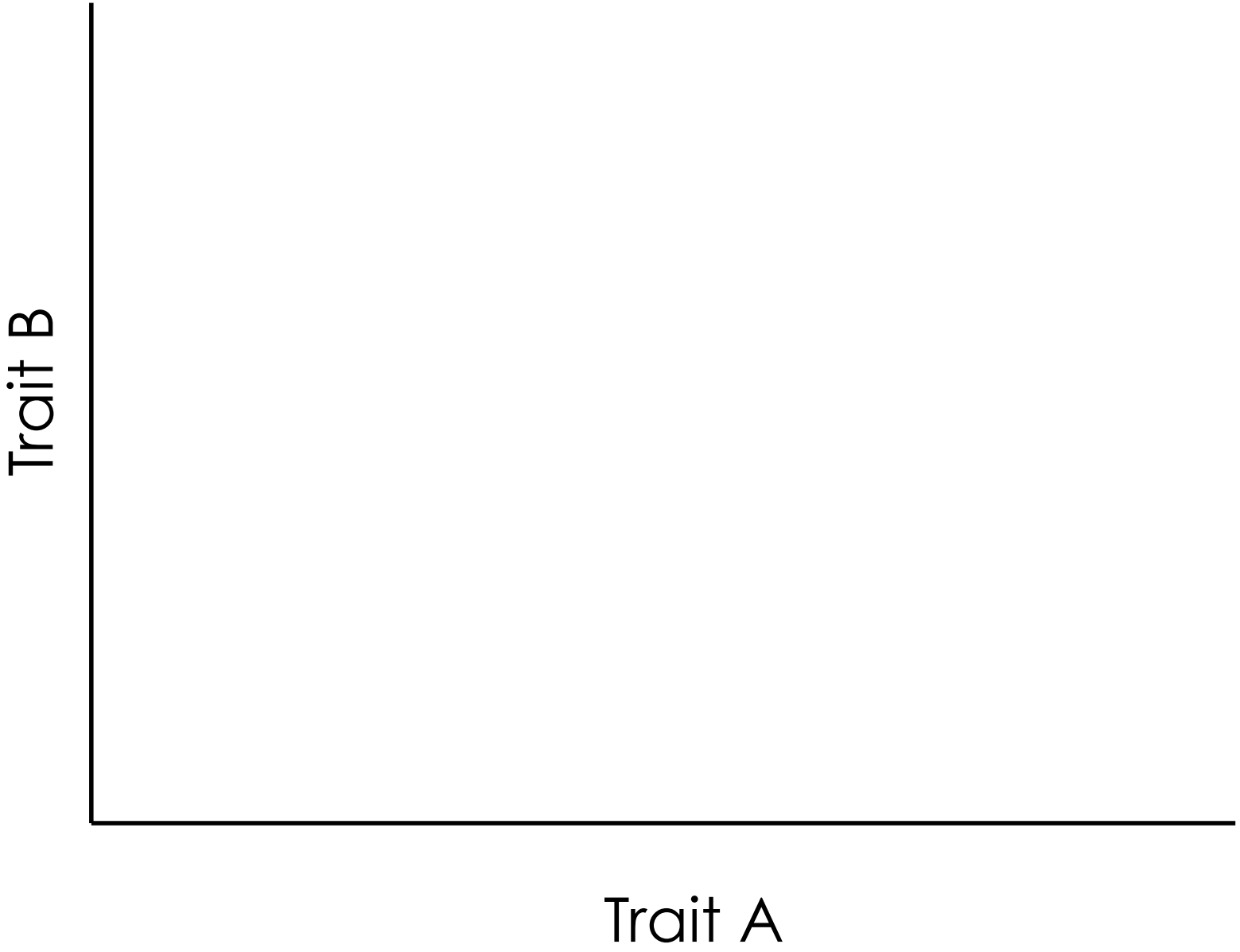
OLS: significant

PGLS: not significant

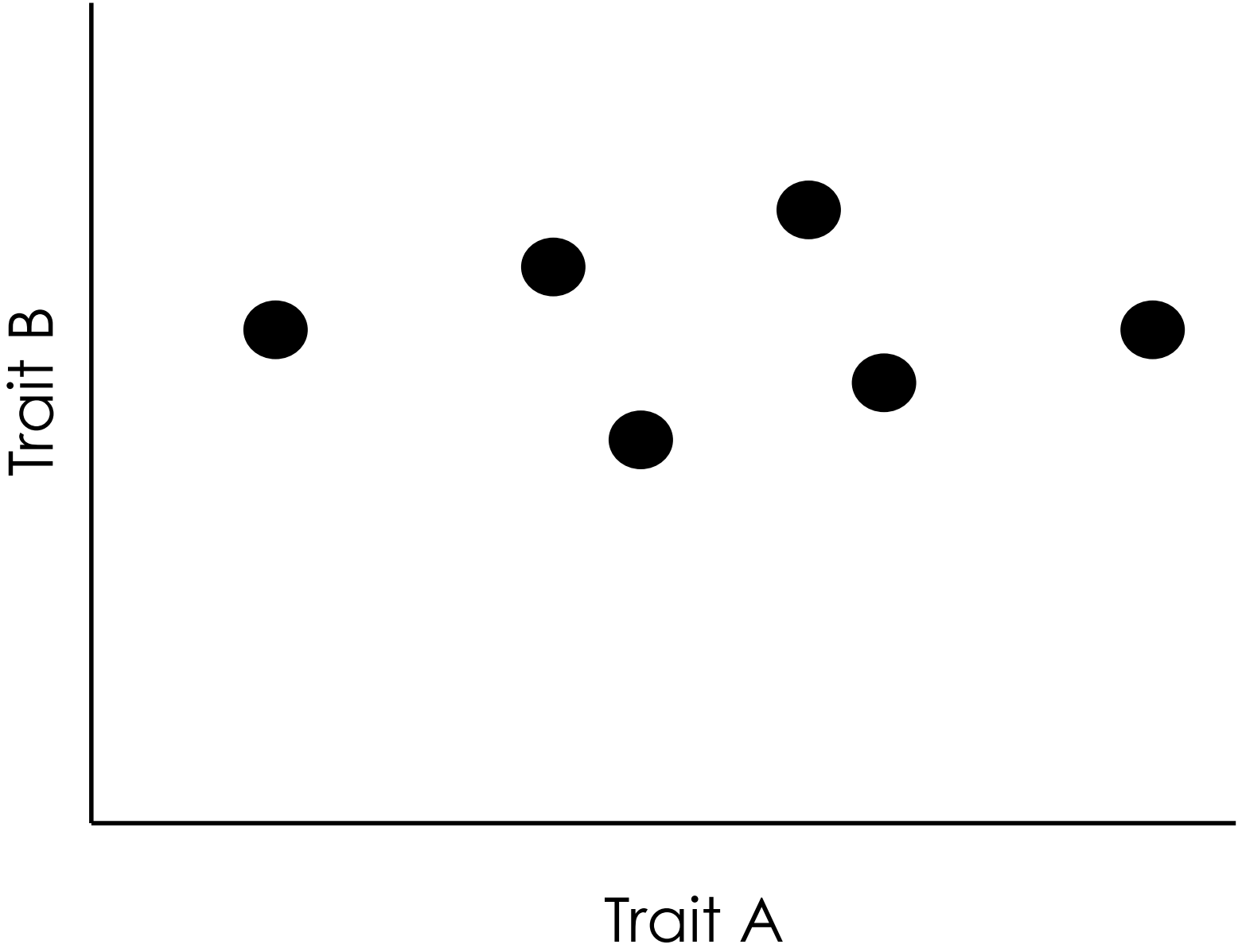


from Müller et al. (2013) CBP A

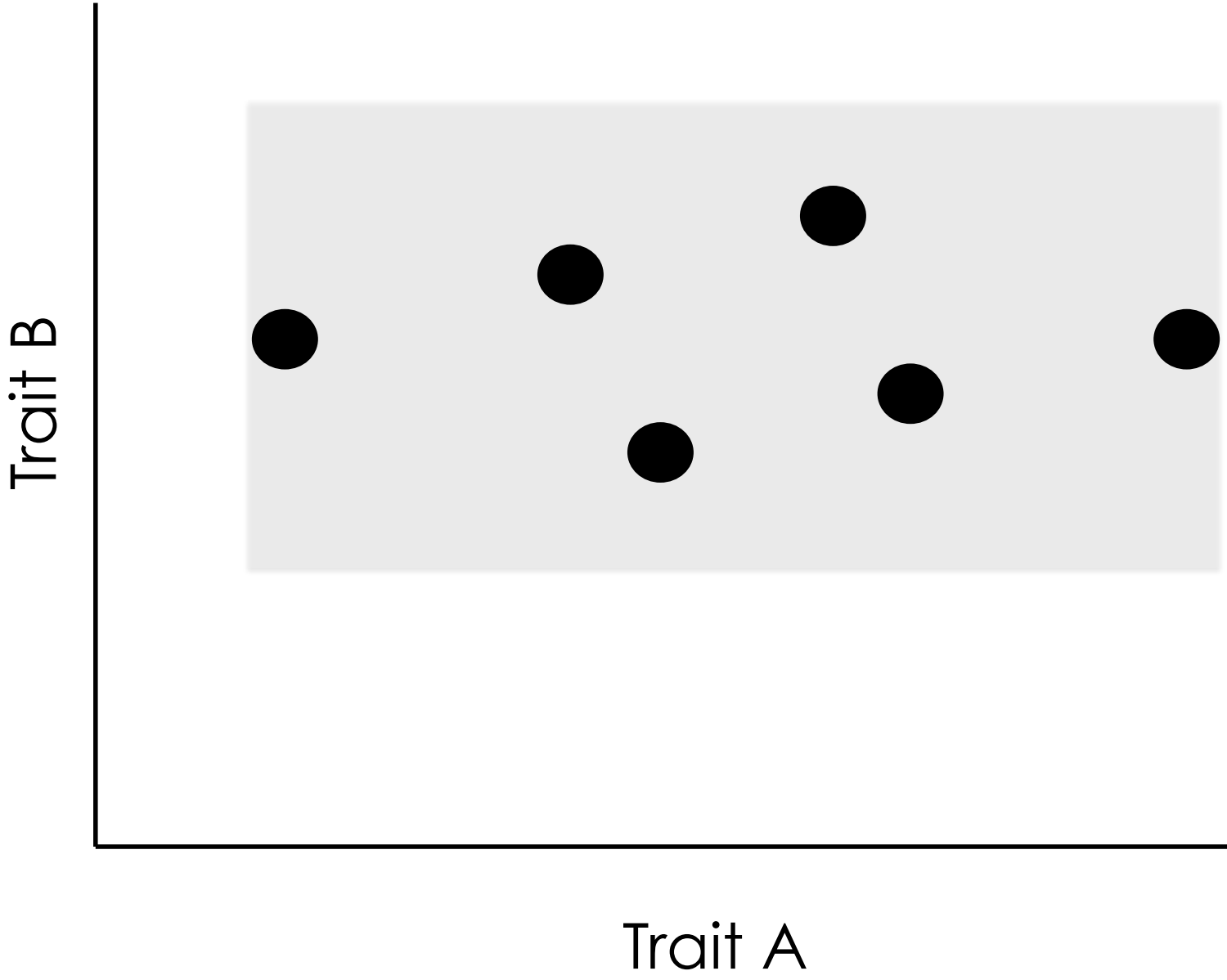
Accounting for phylogeny



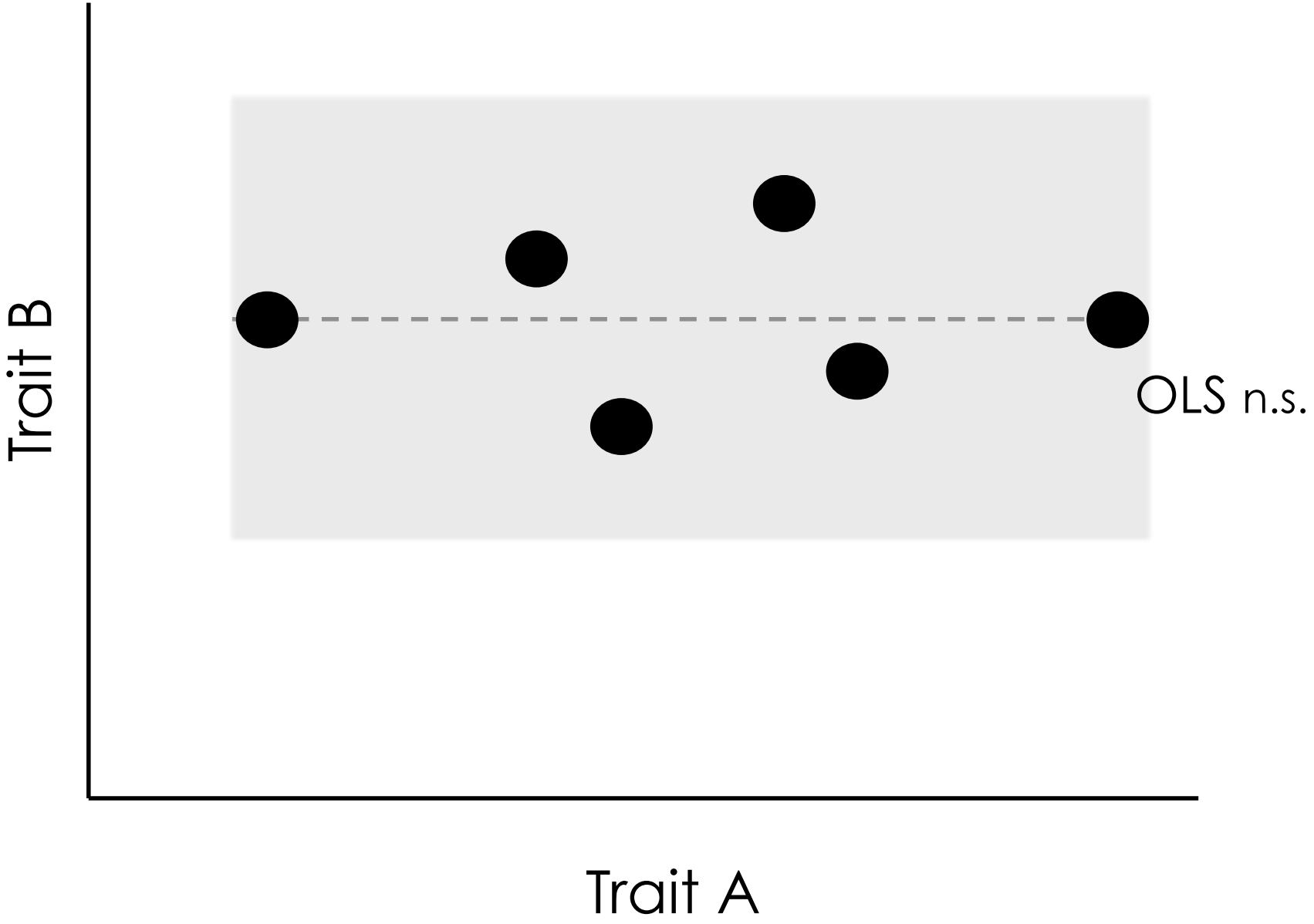
Accounting for phylogeny



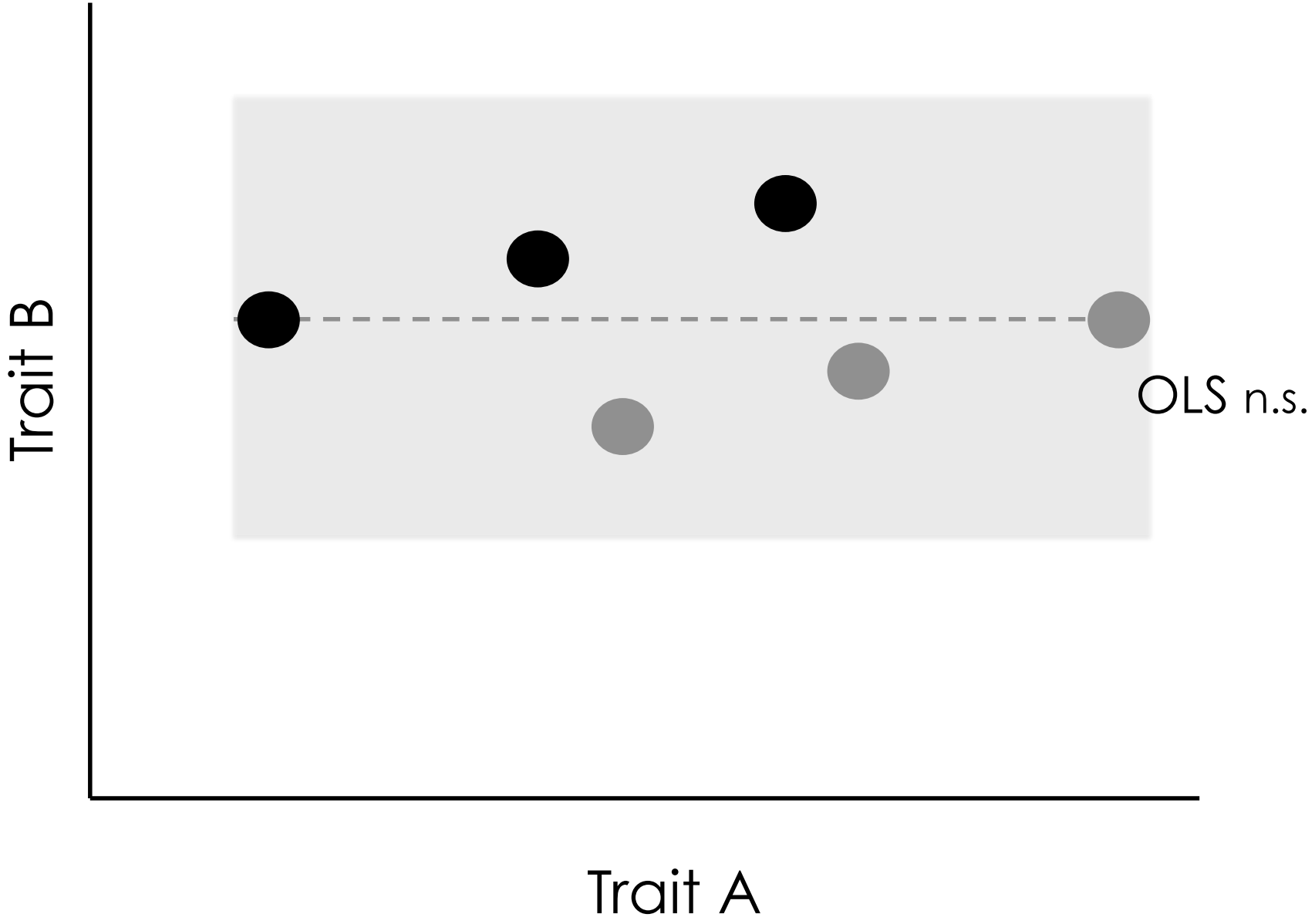
Accounting for phylogeny



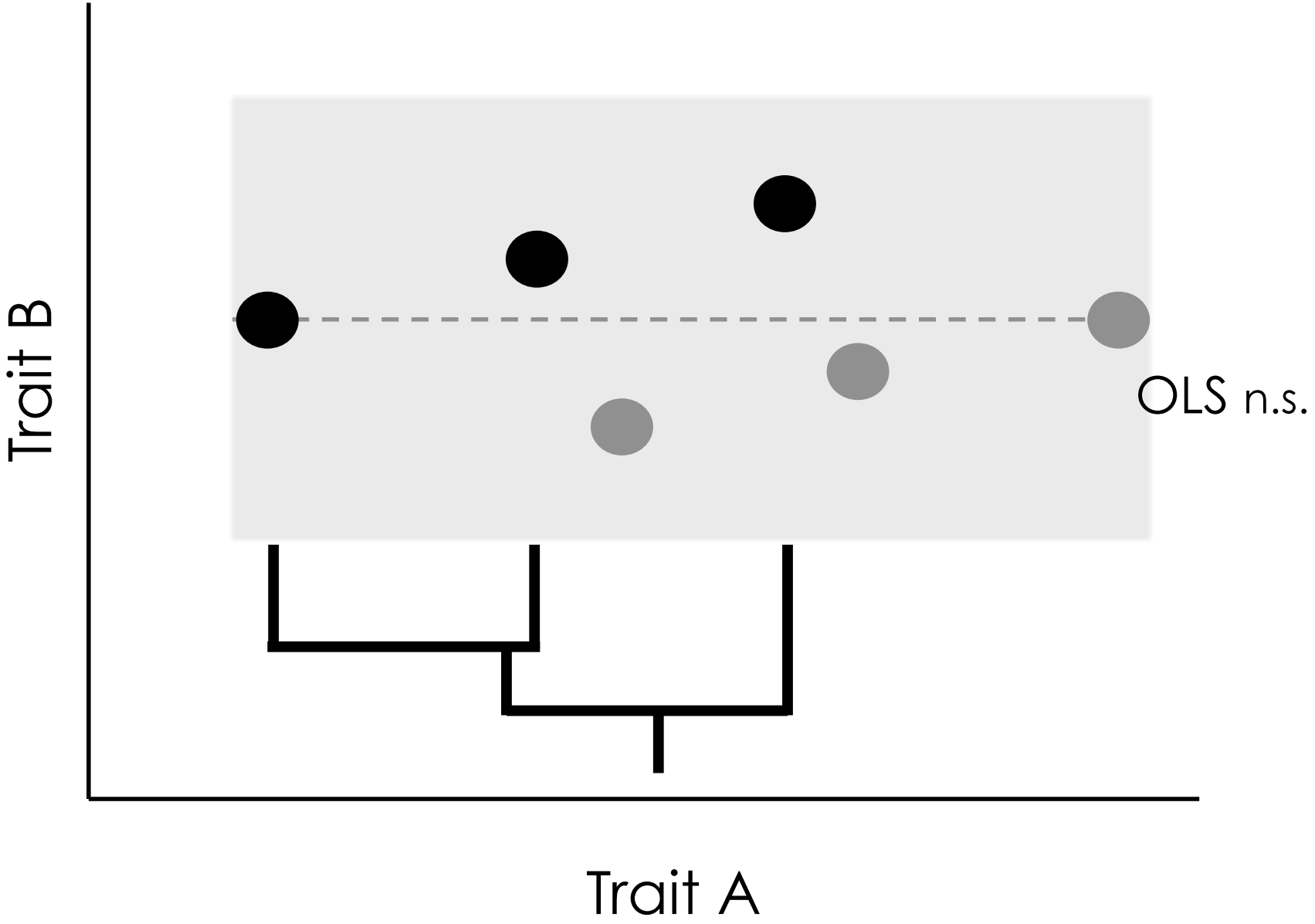
Accounting for phylogeny



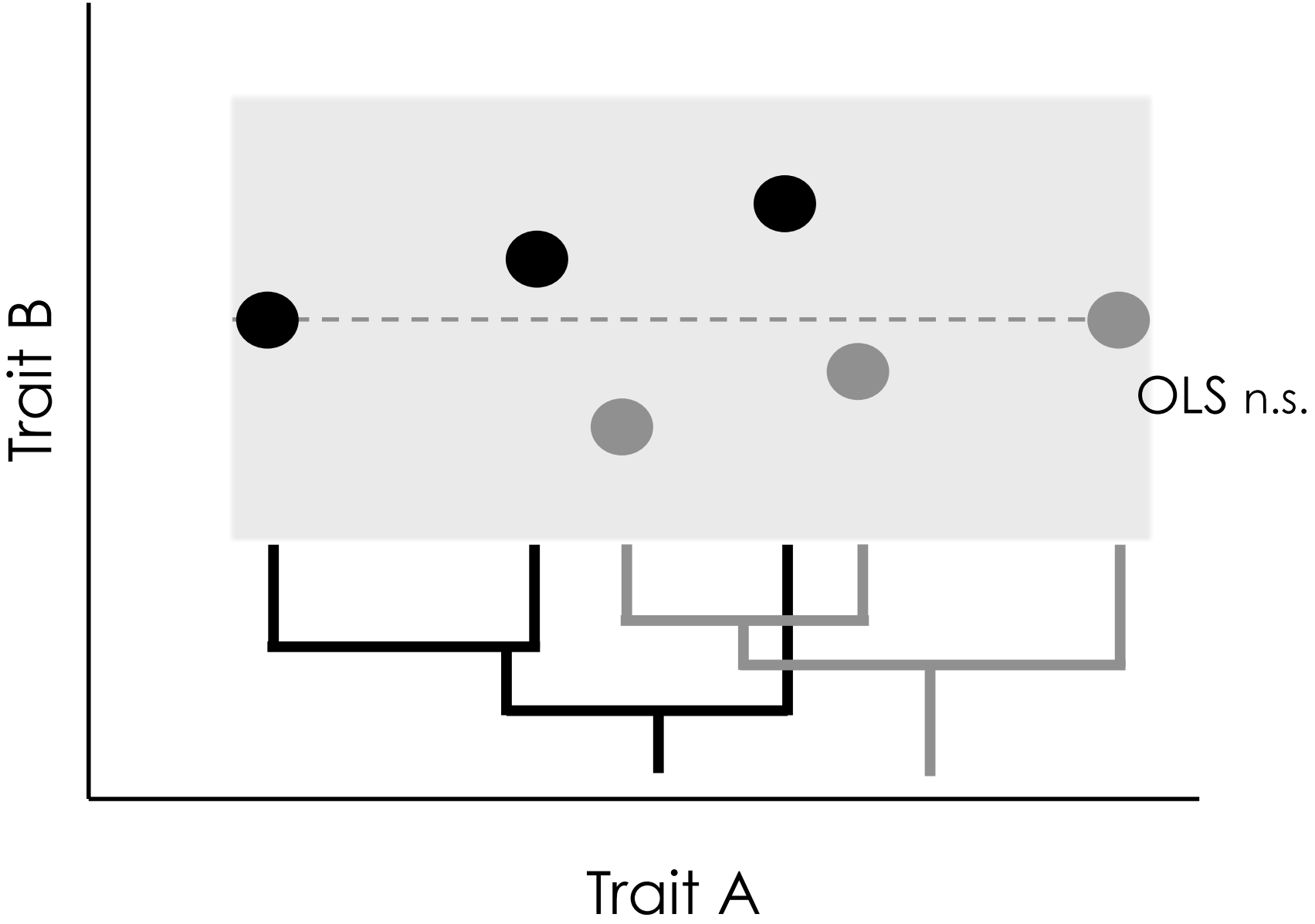
Accounting for phylogeny



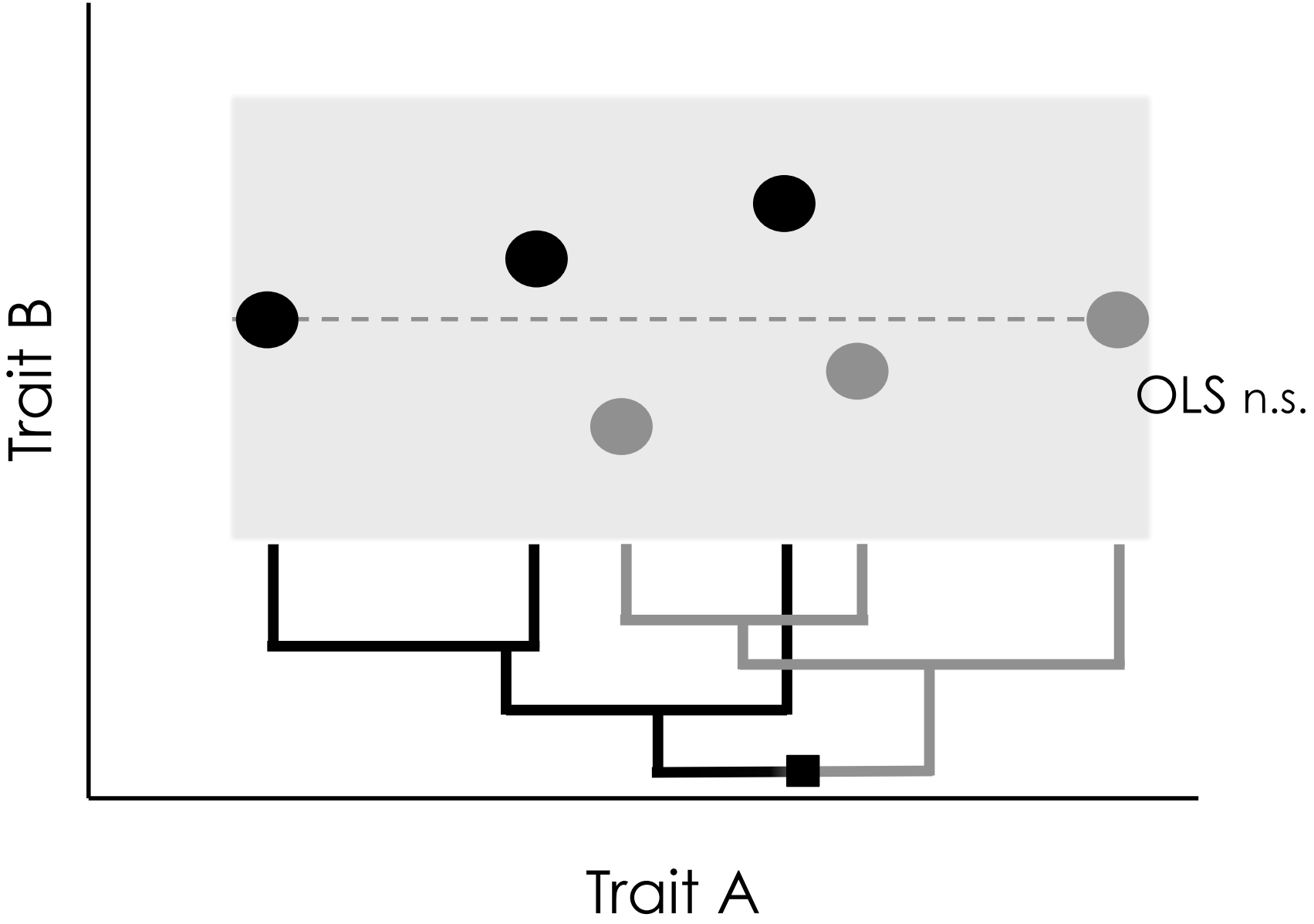
Accounting for phylogeny



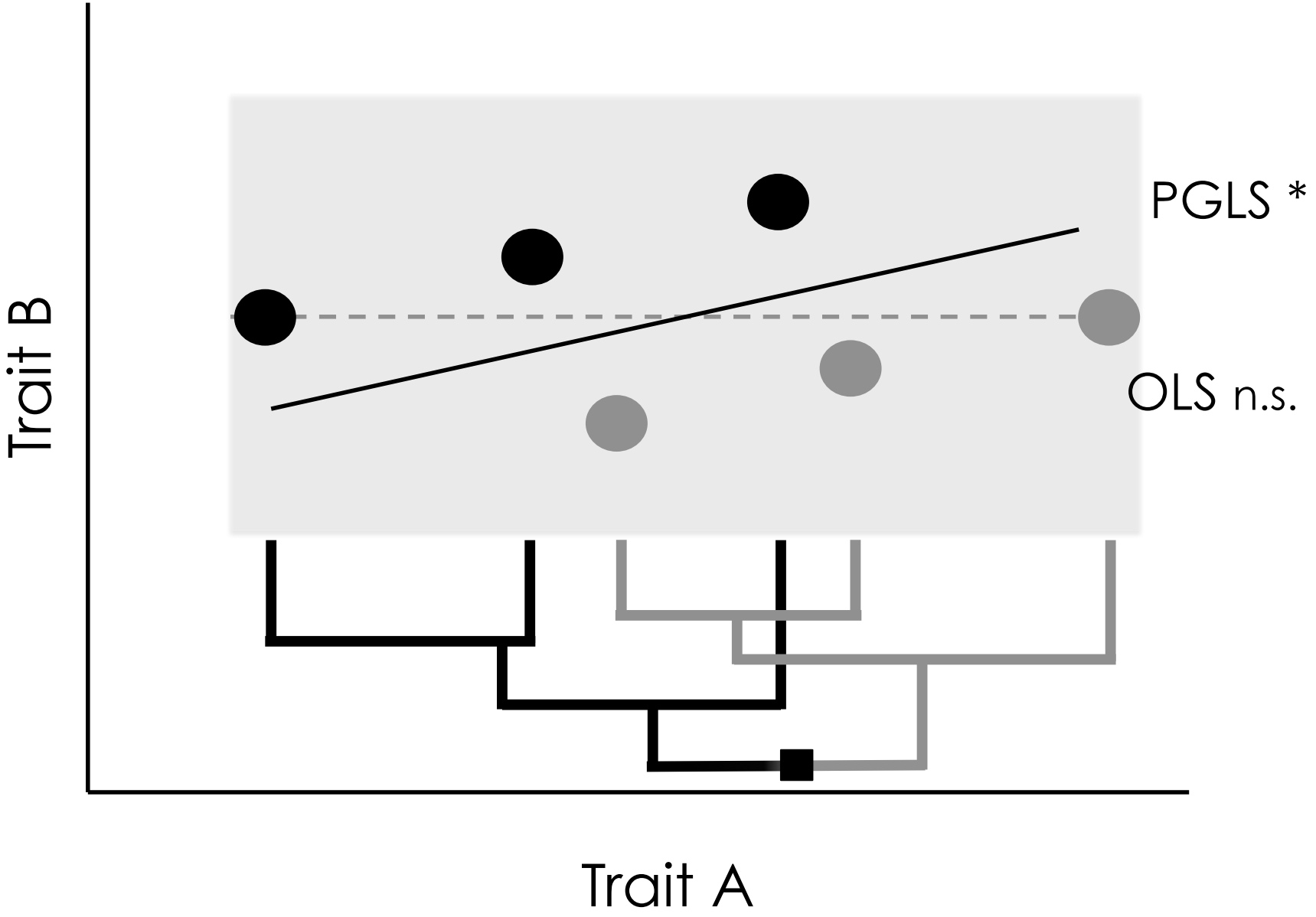
Accounting for phylogeny



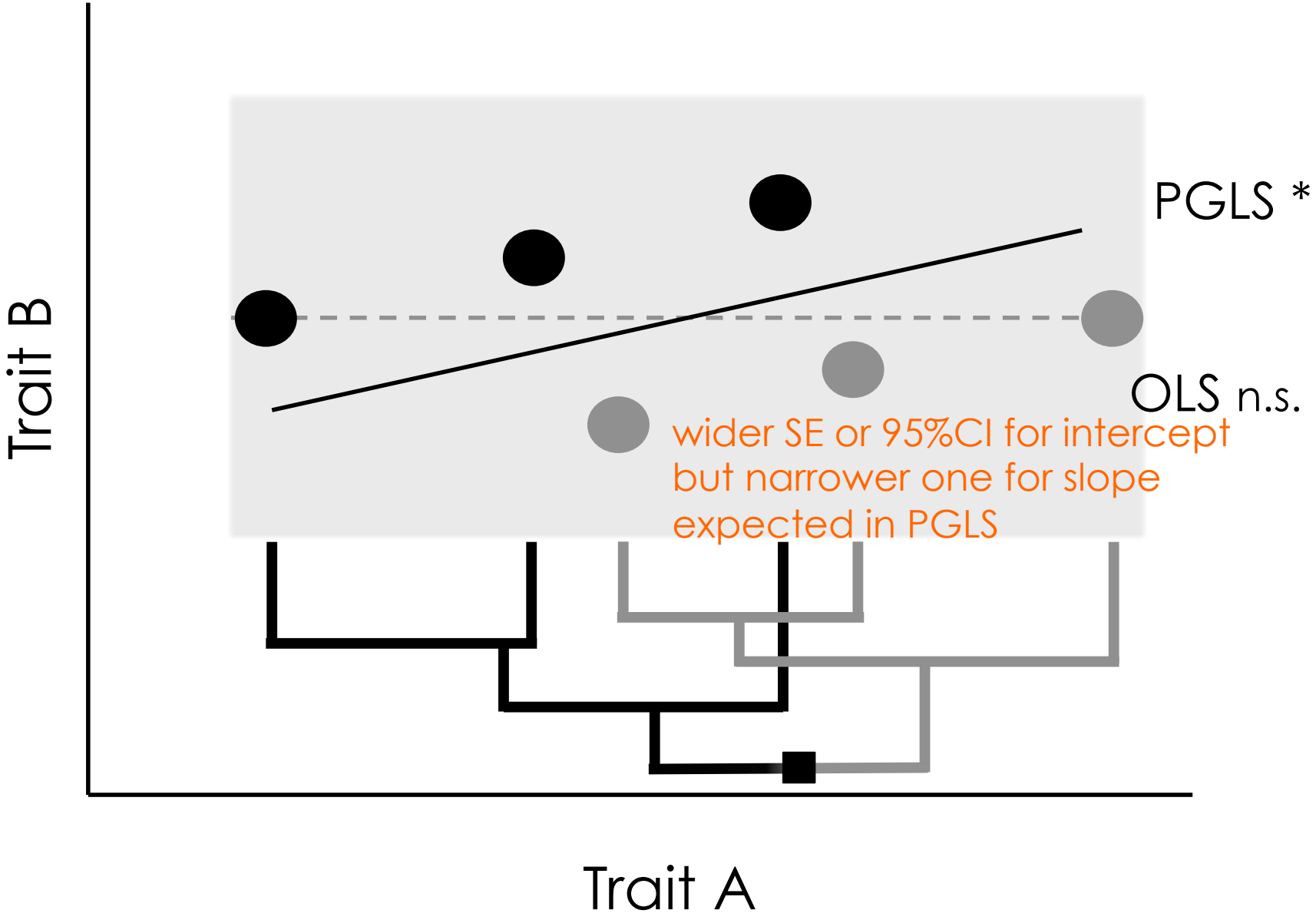
Accounting for phylogeny



Accounting for phylogeny



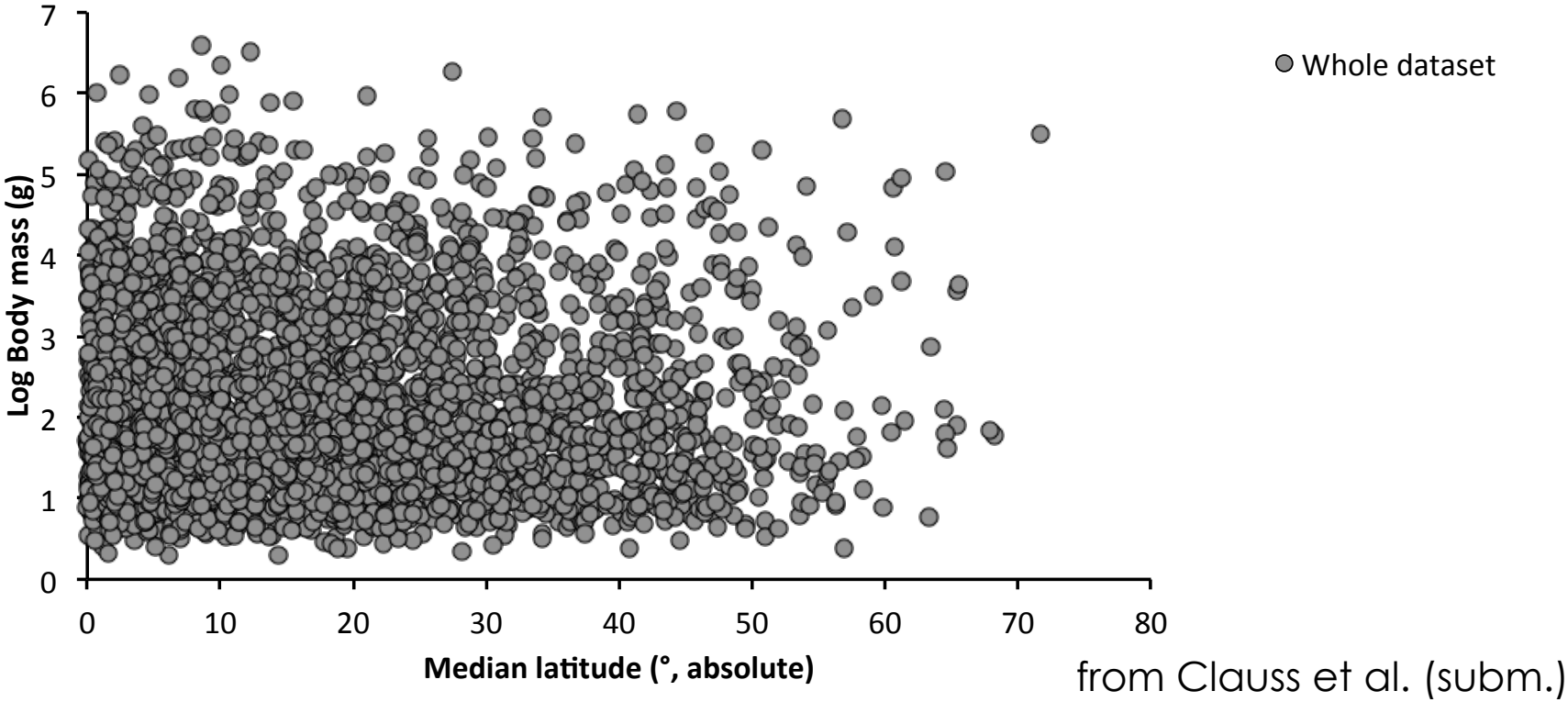
Accounting for phylogeny



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.

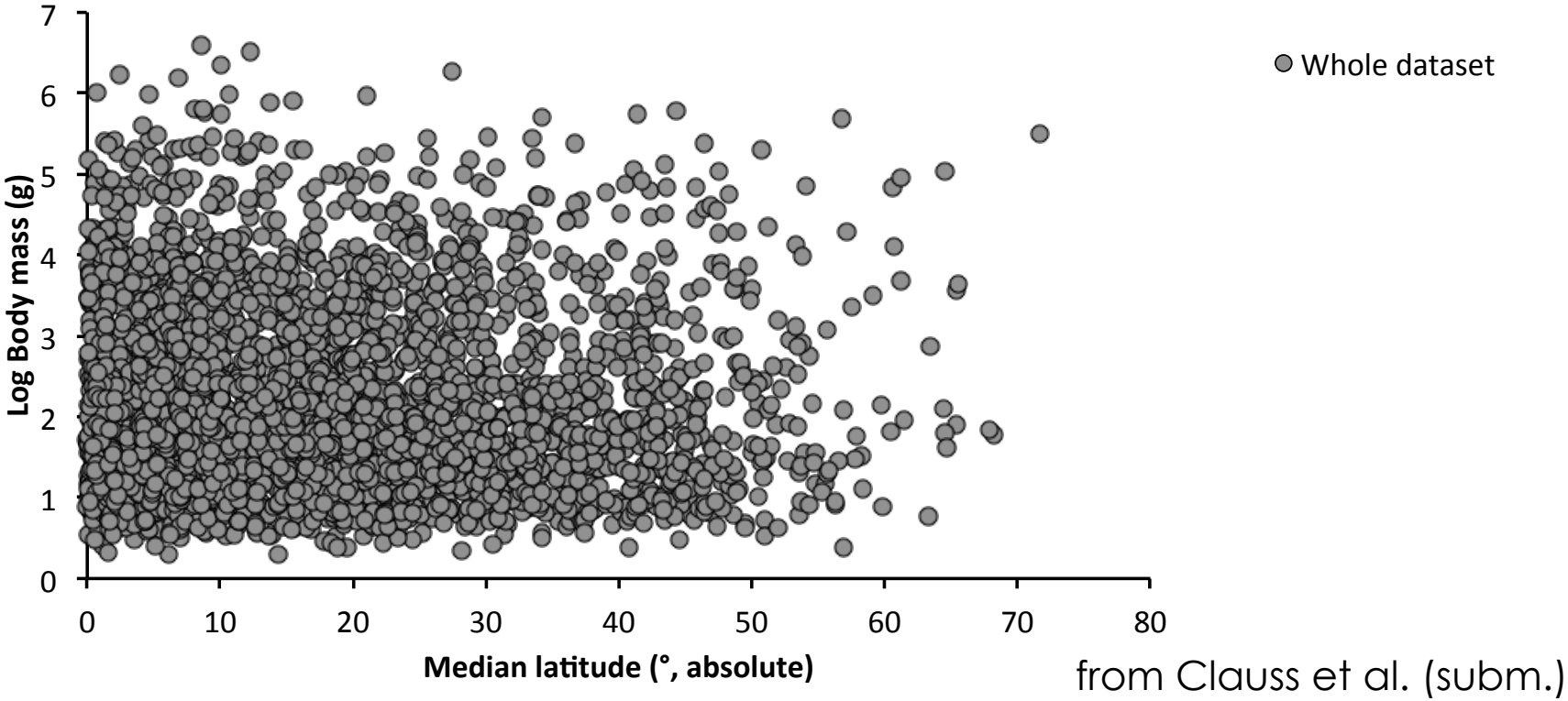


from Clauss et al. (subm.)

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.

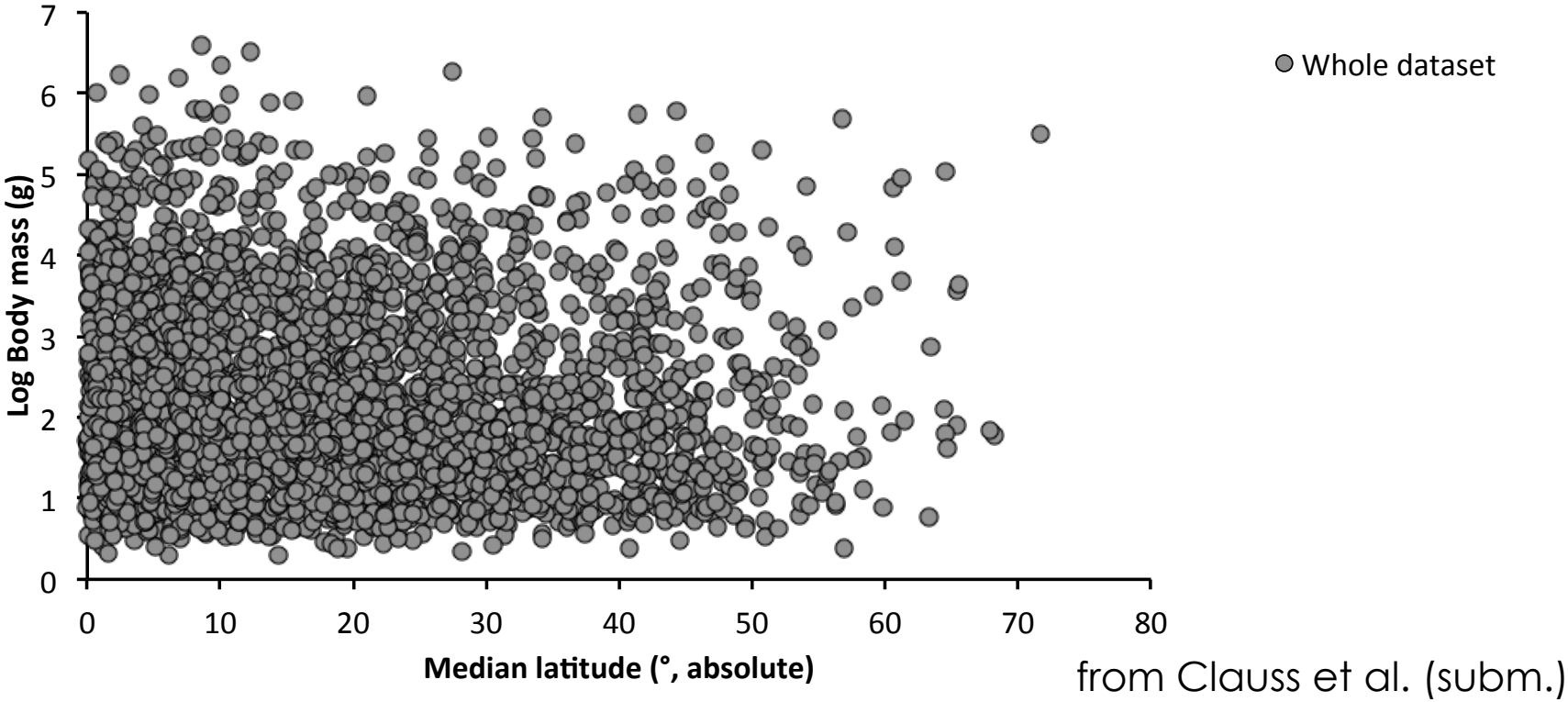


from Clauss et al. (subm.)

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.

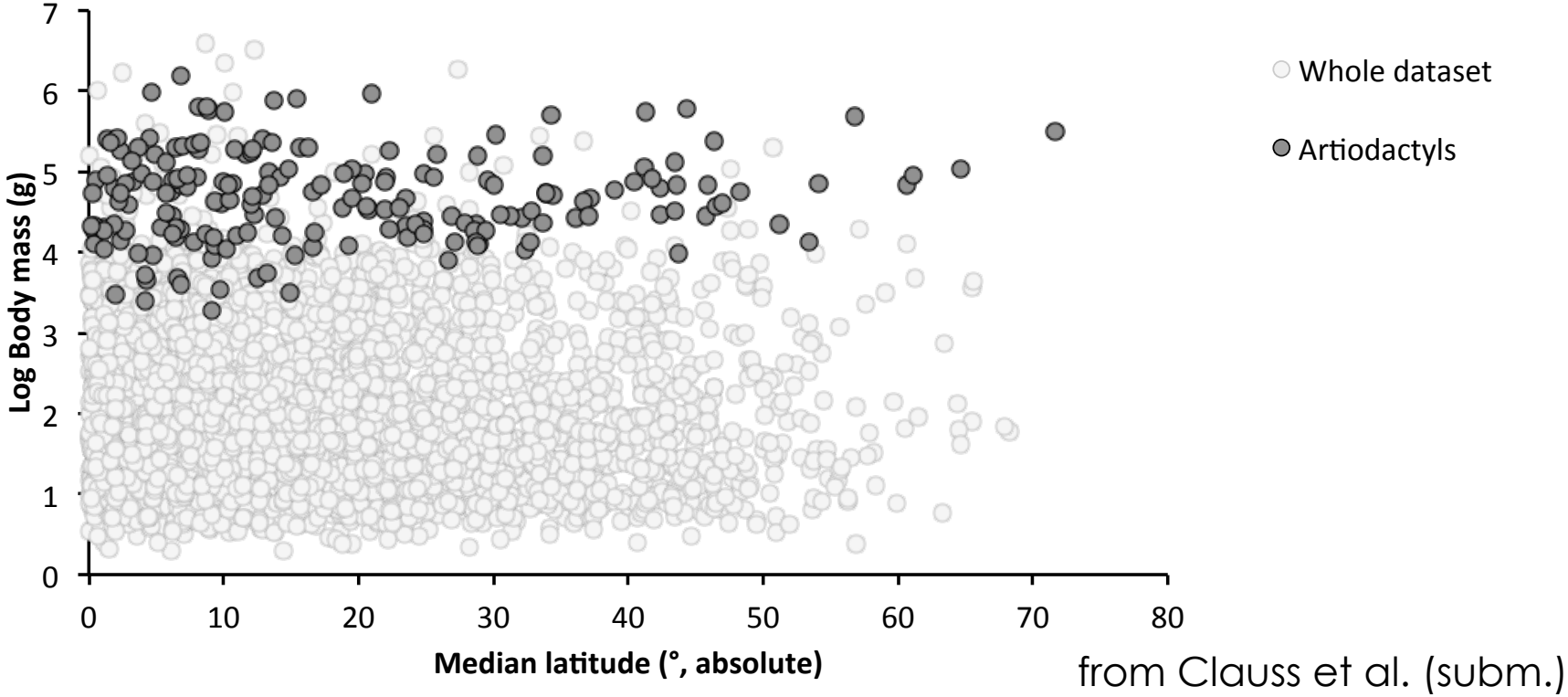


from Clauss et al. (subm.)

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.

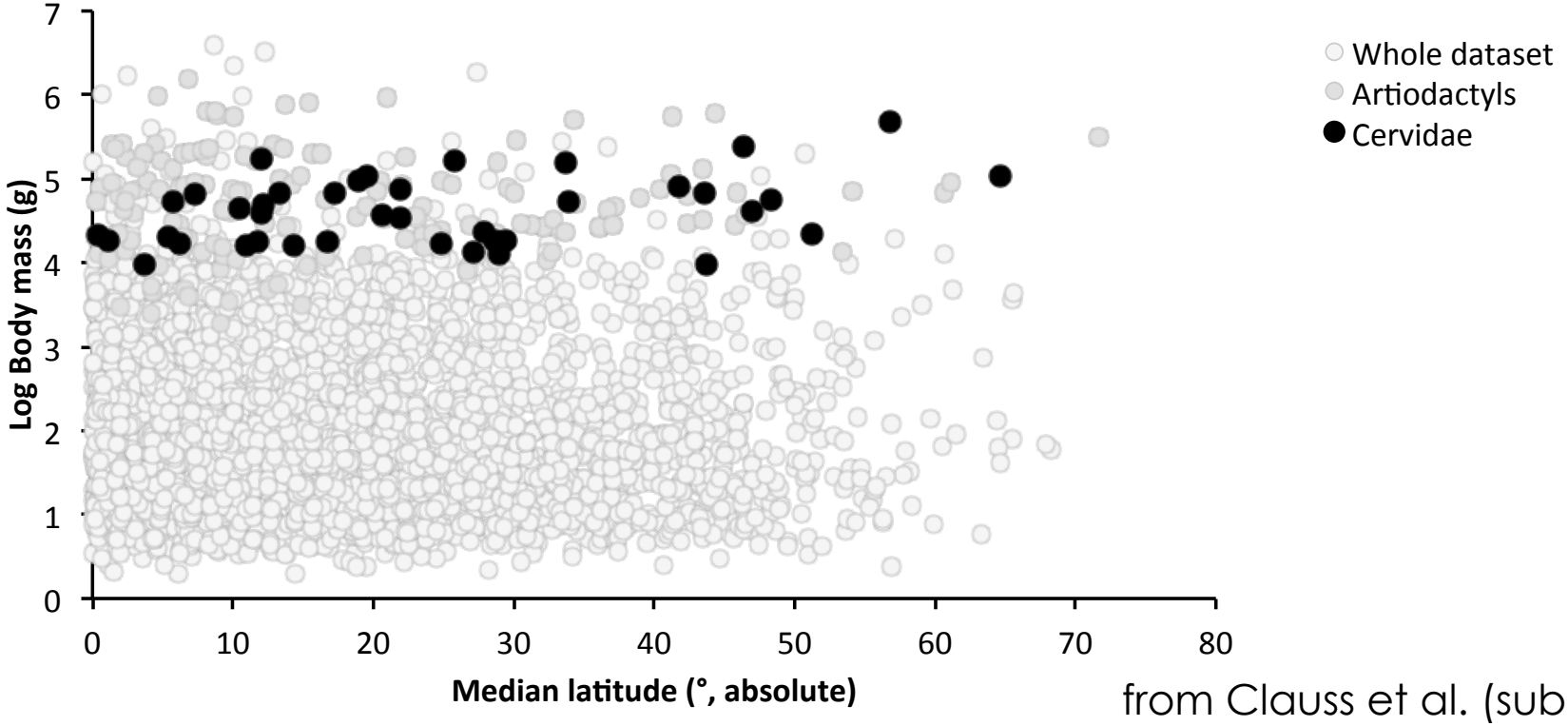


from Clauss et al. (subm.)

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.

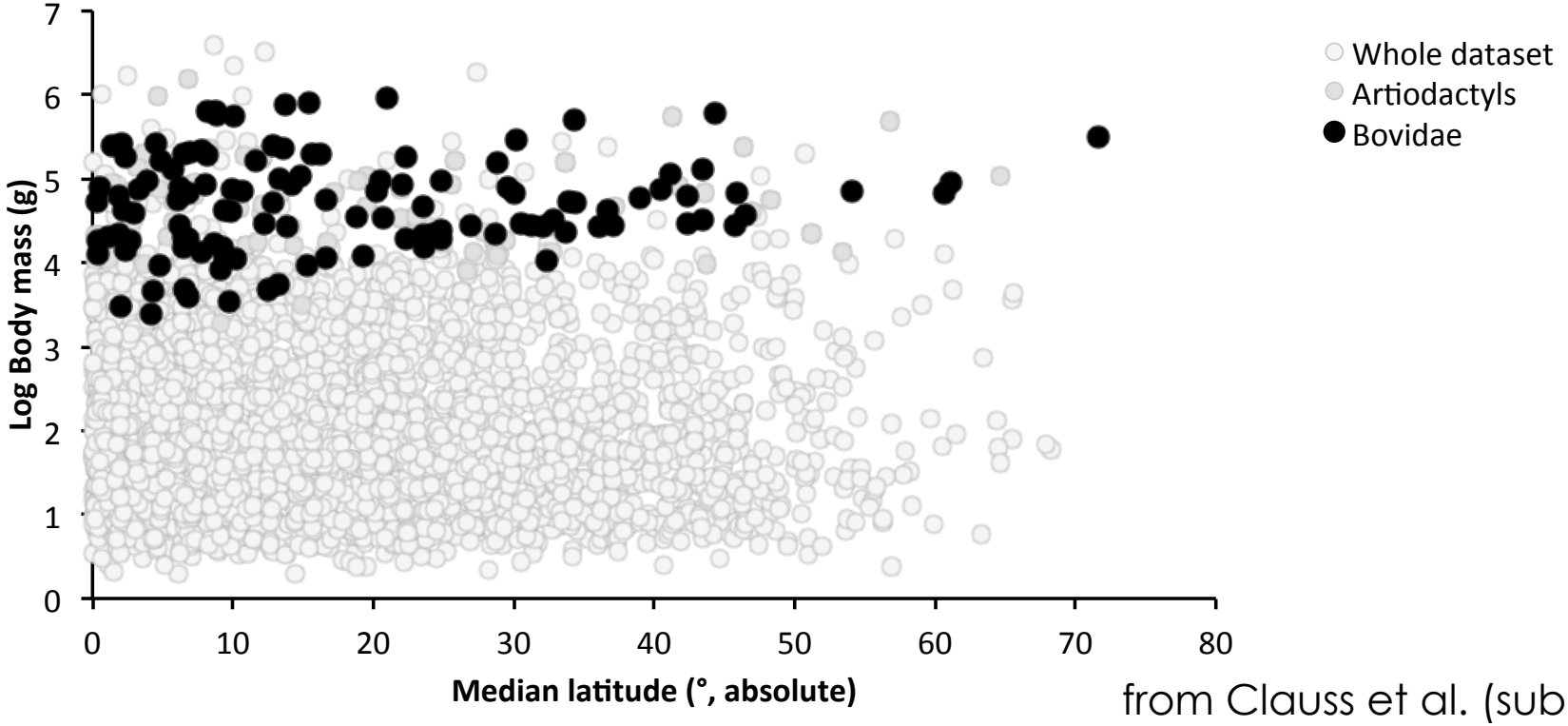


from Clauss et al. (subm.)

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.

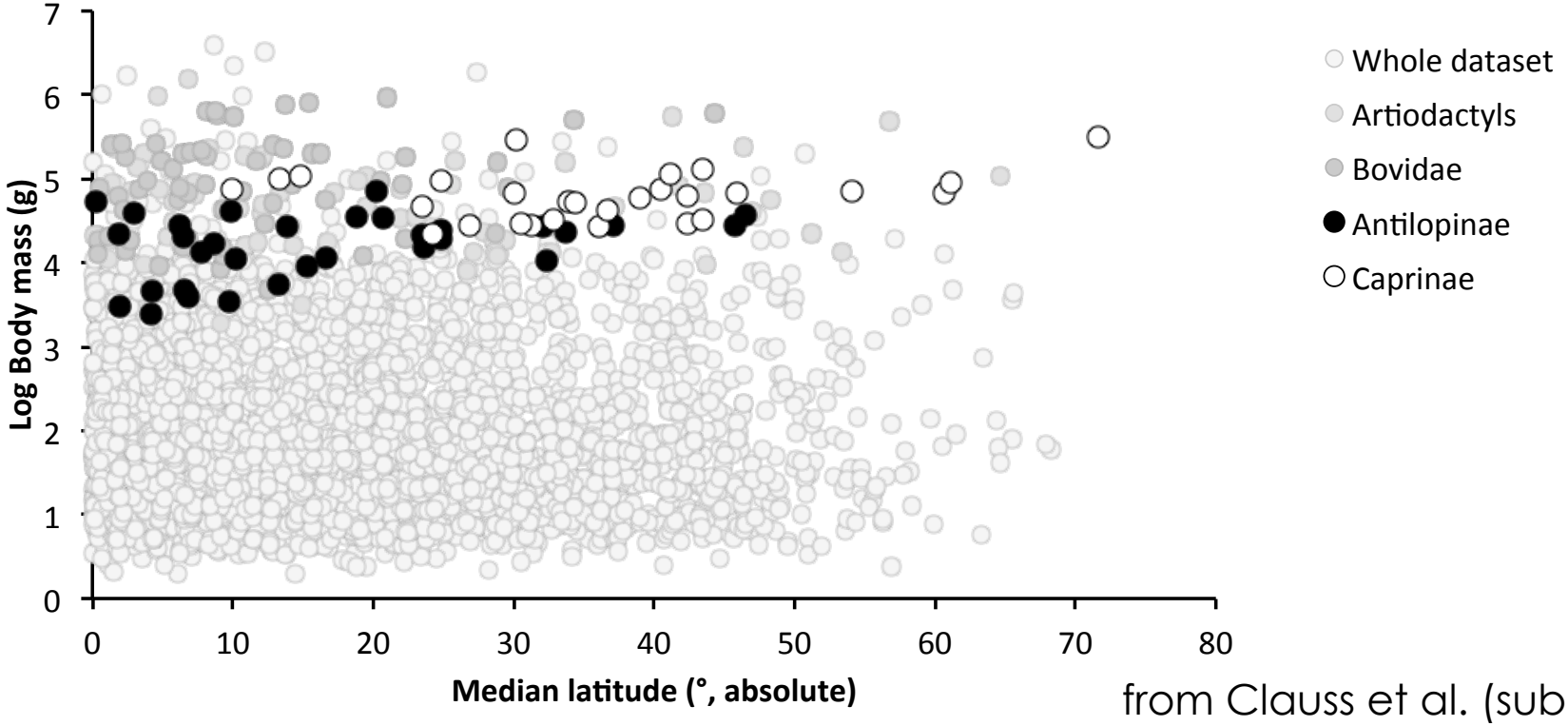


from Clauss et al. (subm.)

Example IV: Bergmann's rule

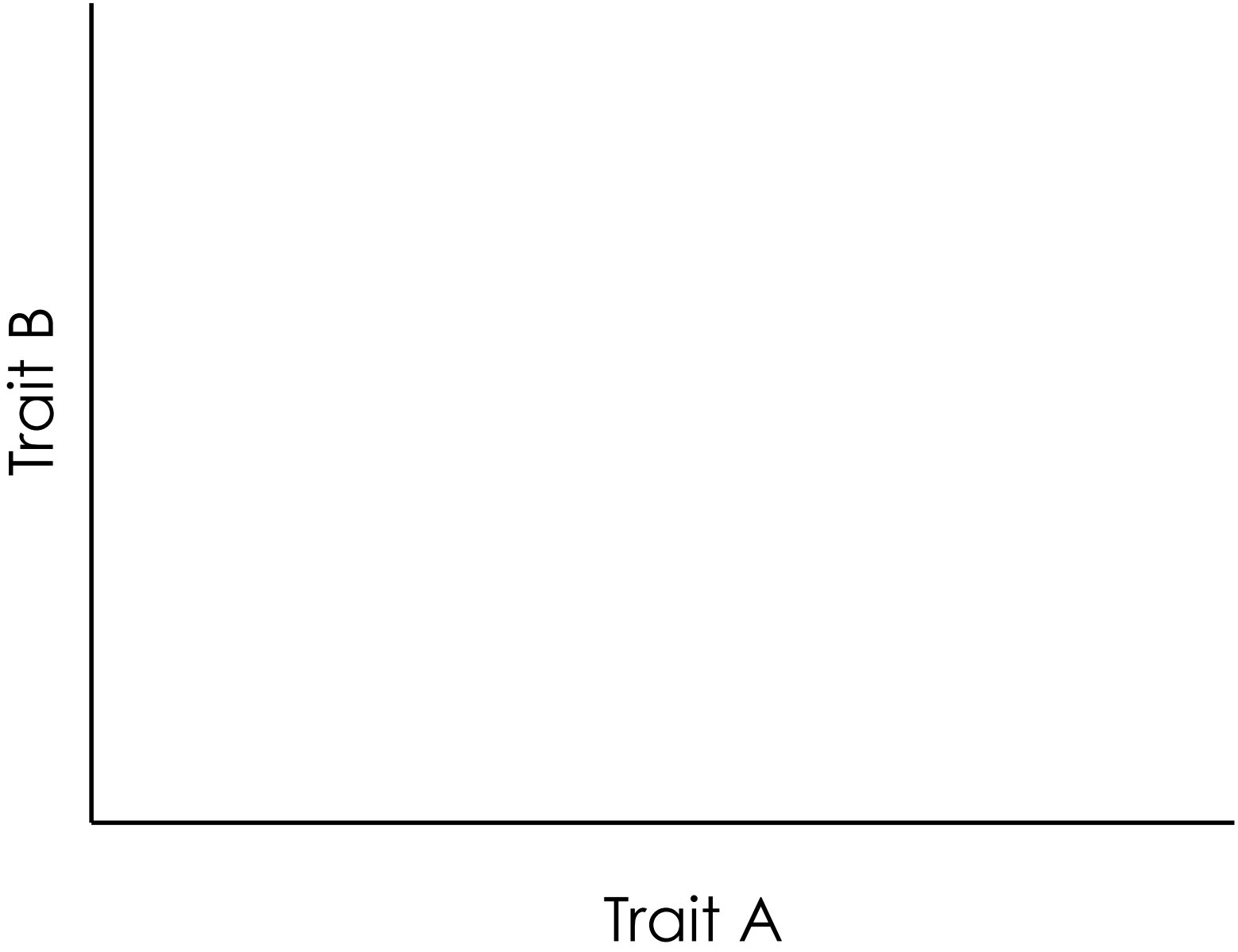
OLS: 2.19 (±0.03) - 0.0012 (±0.0013) Lat.

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

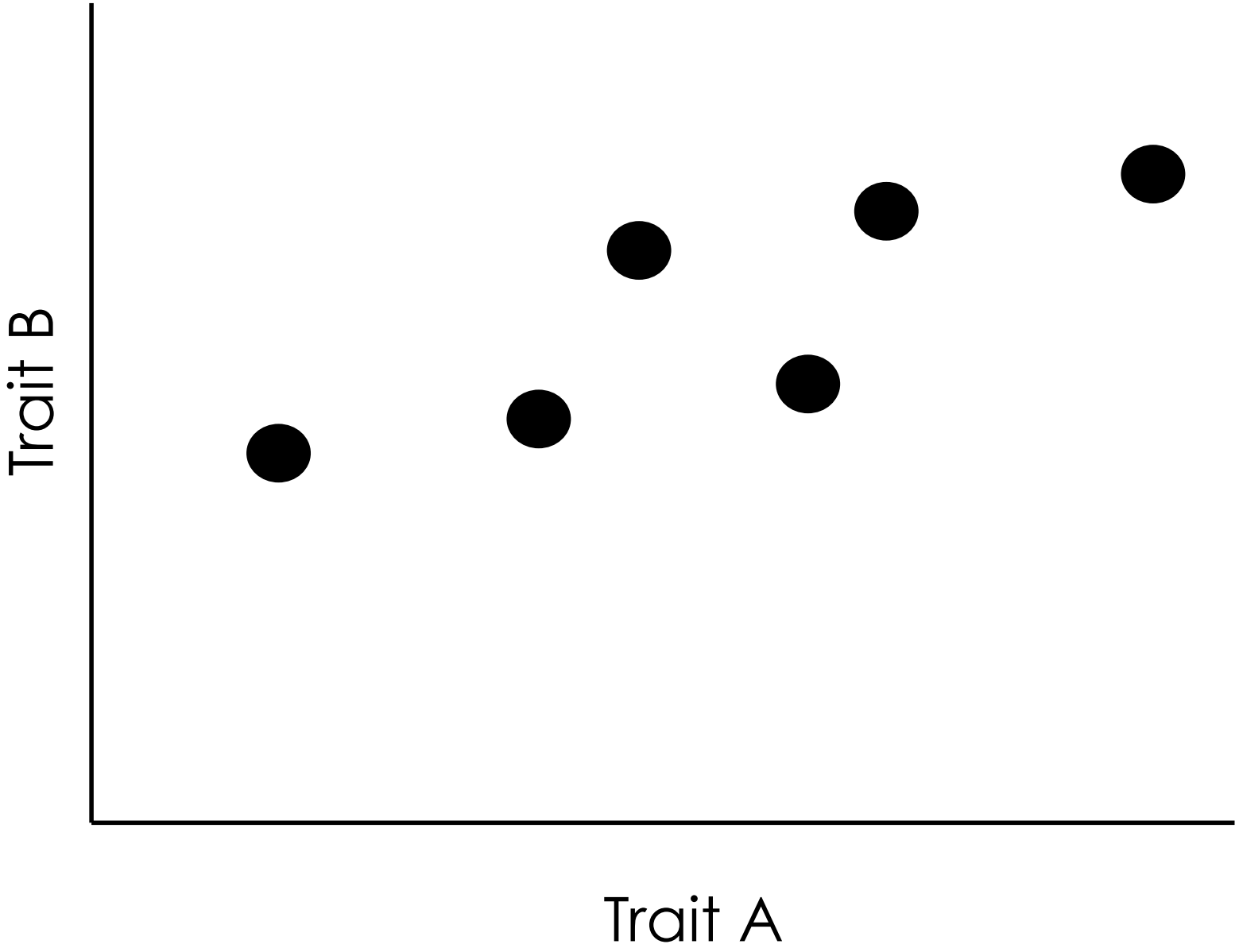


from Clauss et al. (subm.)

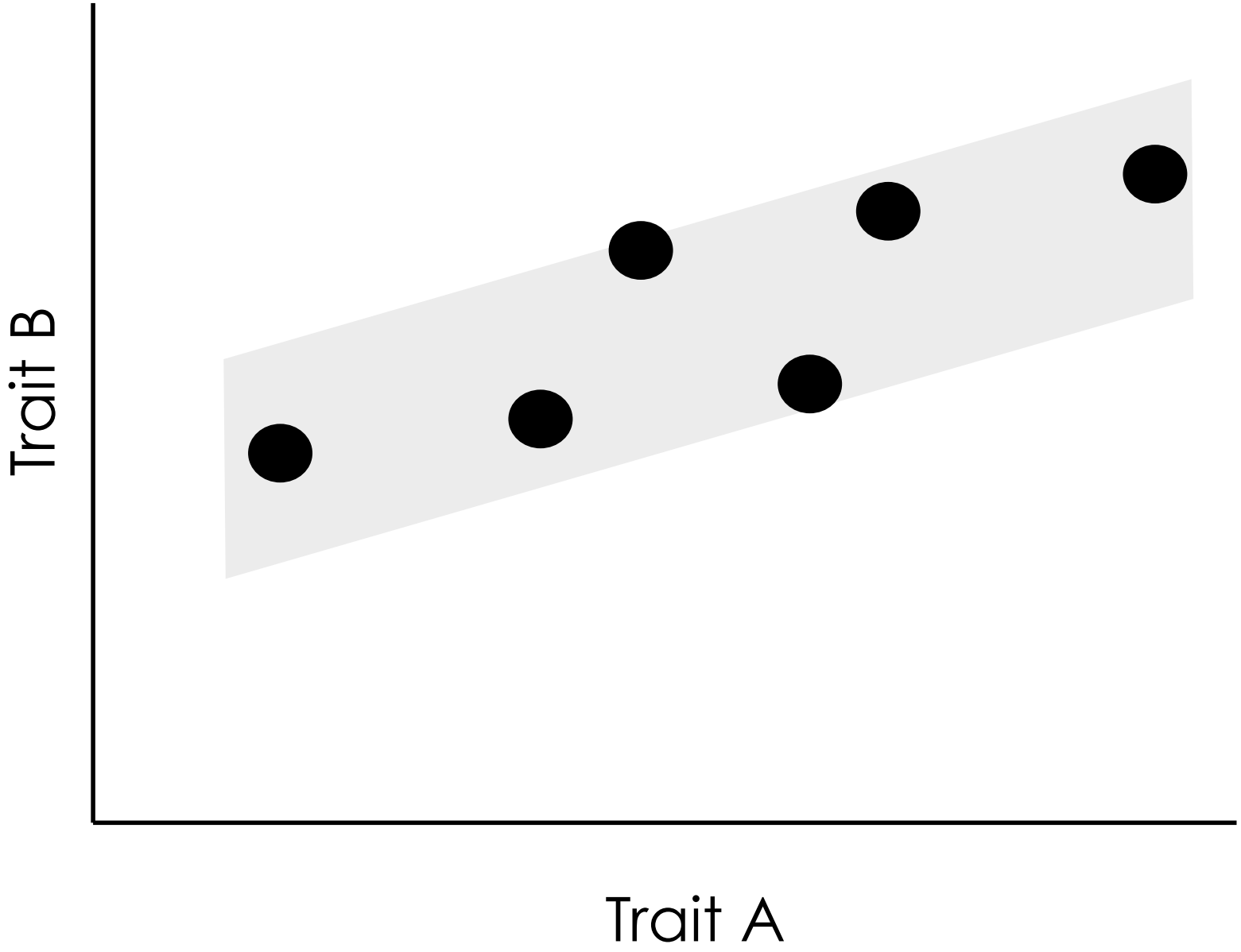
Accounting for phylogeny



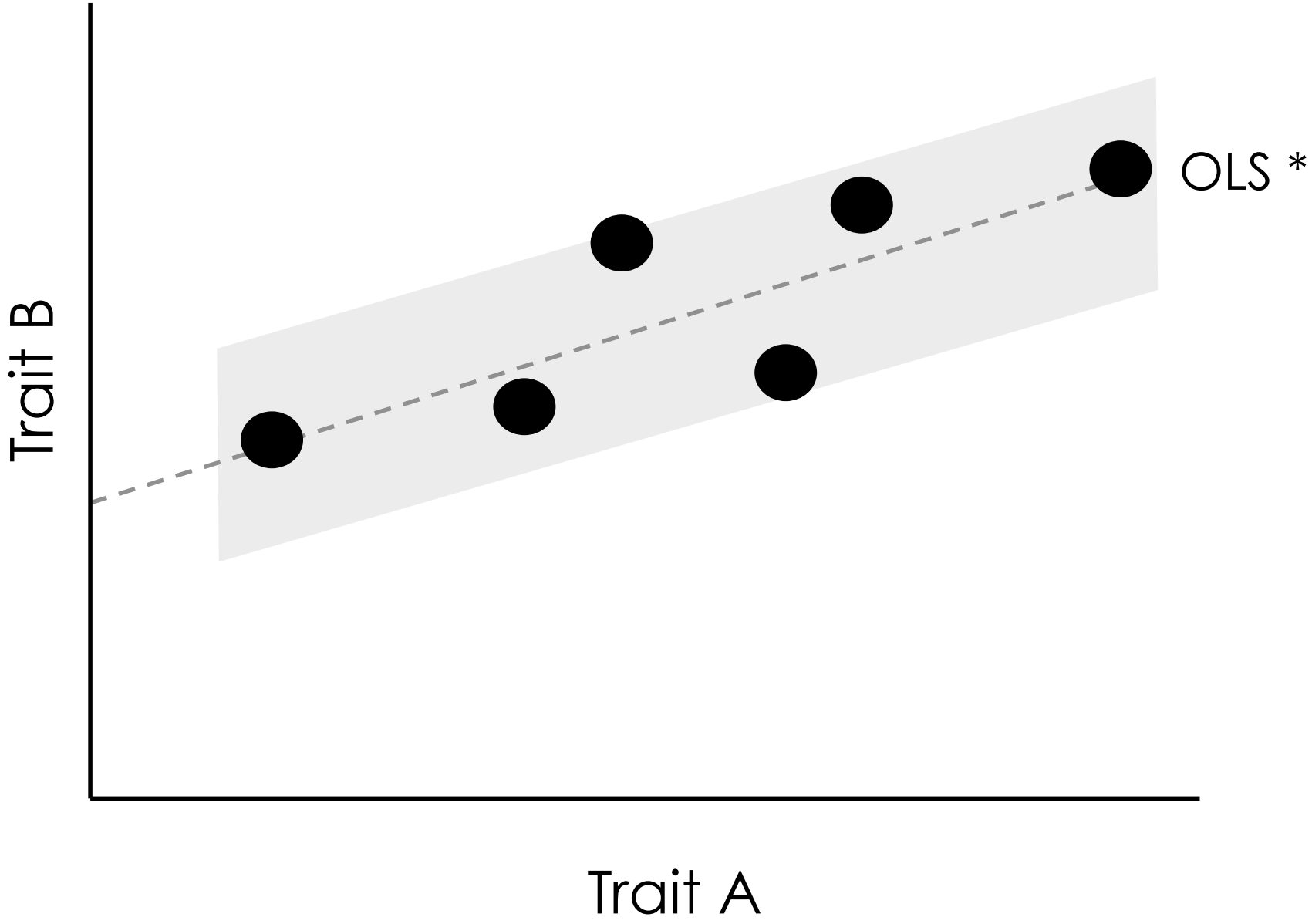
Accounting for phylogeny



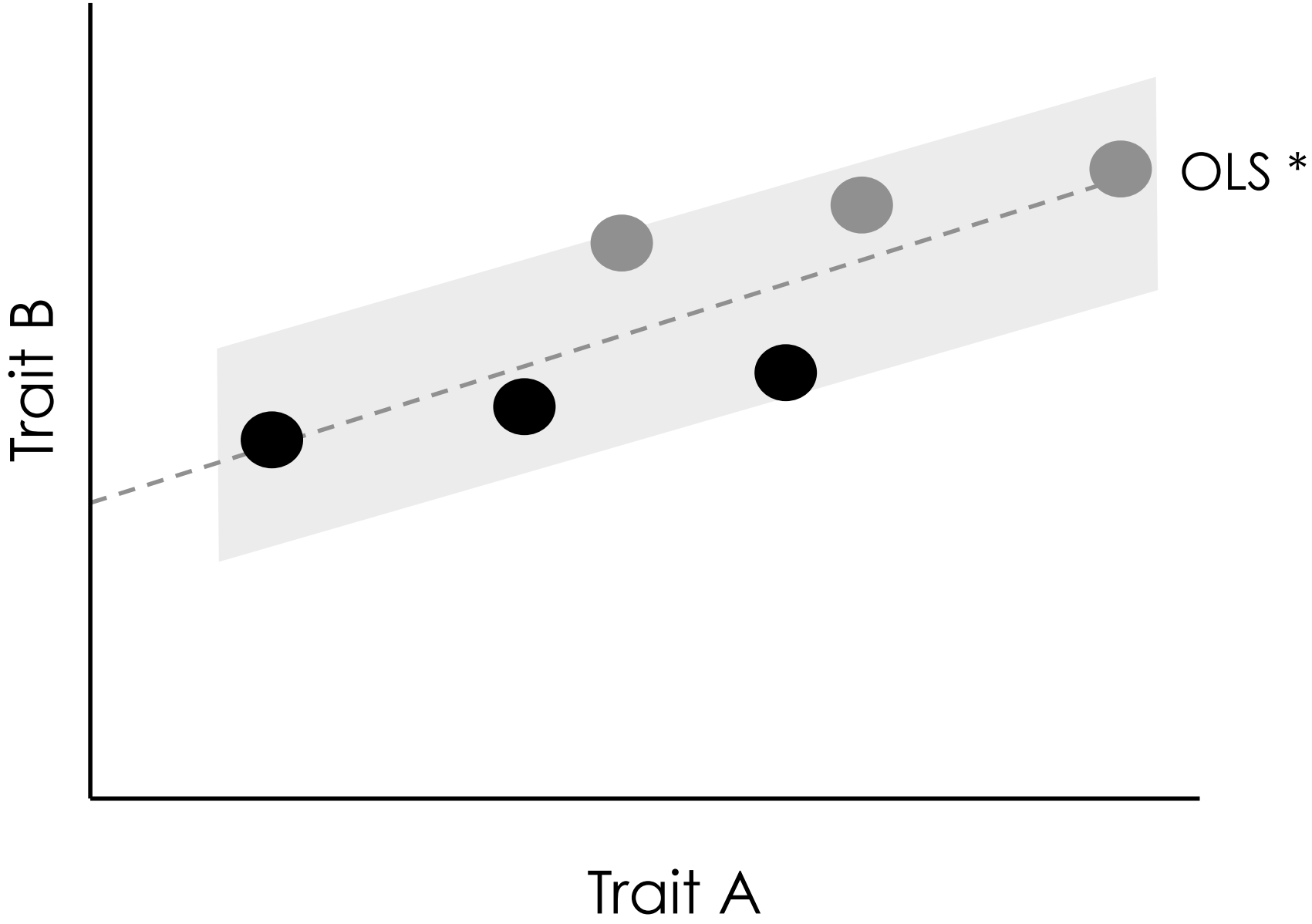
Accounting for phylogeny



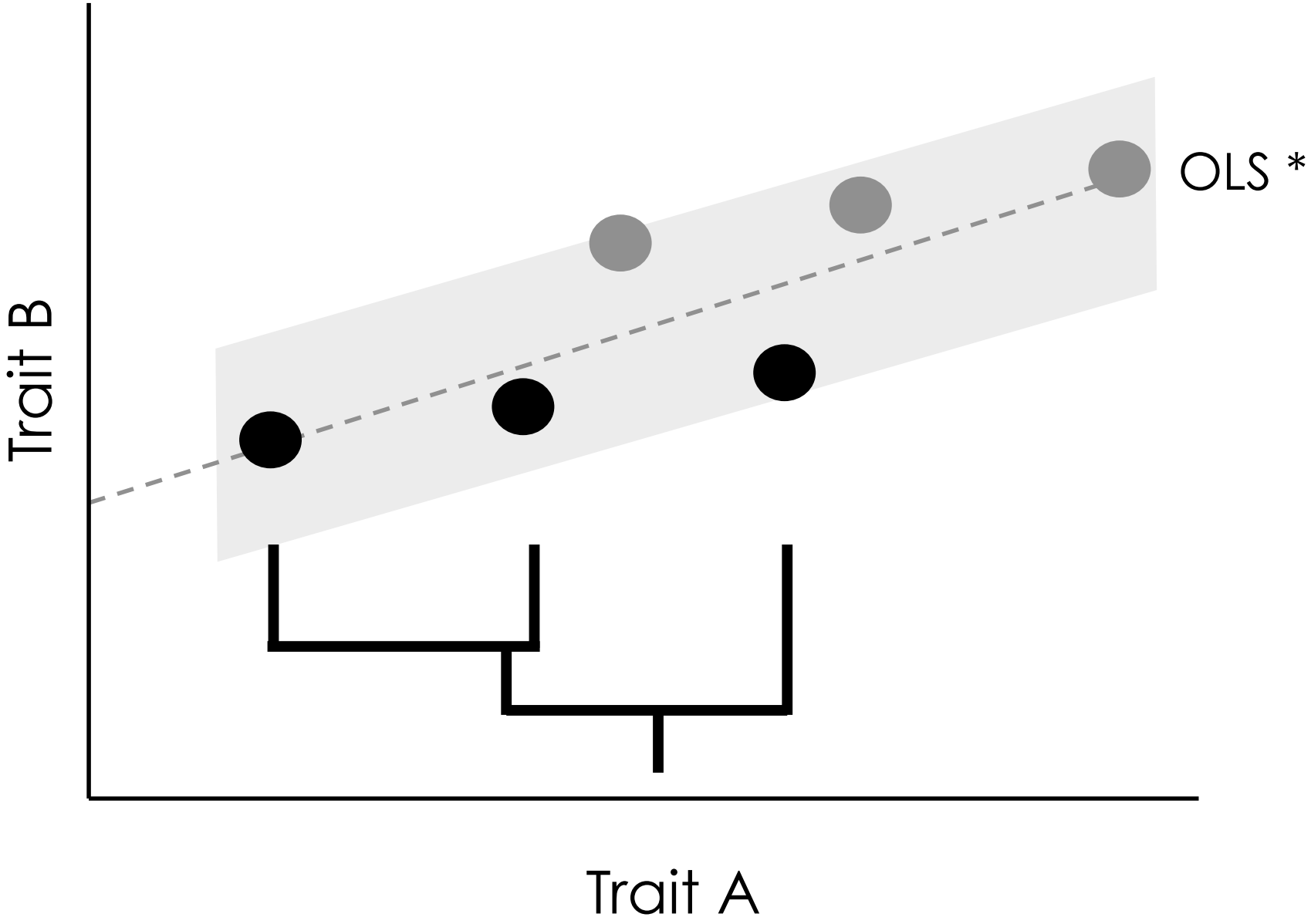
Accounting for phylogeny



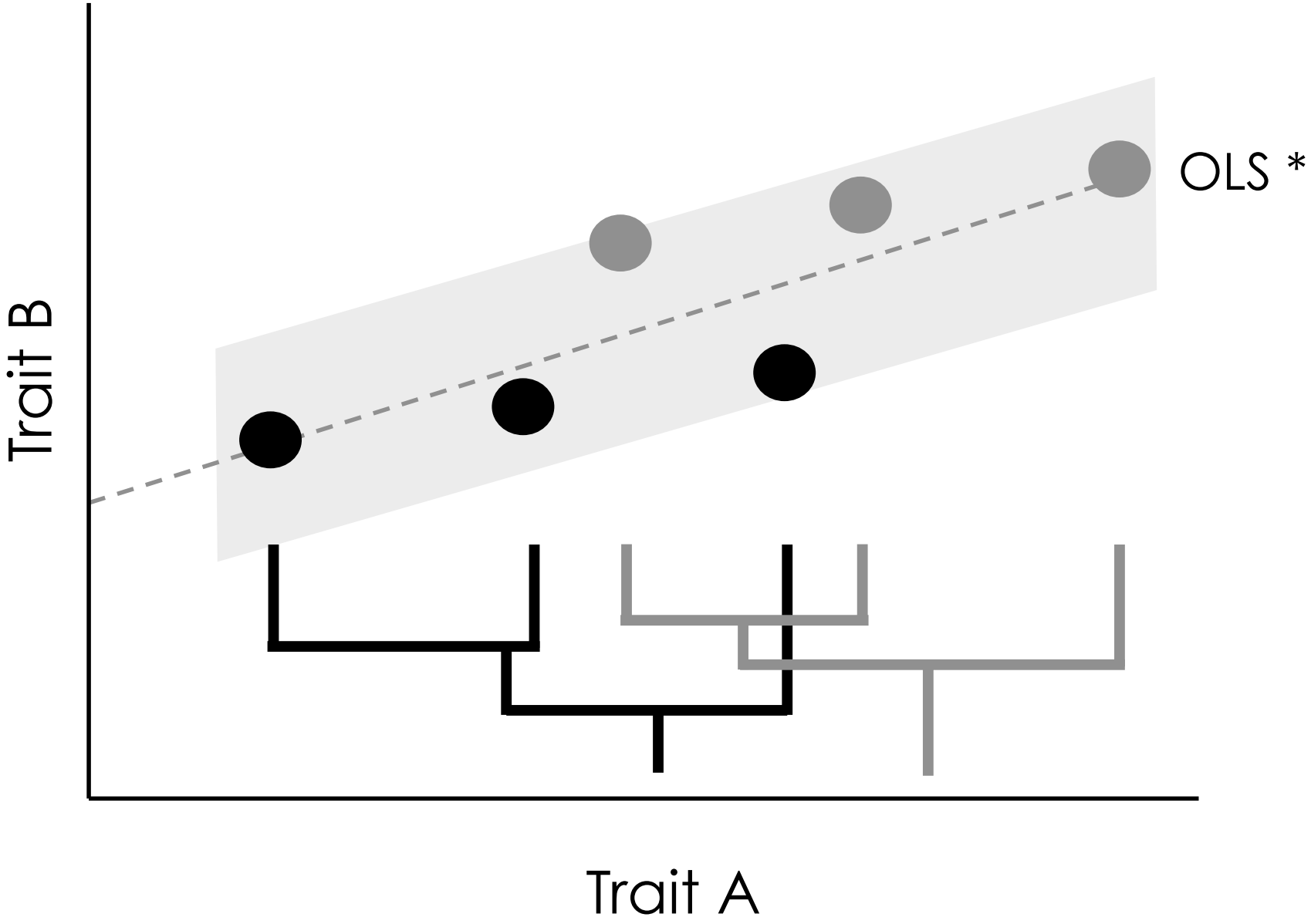
Accounting for phylogeny



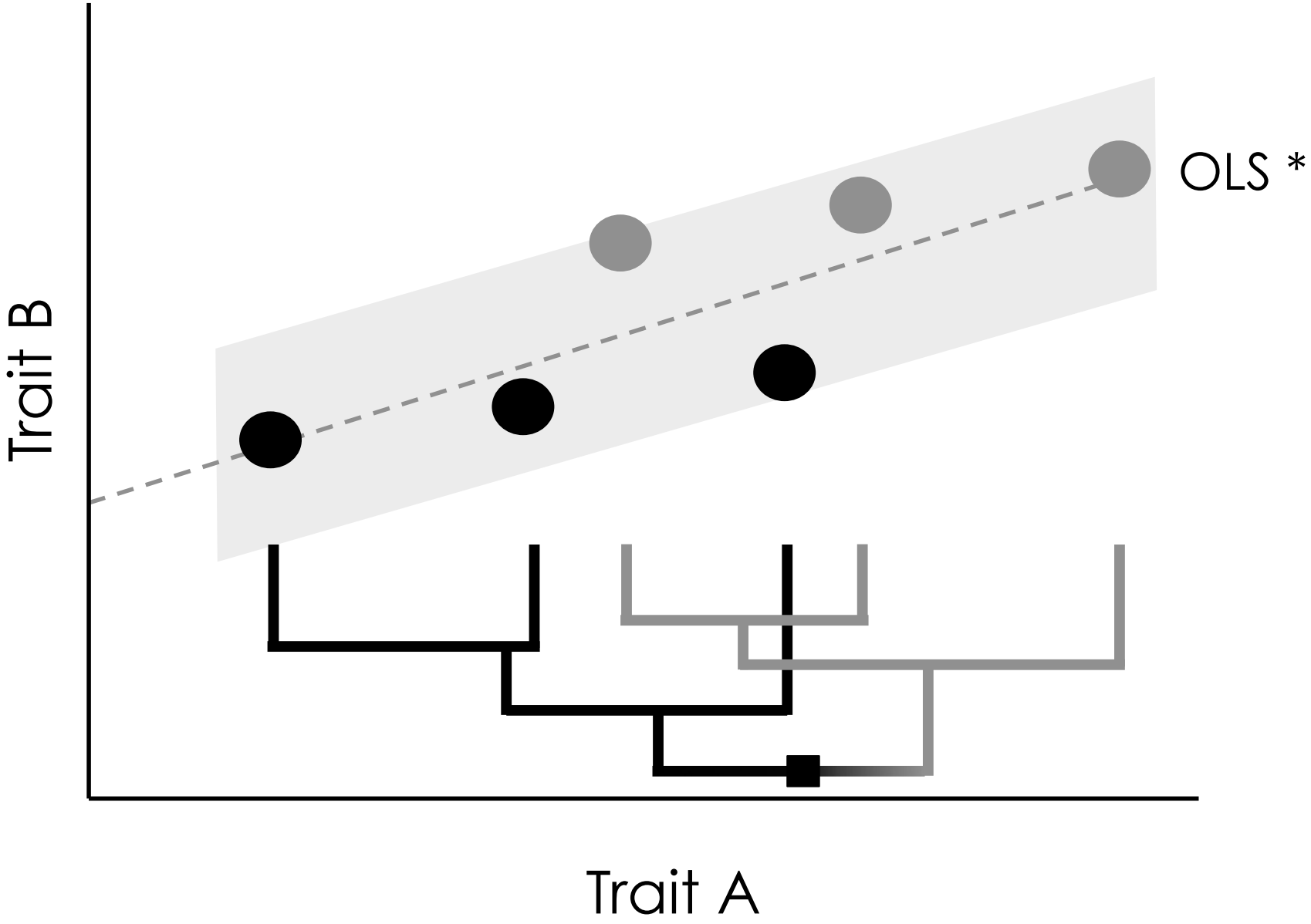
Accounting for phylogeny



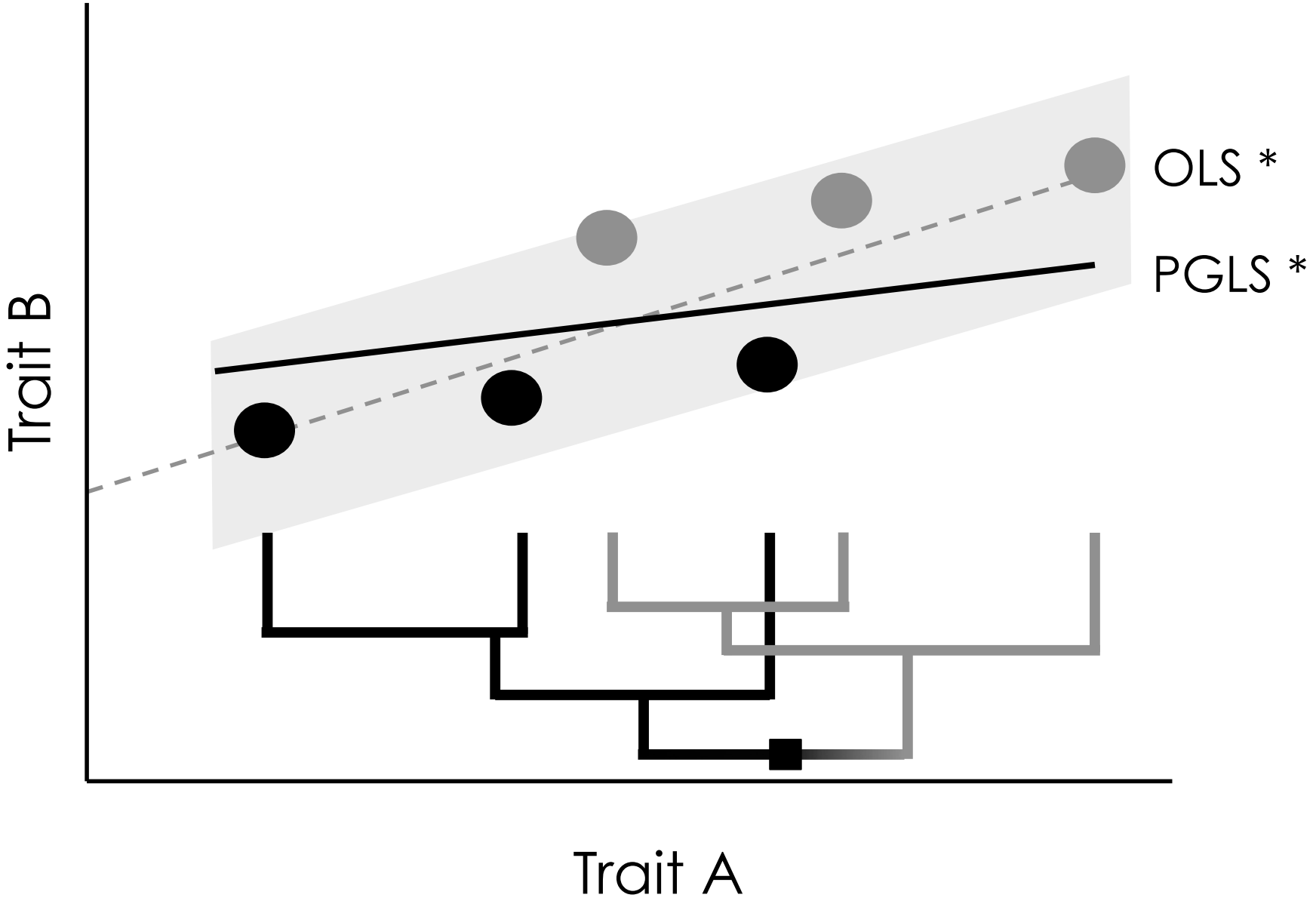
Accounting for phylogeny



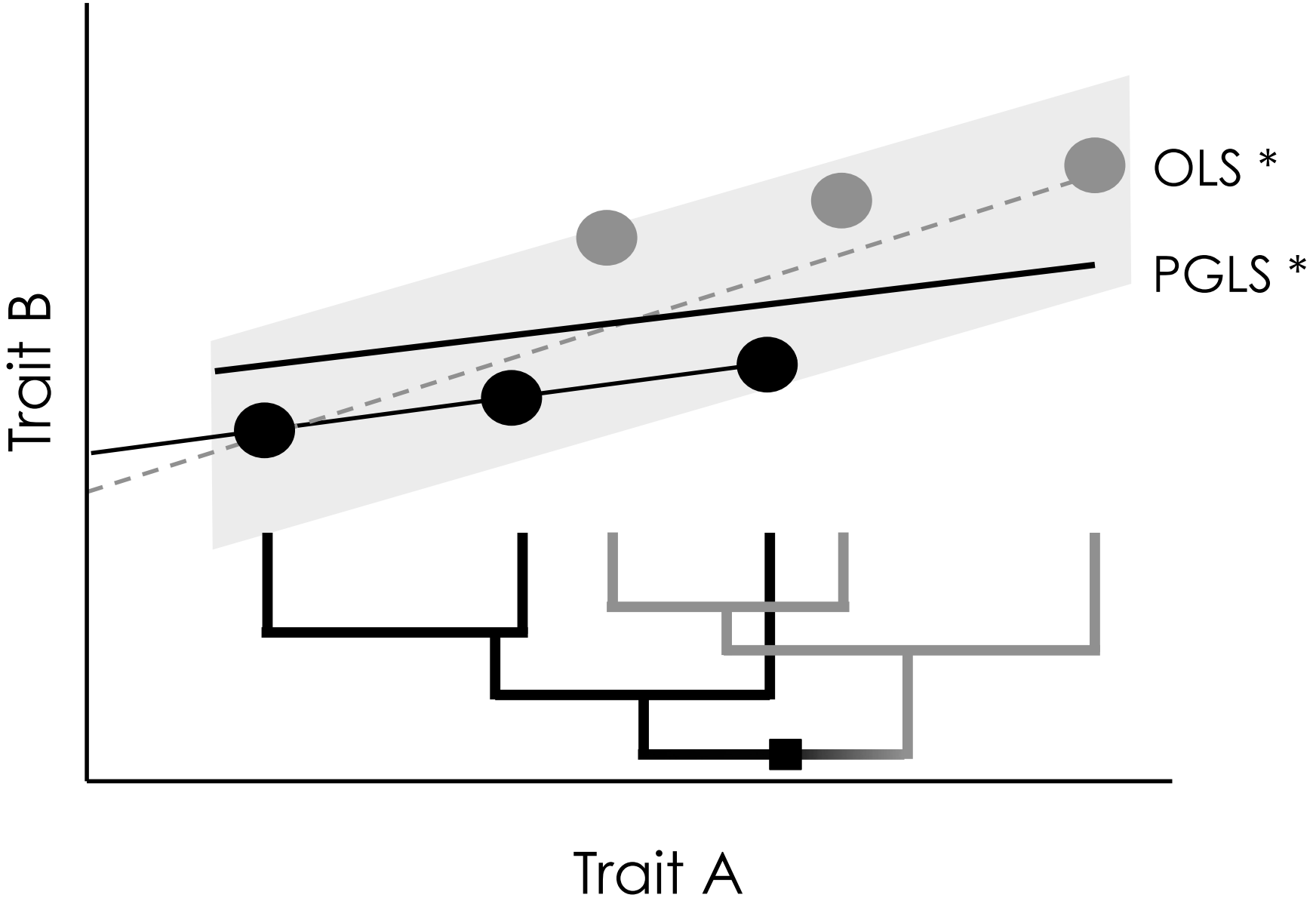
Accounting for phylogeny



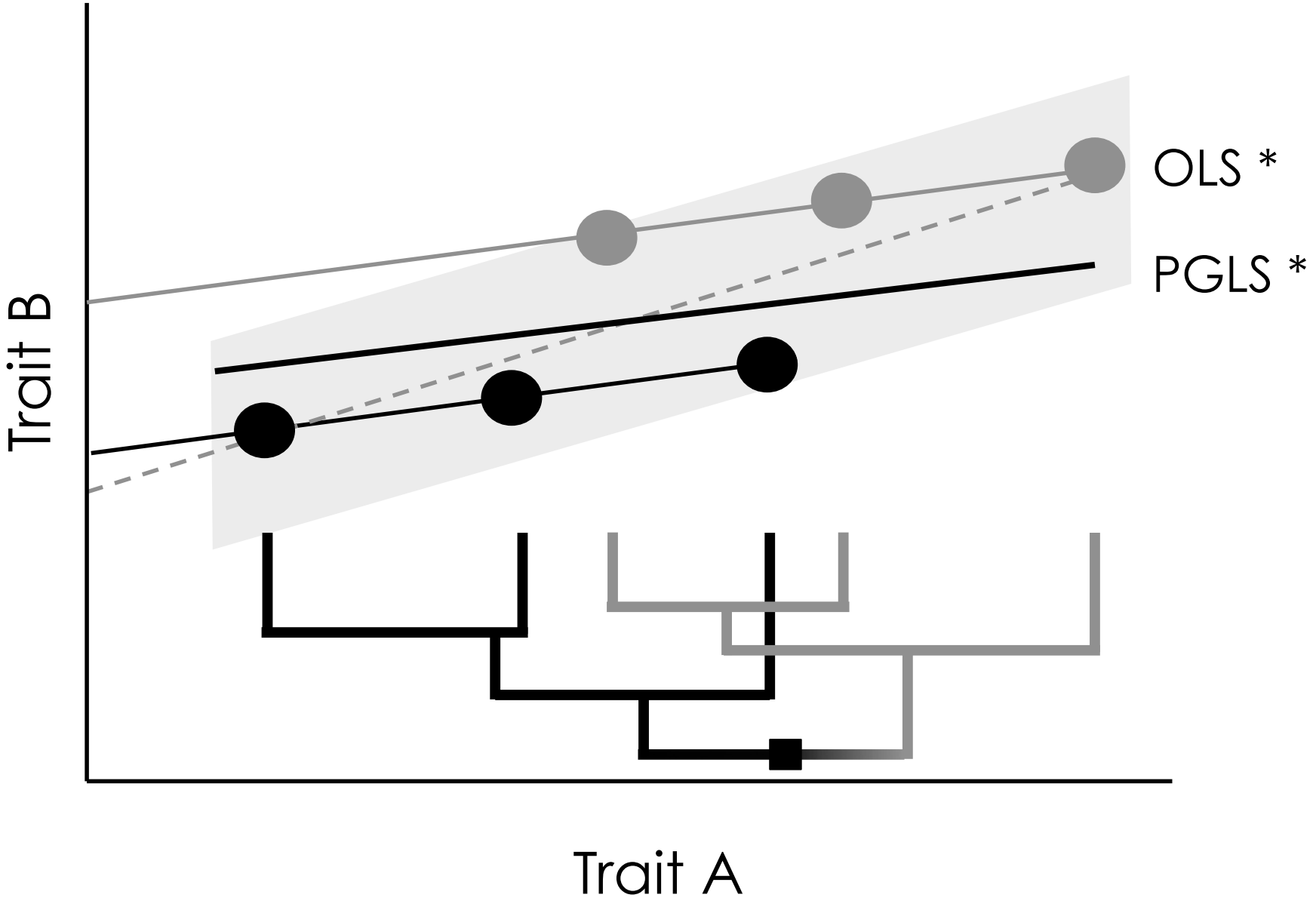
Accounting for phylogeny



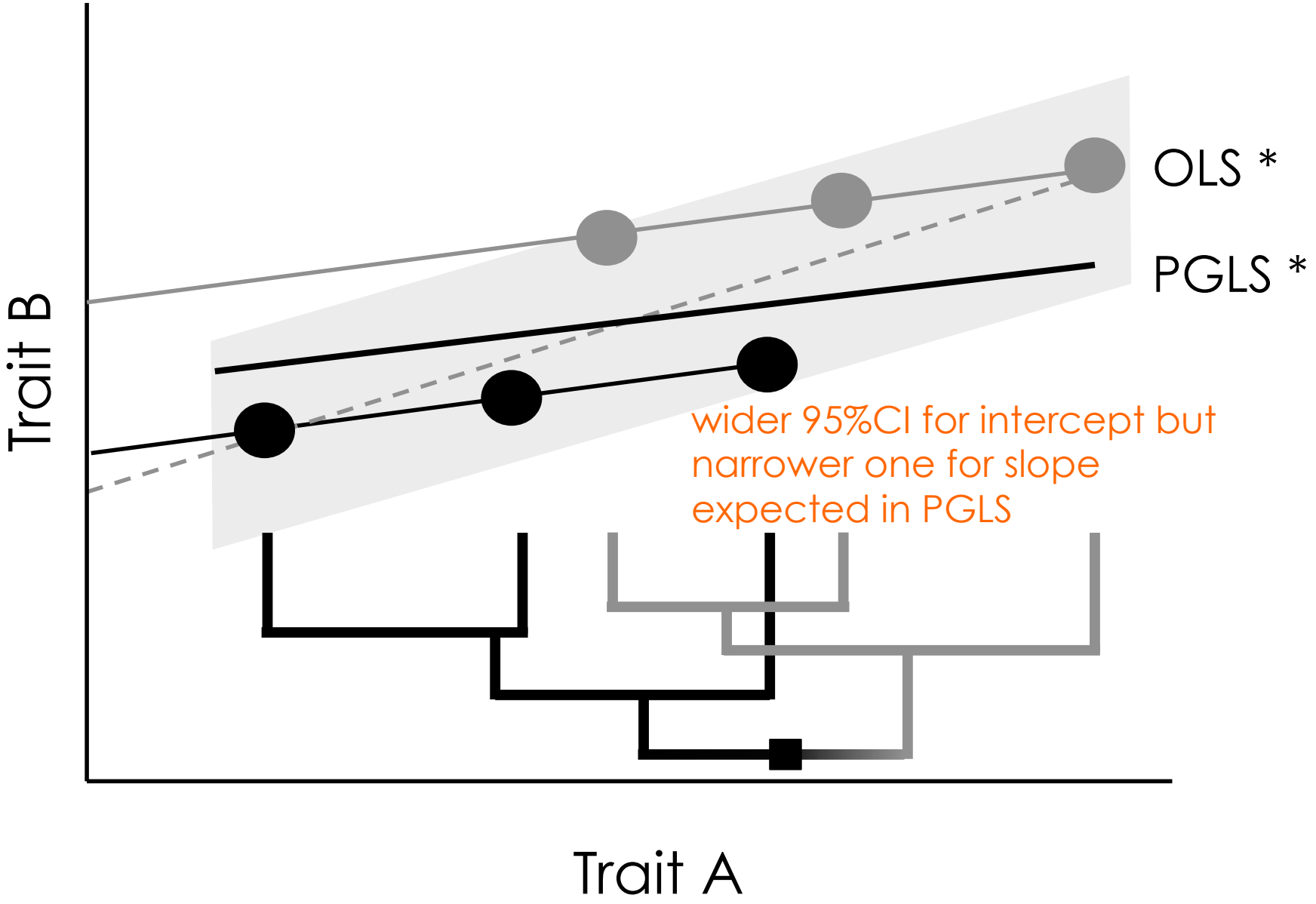
Accounting for phylogeny



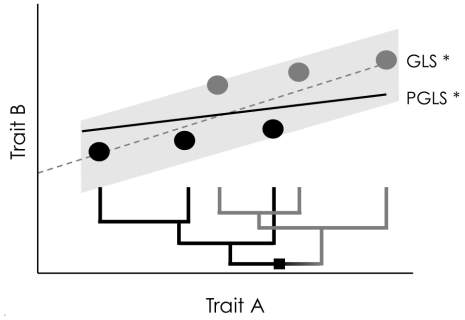
Accounting for phylogeny



Accounting for phylogeny

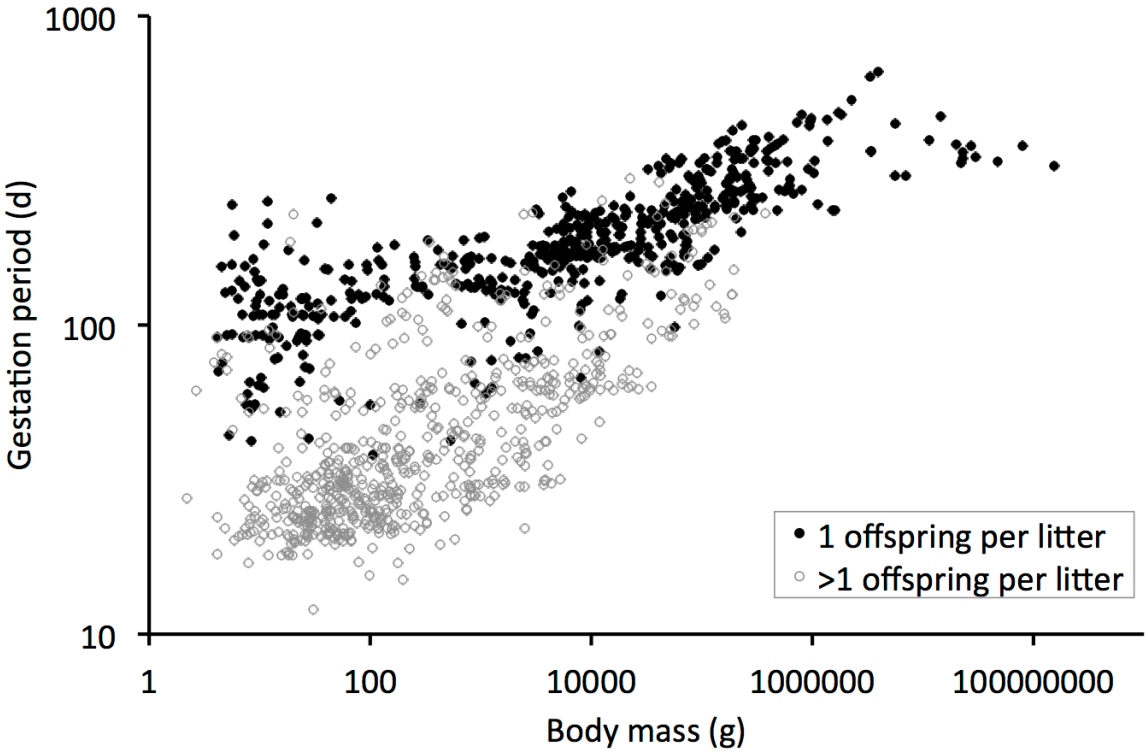


Example V: Gestation time



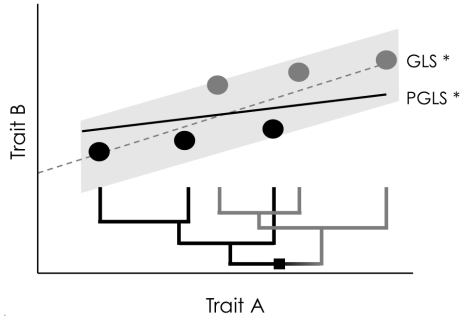
OLS: 21.5 (19.9-23.3) $BM^{0.19\ (0.18\text{-}0.20)}$

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



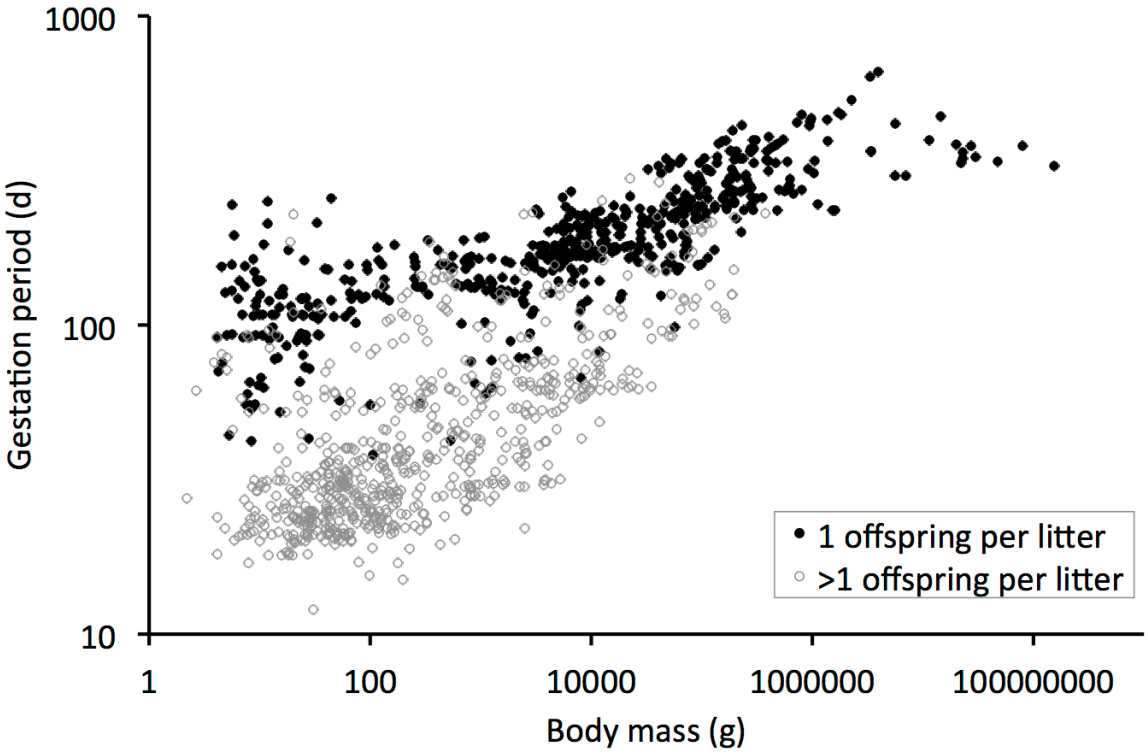
from Clauss et al. (in press)

Example V: Gestation time



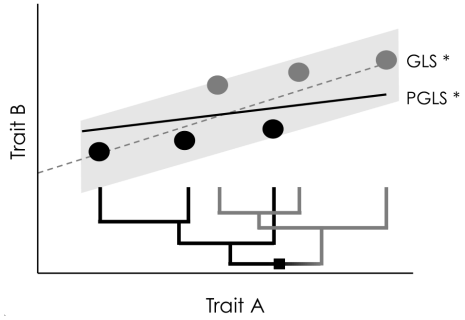
OLS: 21.5 (19.9-23.3) $BM^{0.19\ (0.18\text{-}0.20)}$

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



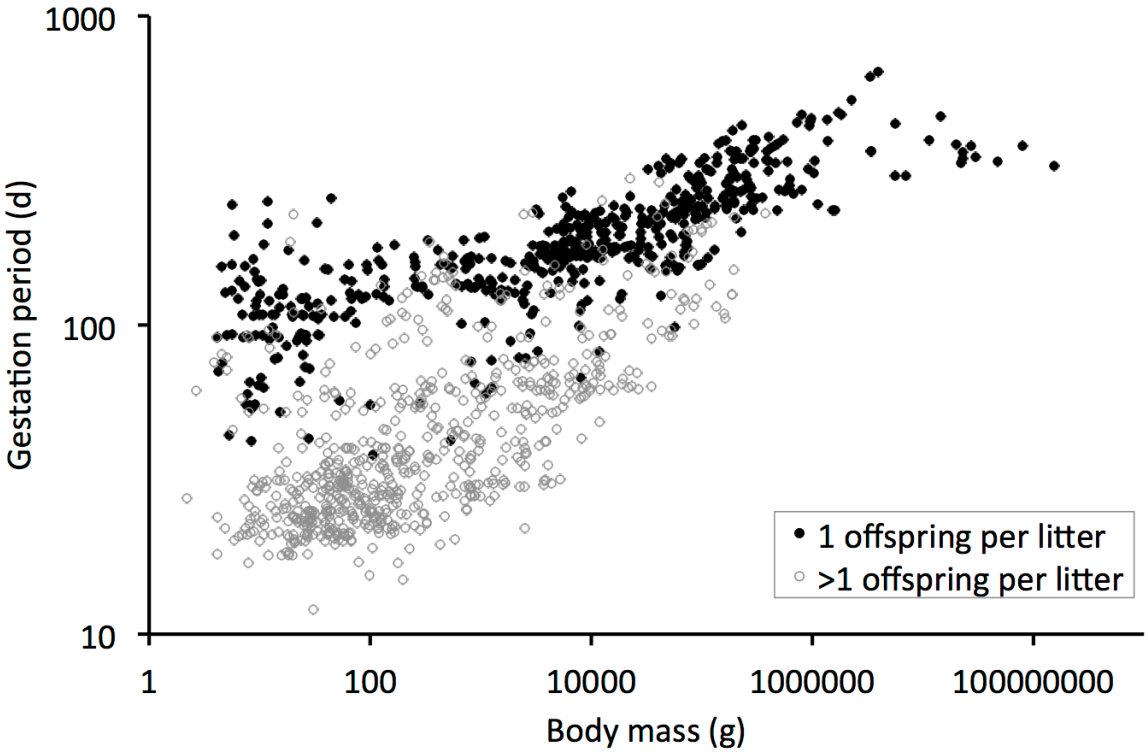
from Clauss et al. (in press)

Example V: Gestation time



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)

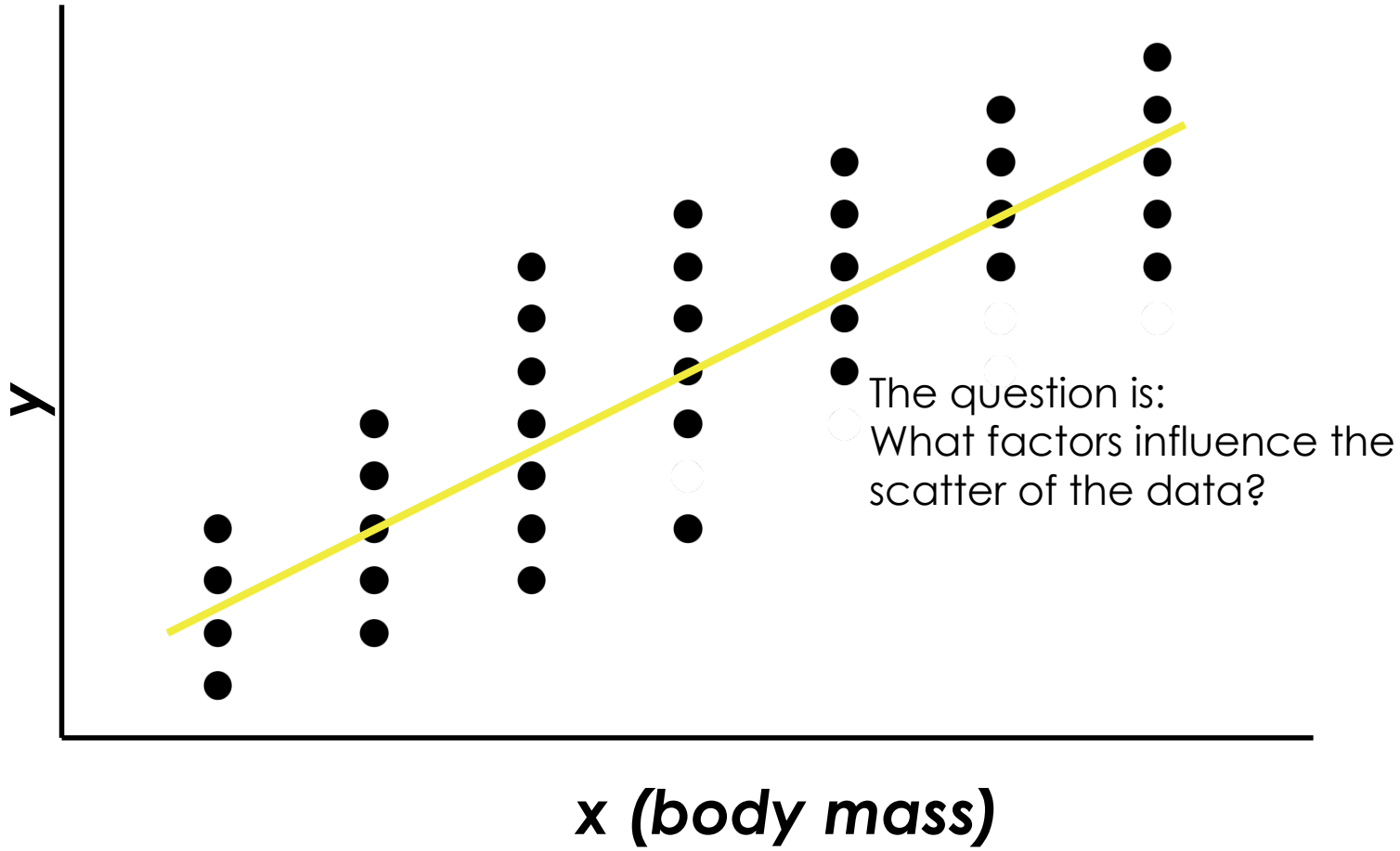


from Clauss et al. (in press)

Allometries as snapshots in evolutionary time

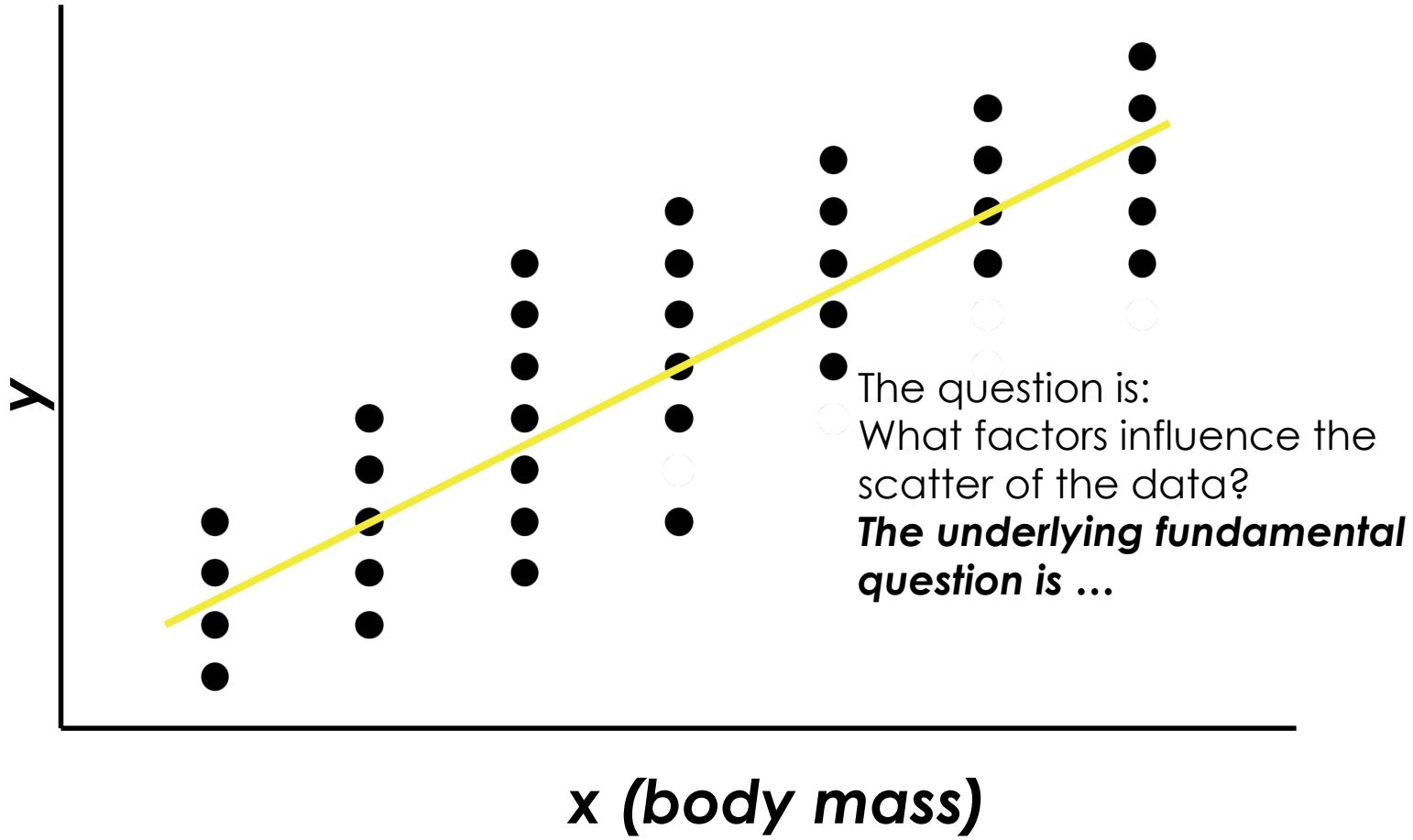
Interpreting allometries

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



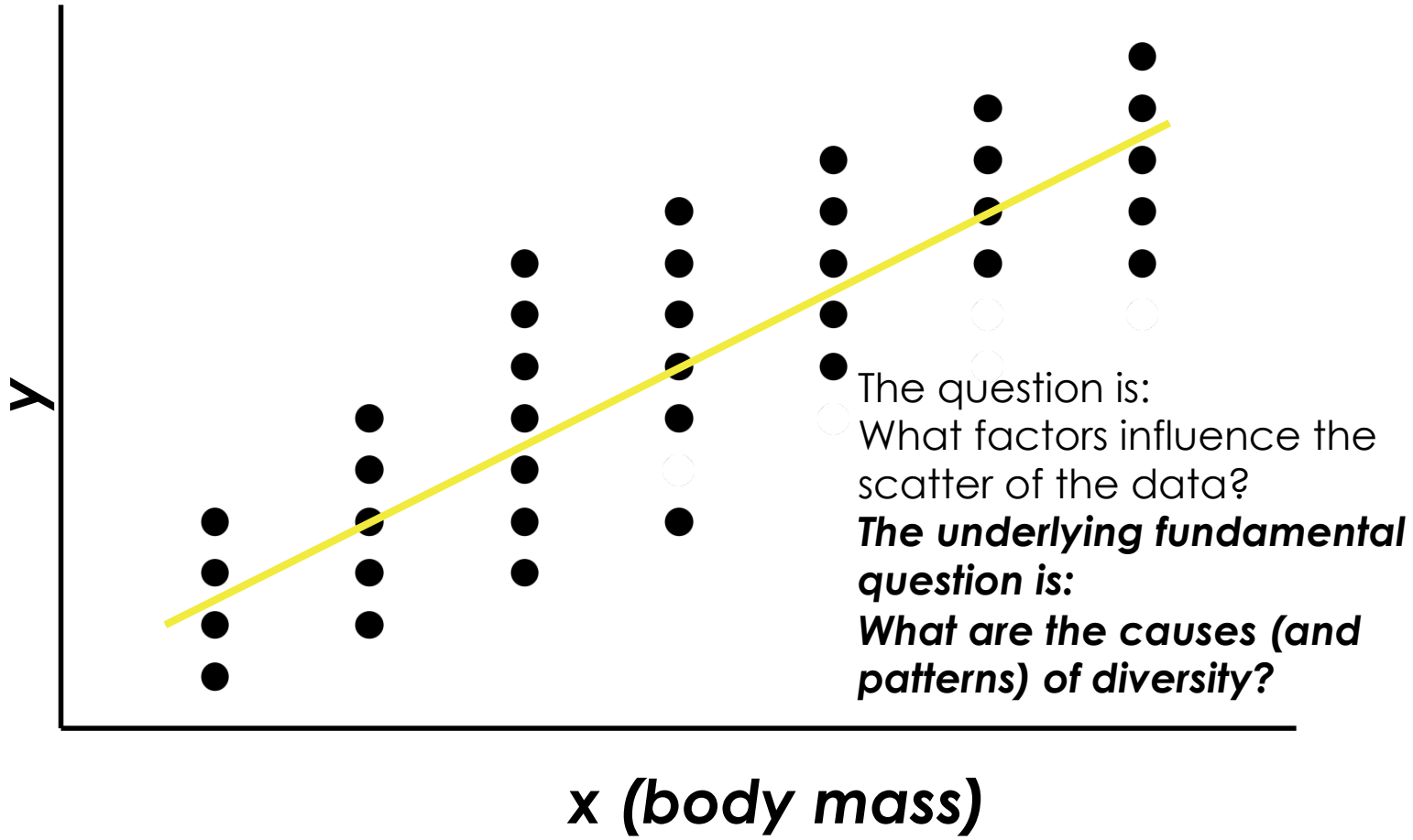
Interpreting allometries

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



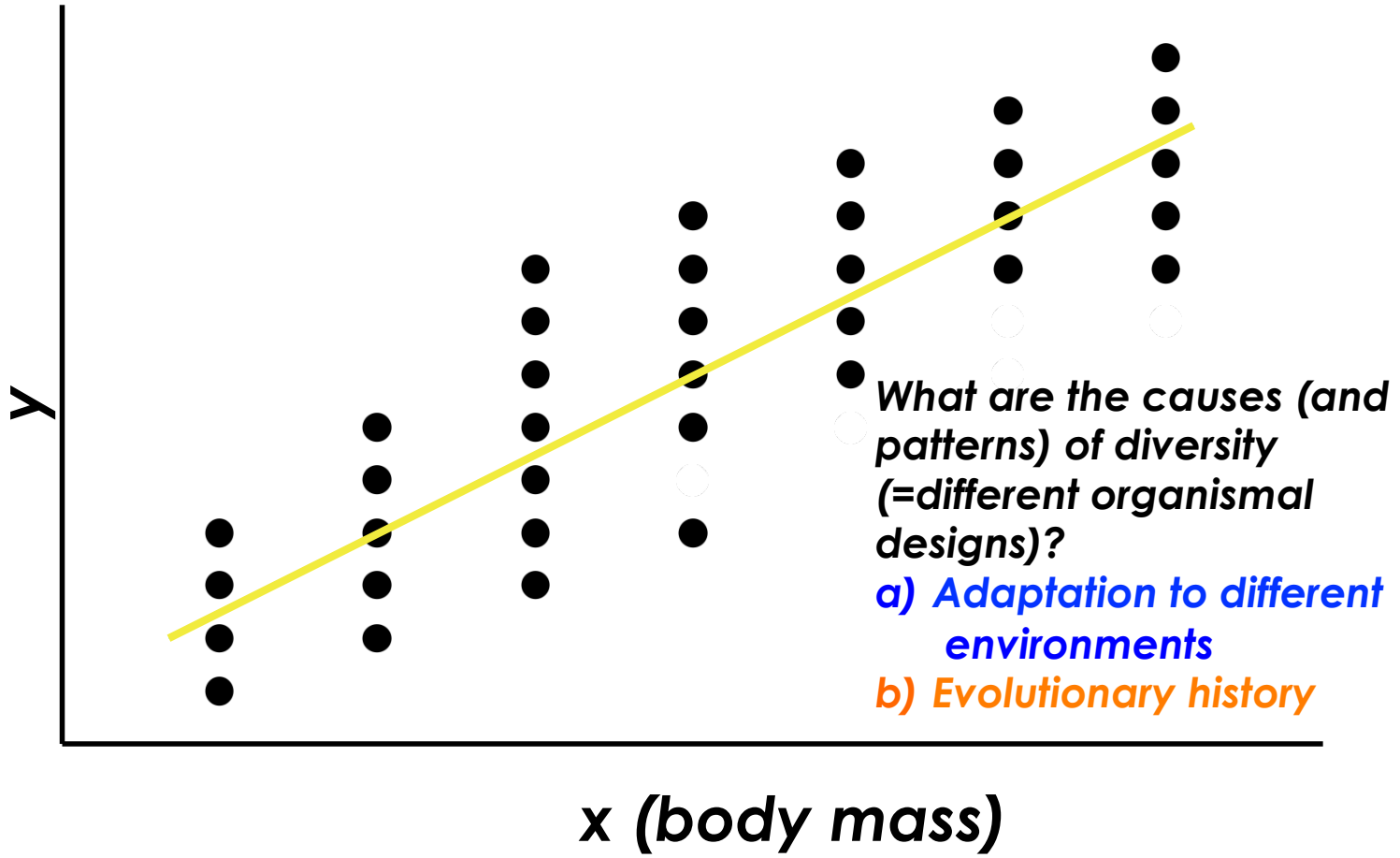
Interpreting allometries

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



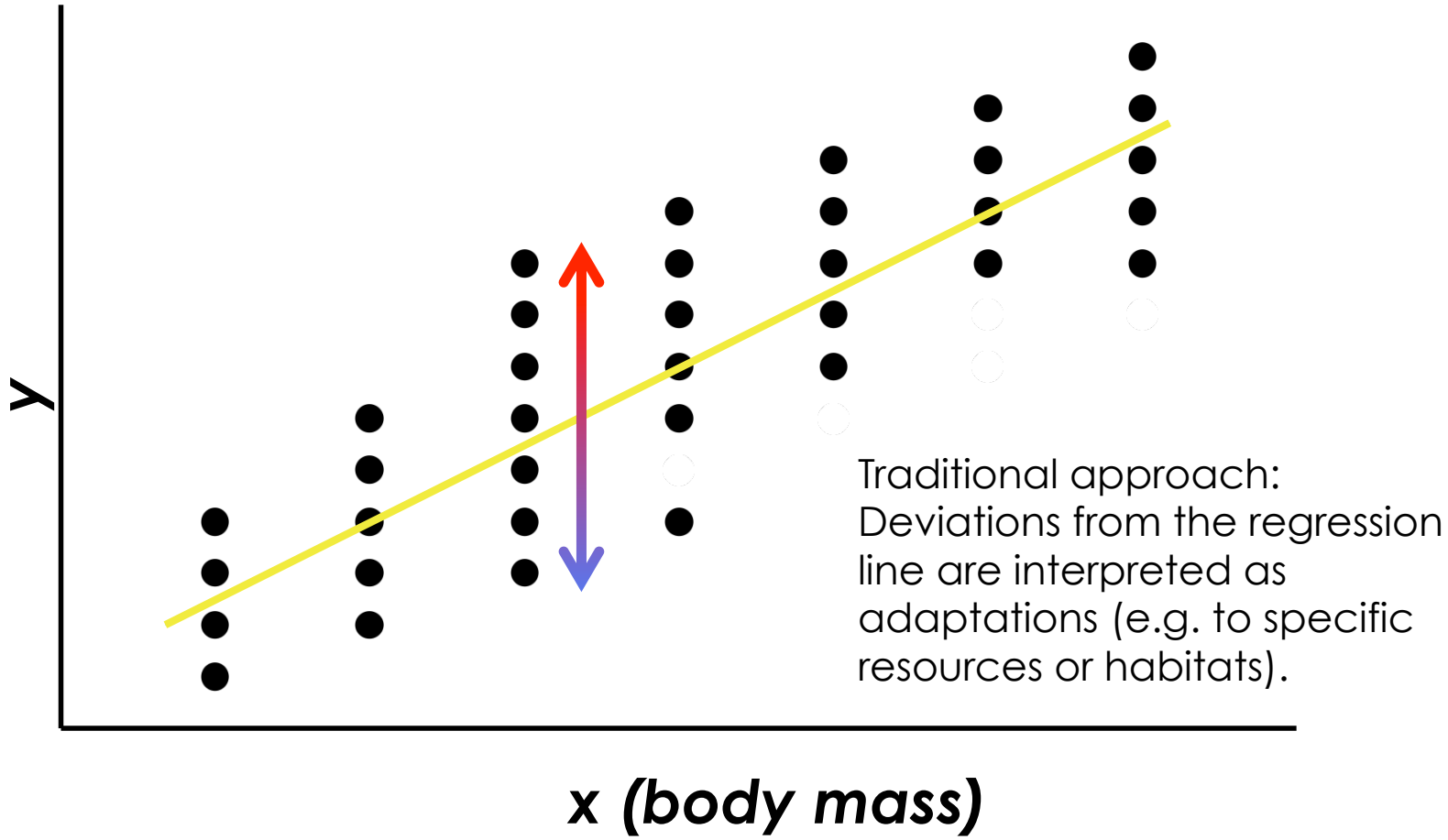
Interpreting allometries

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



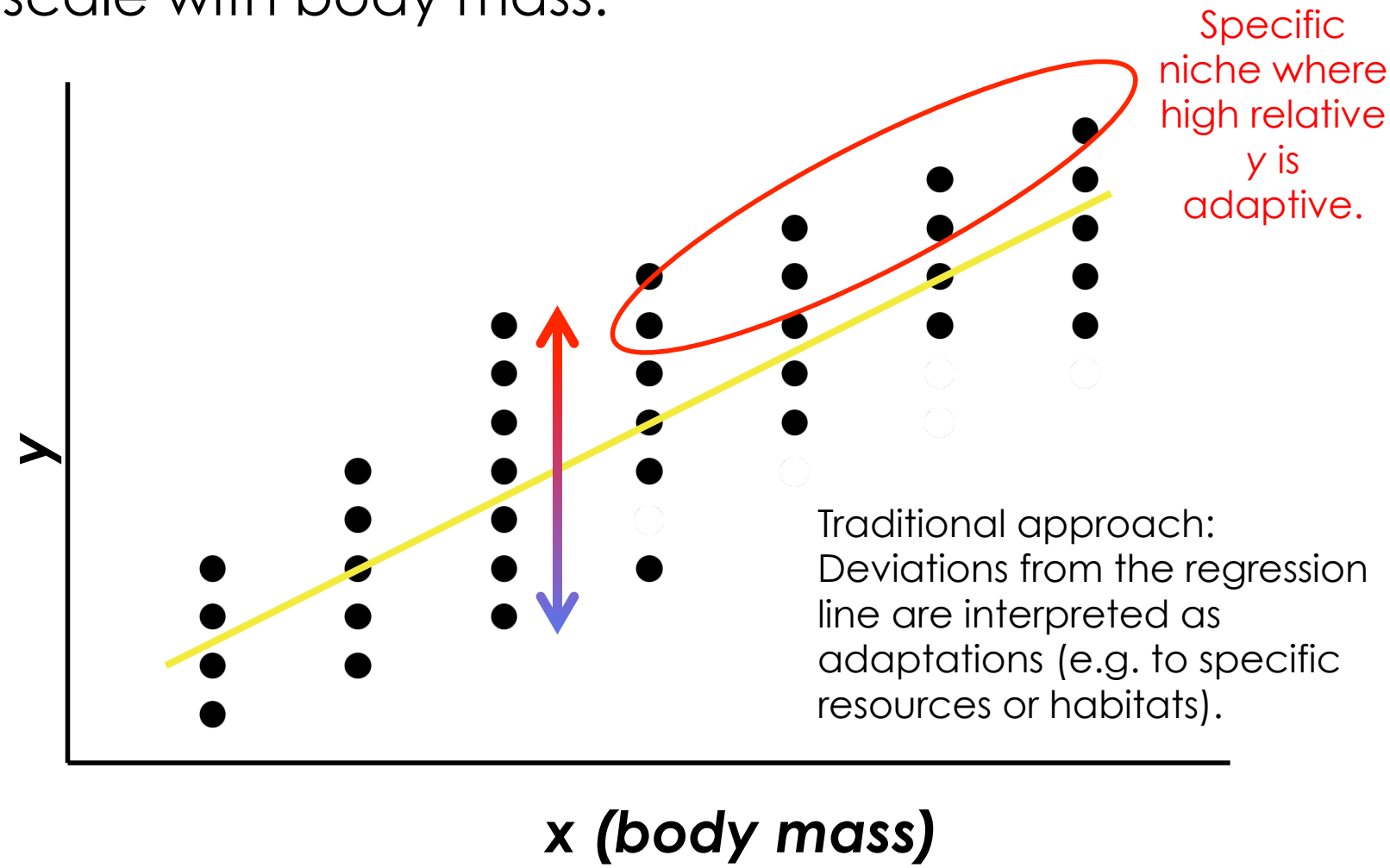
Interpreting allometries

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



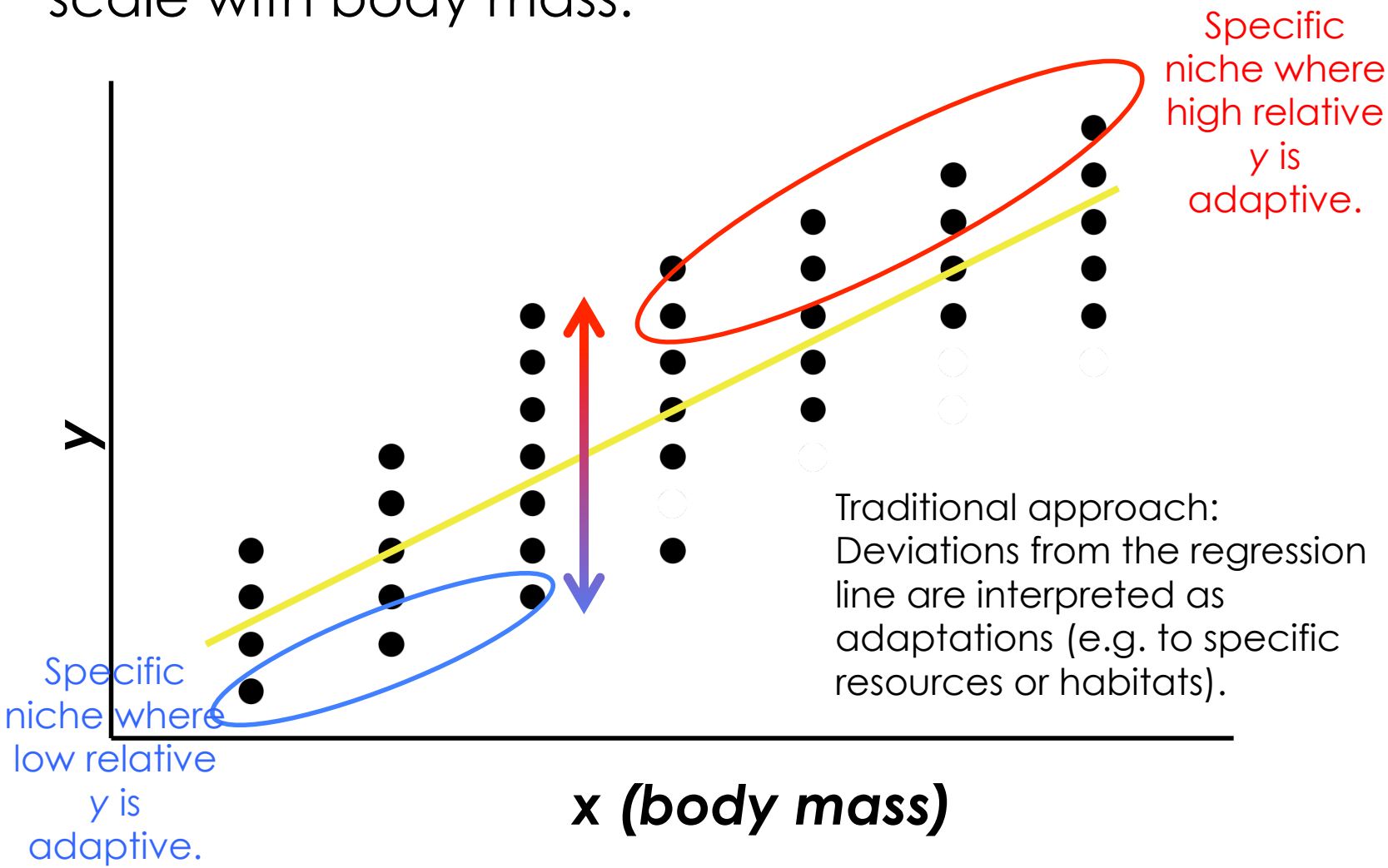
Interpreting allometries

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



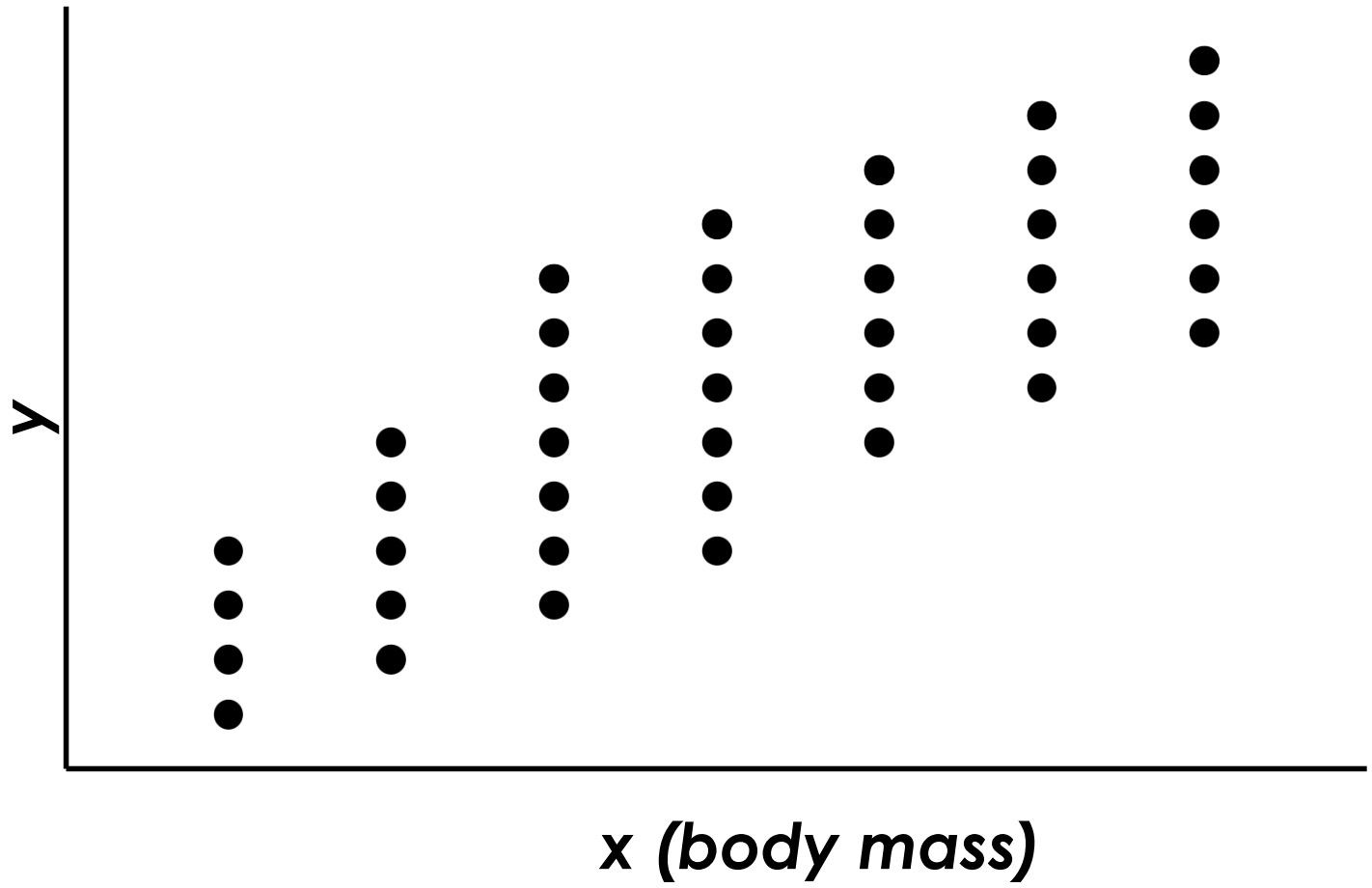
Interpreting allometries

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



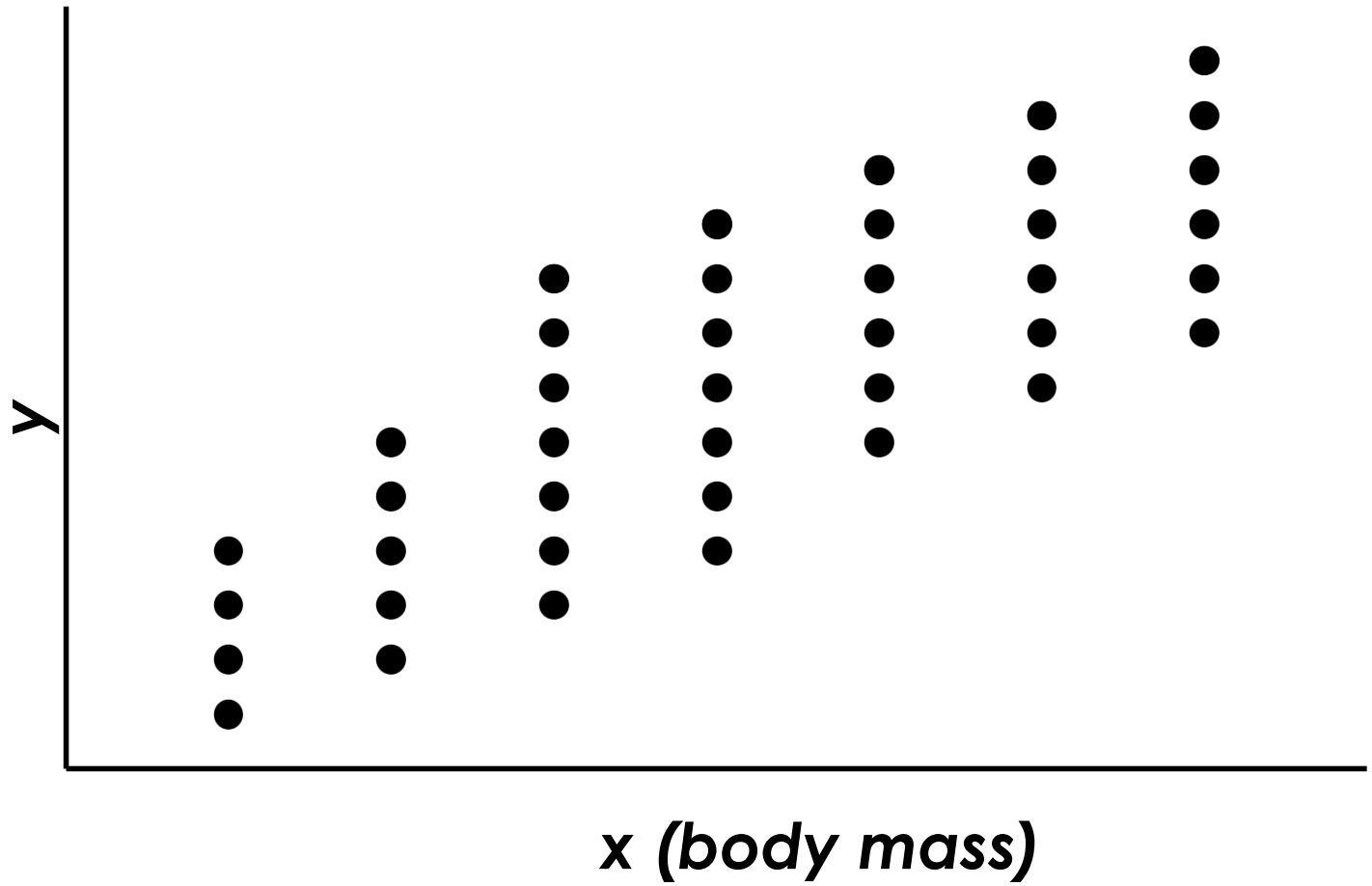
Interpreting allometries

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



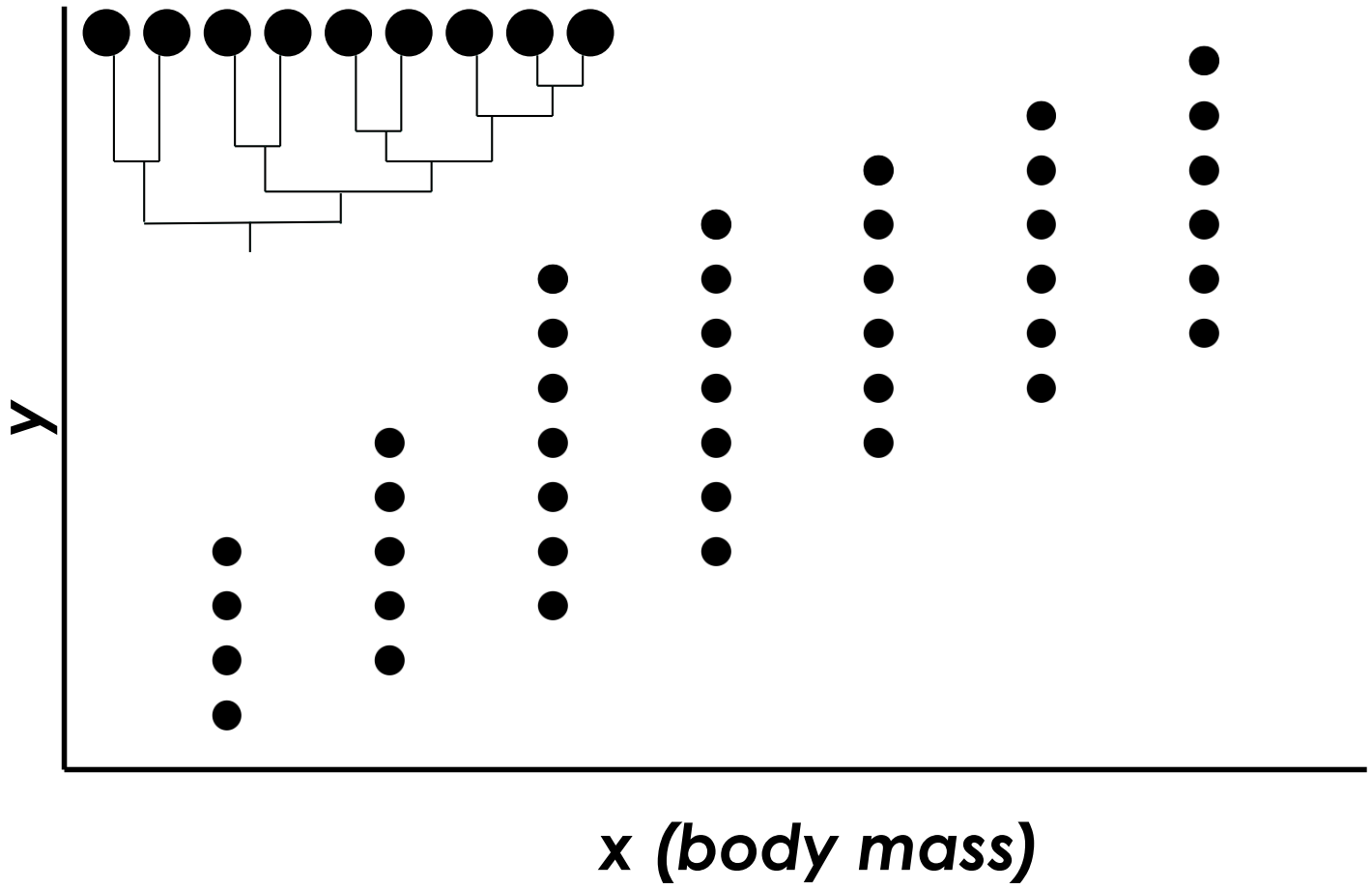
Interpreting allometries

Is there a systematic phylogenetic structure in the dataset?



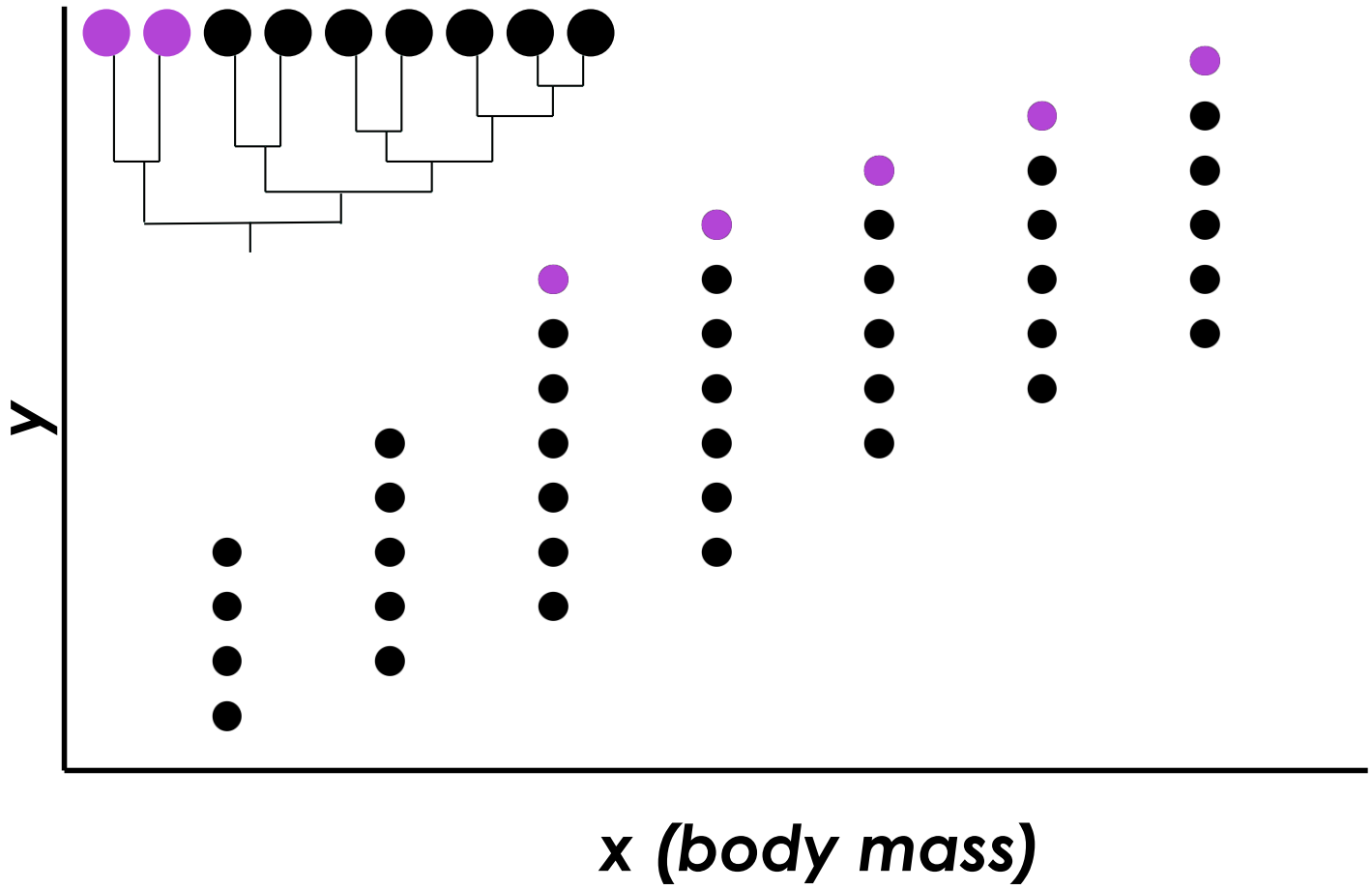
Interpreting allometries

Is there a systematic phylogenetic structure in the dataset?



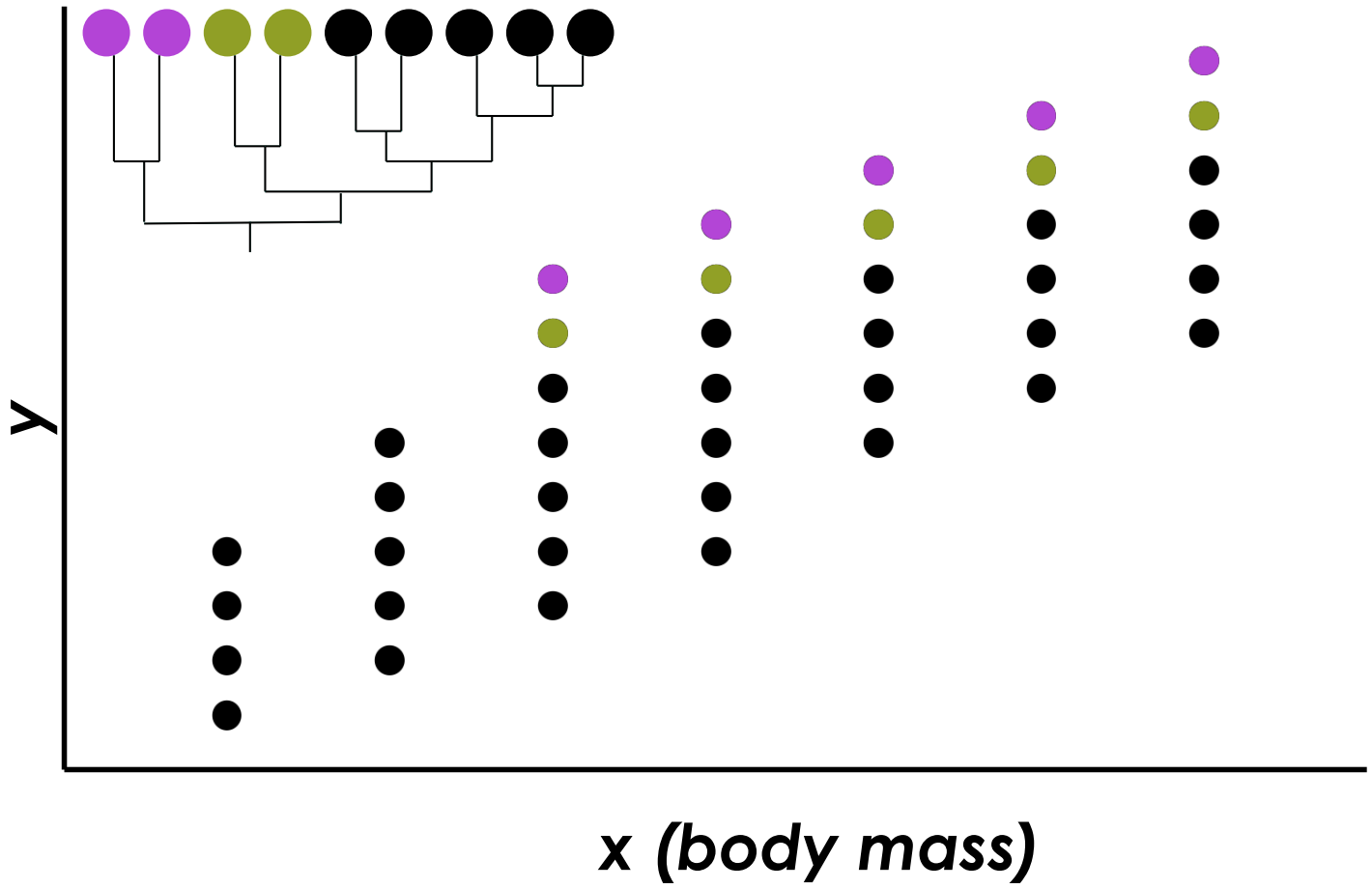
Interpreting allometries

Is there a systematic phylogenetic structure in the dataset?



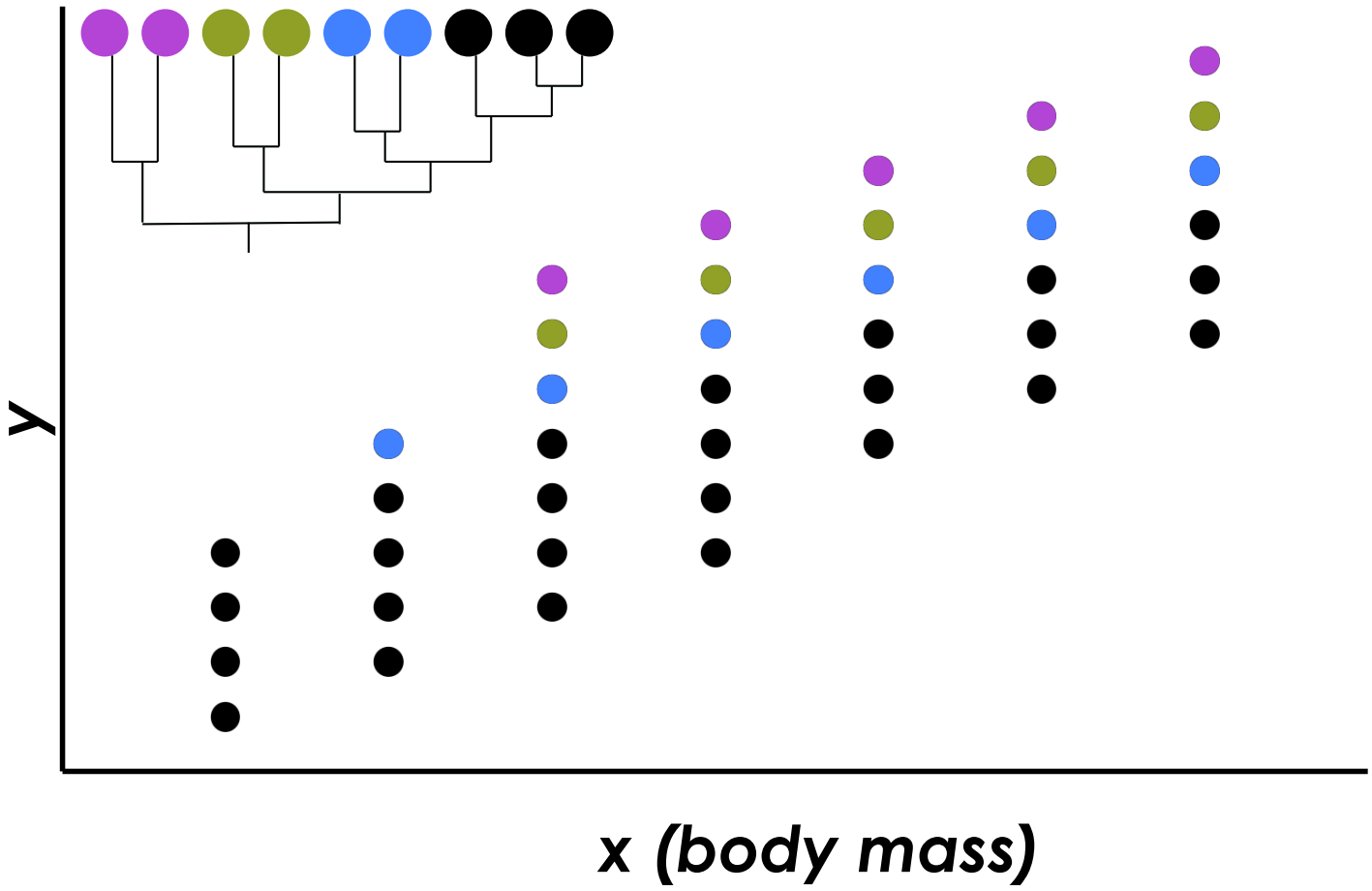
Interpreting allometries

Is there a systematic phylogenetic structure in the dataset?



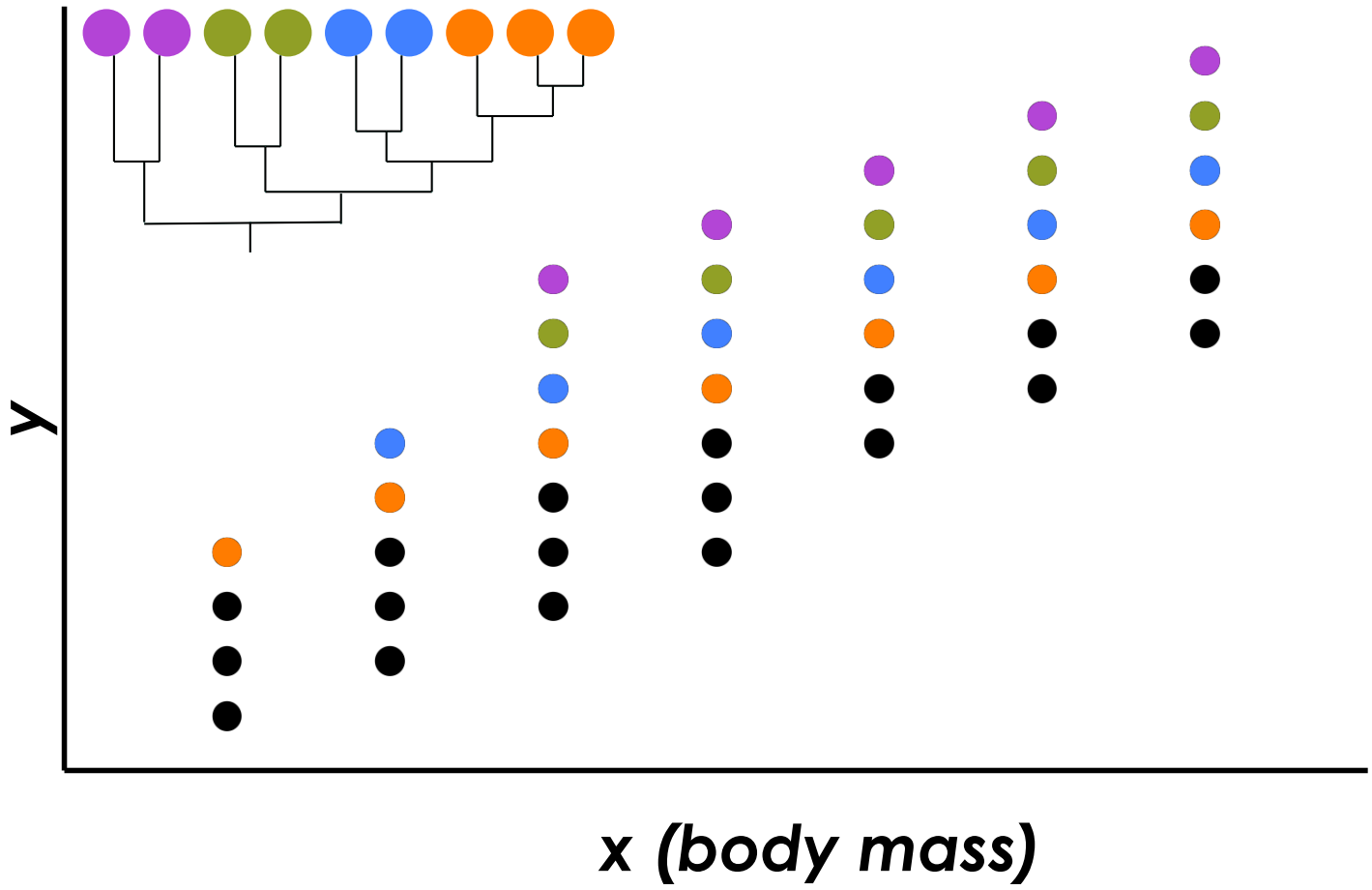
Interpreting allometries

Is there a systematic phylogenetic structure in the dataset?



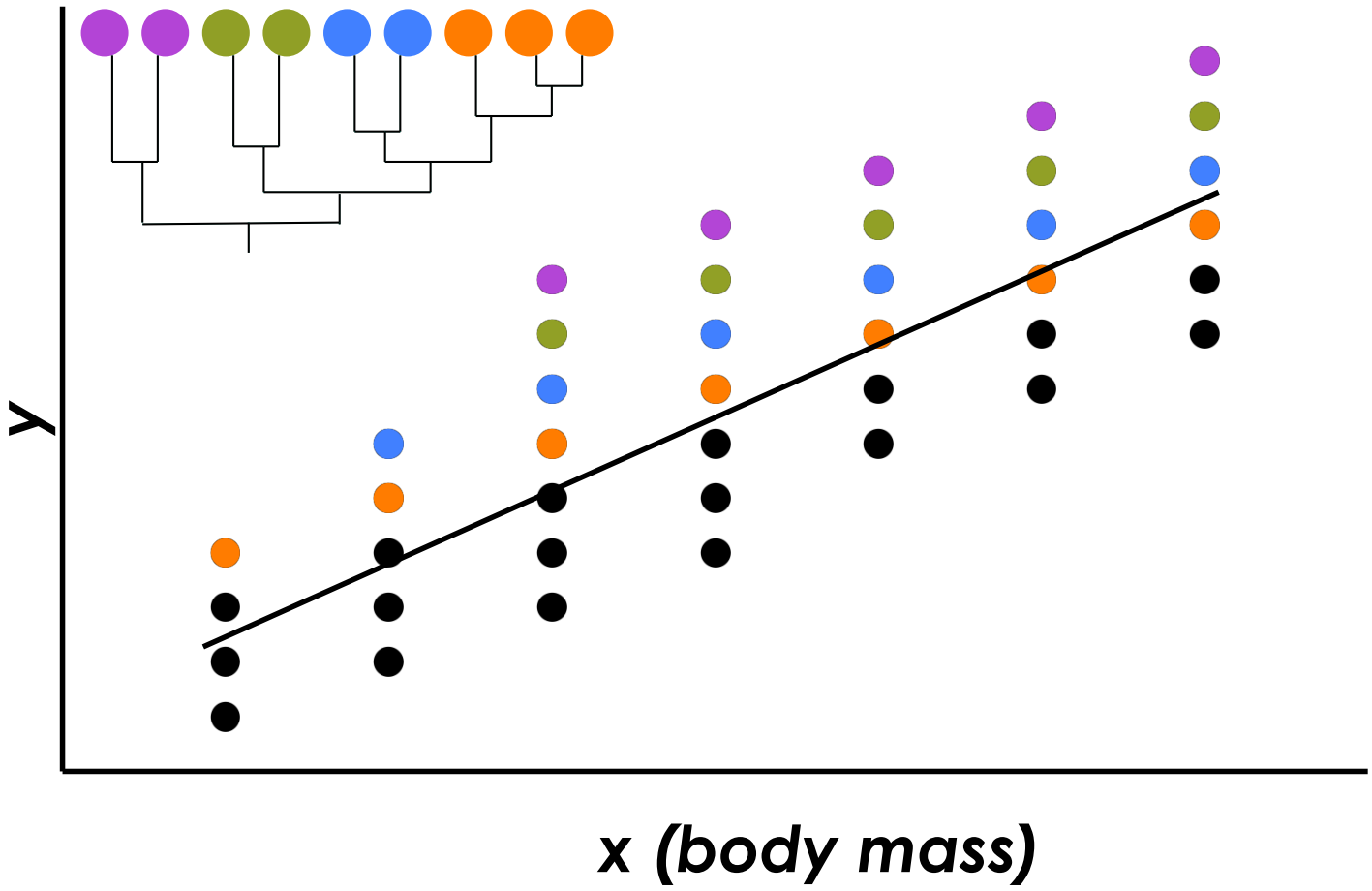
Interpreting allometries

Is there a systematic phylogenetic structure in the dataset?



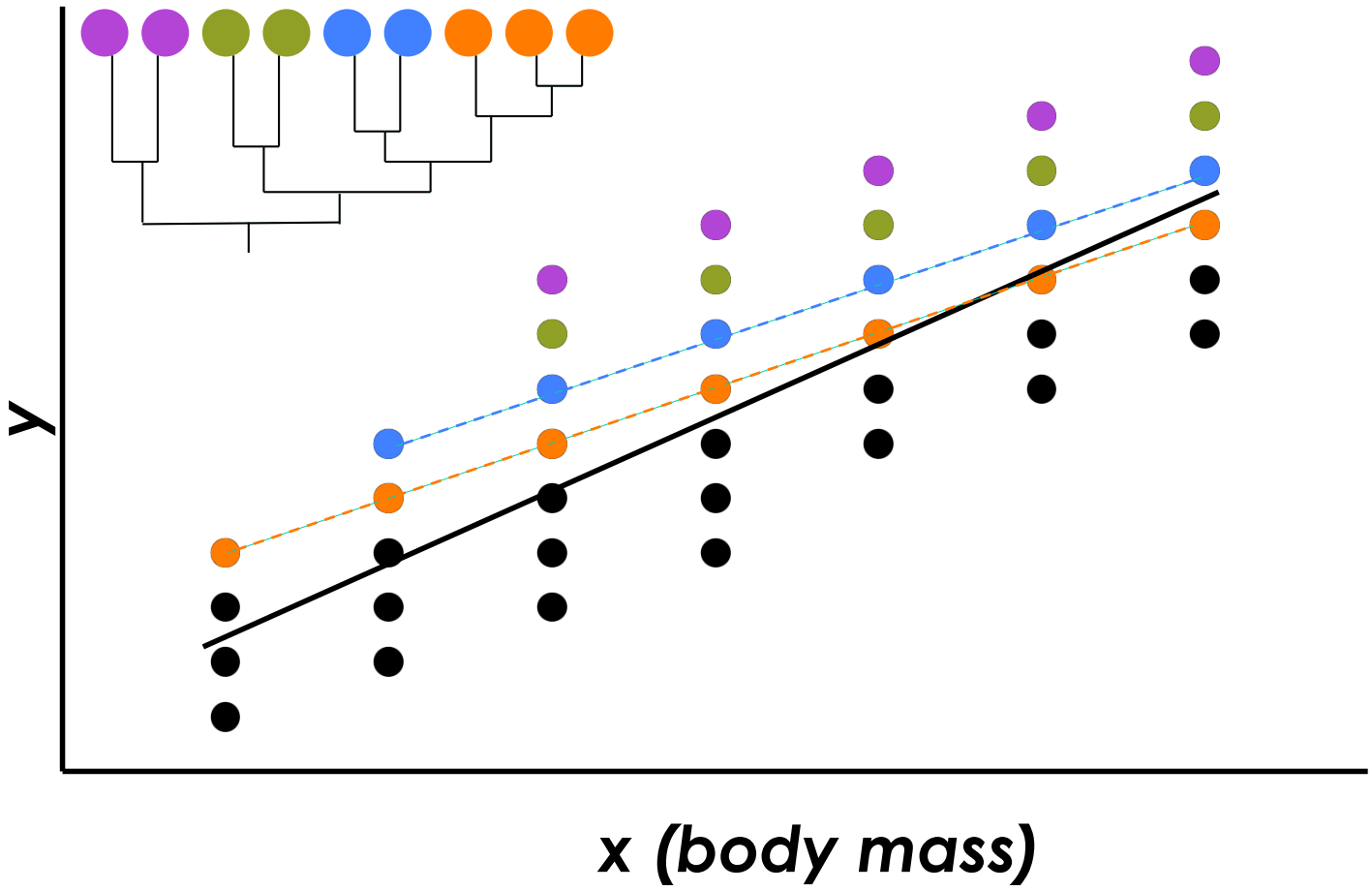
Interpreting allometries

Is there a systematic phylogenetic structure in the dataset?

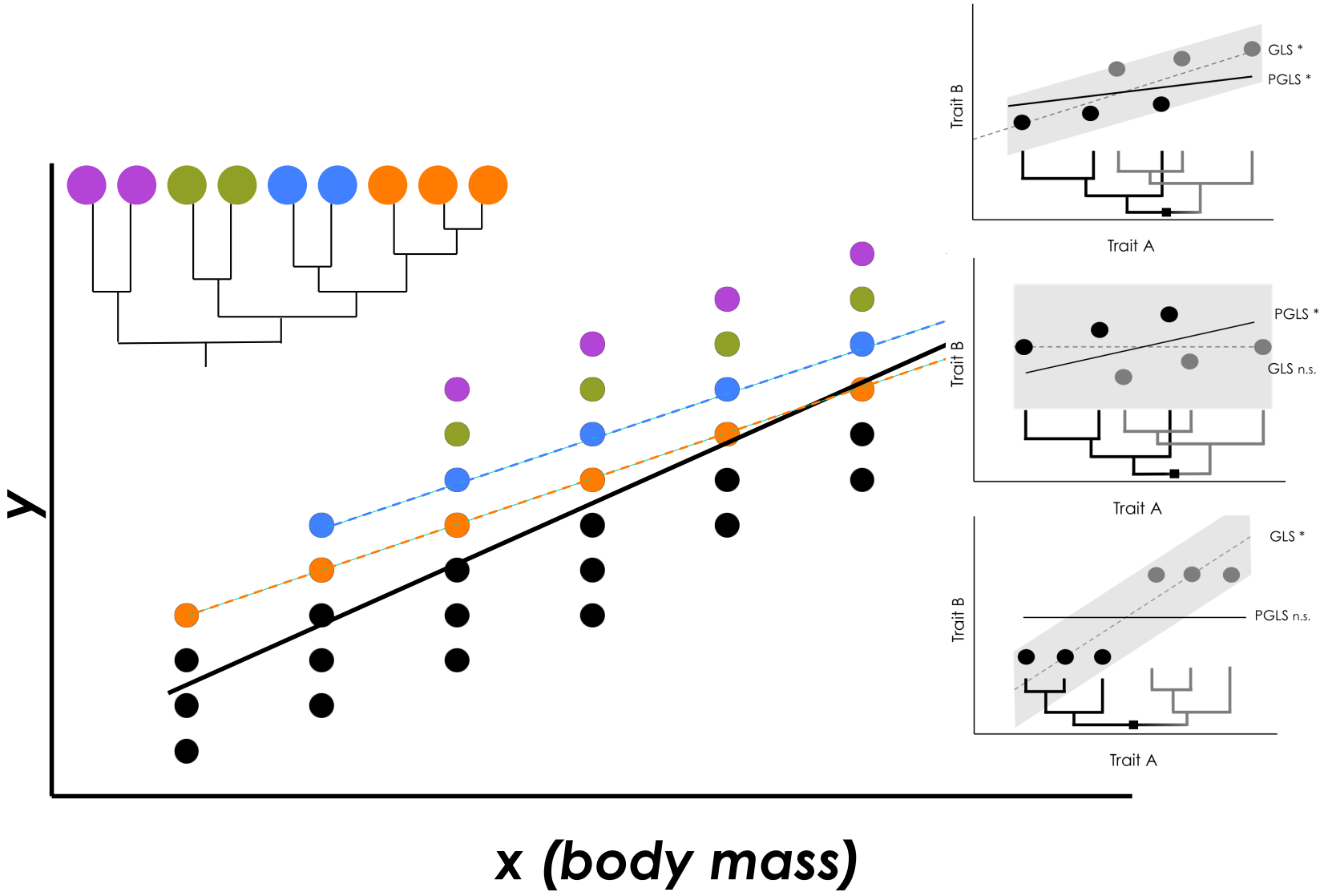


Interpreting allometries

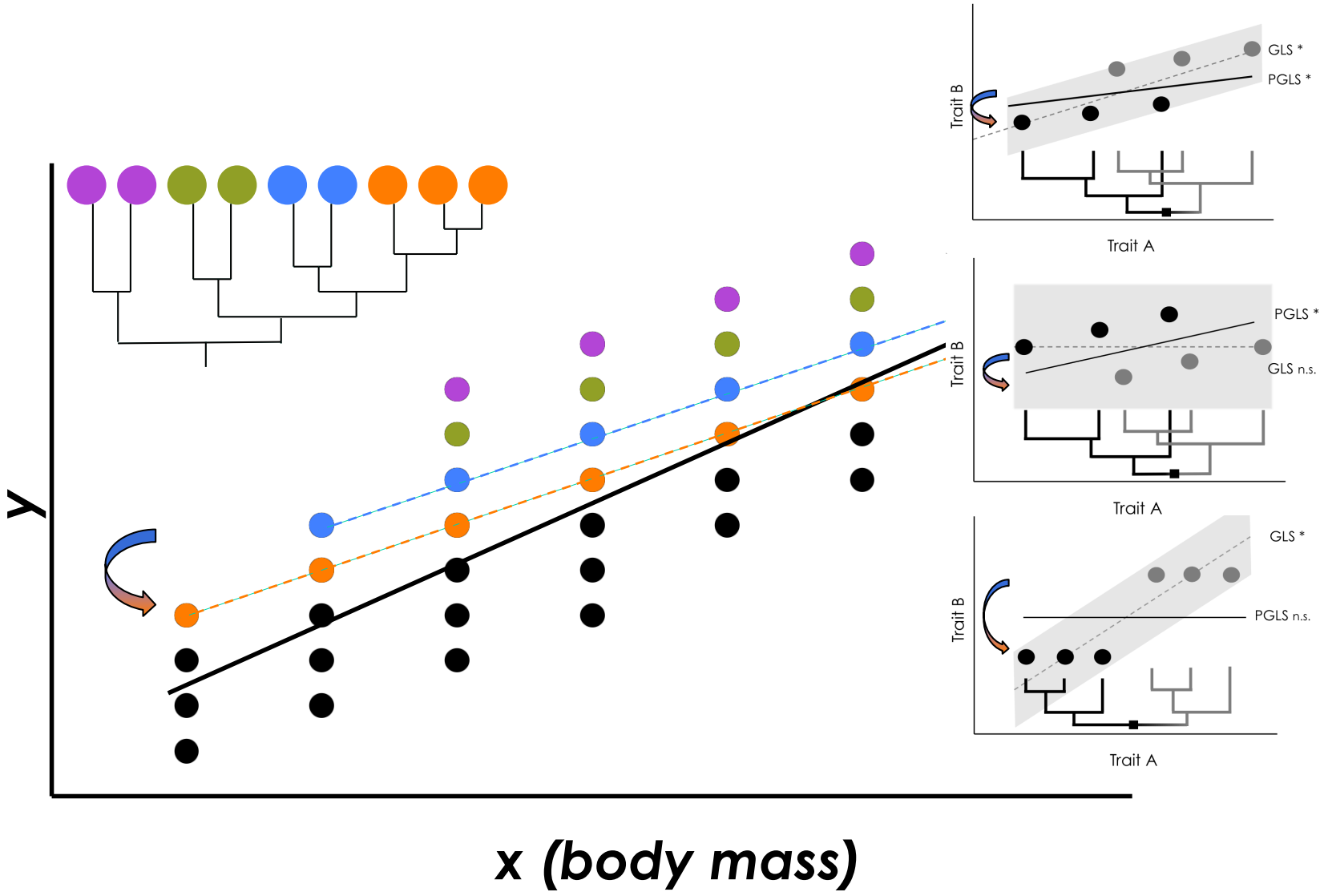
Is there a systematic phylogenetic structure in the dataset?



Interpreting allometries

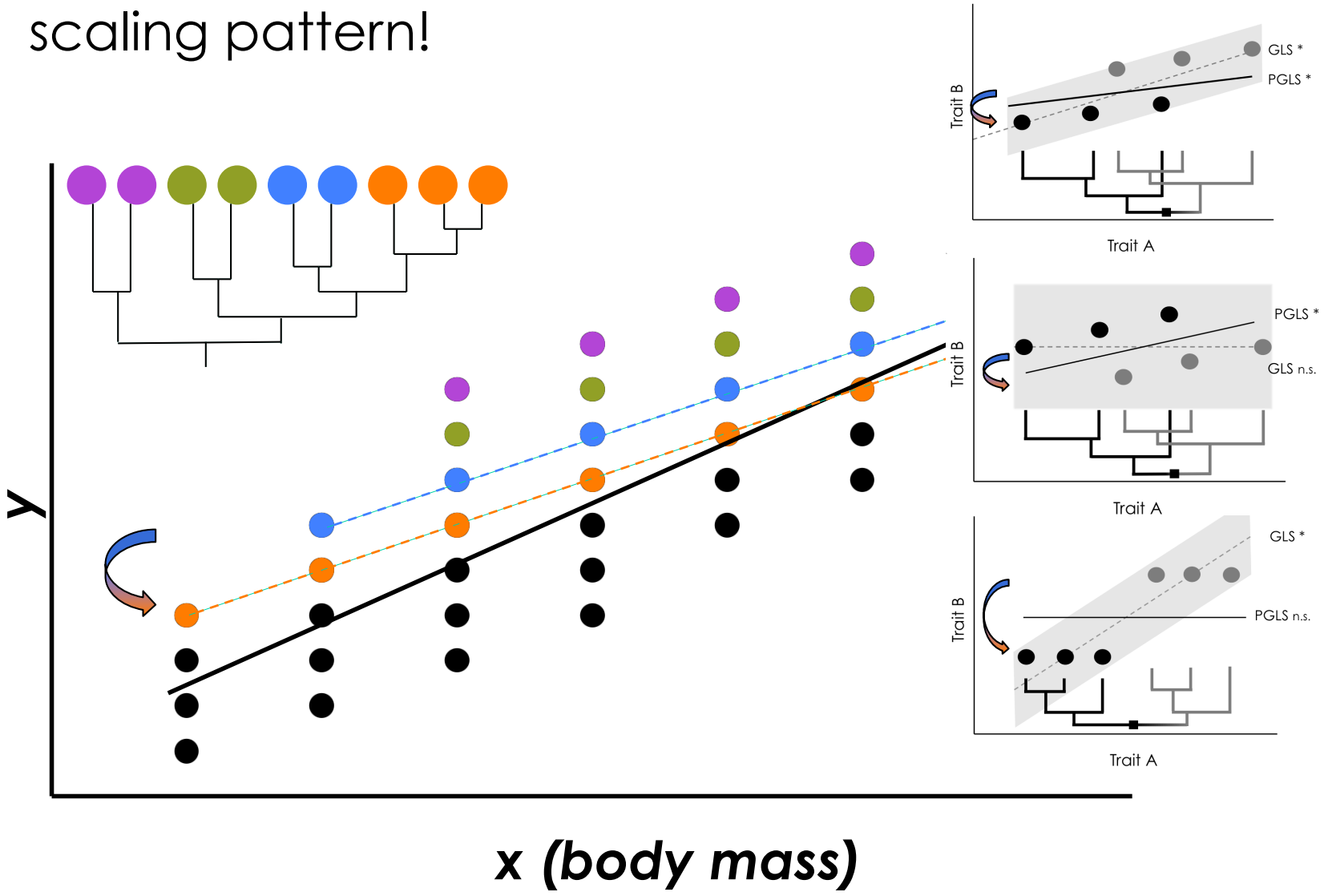


Changing the intercept



Changing the intercept

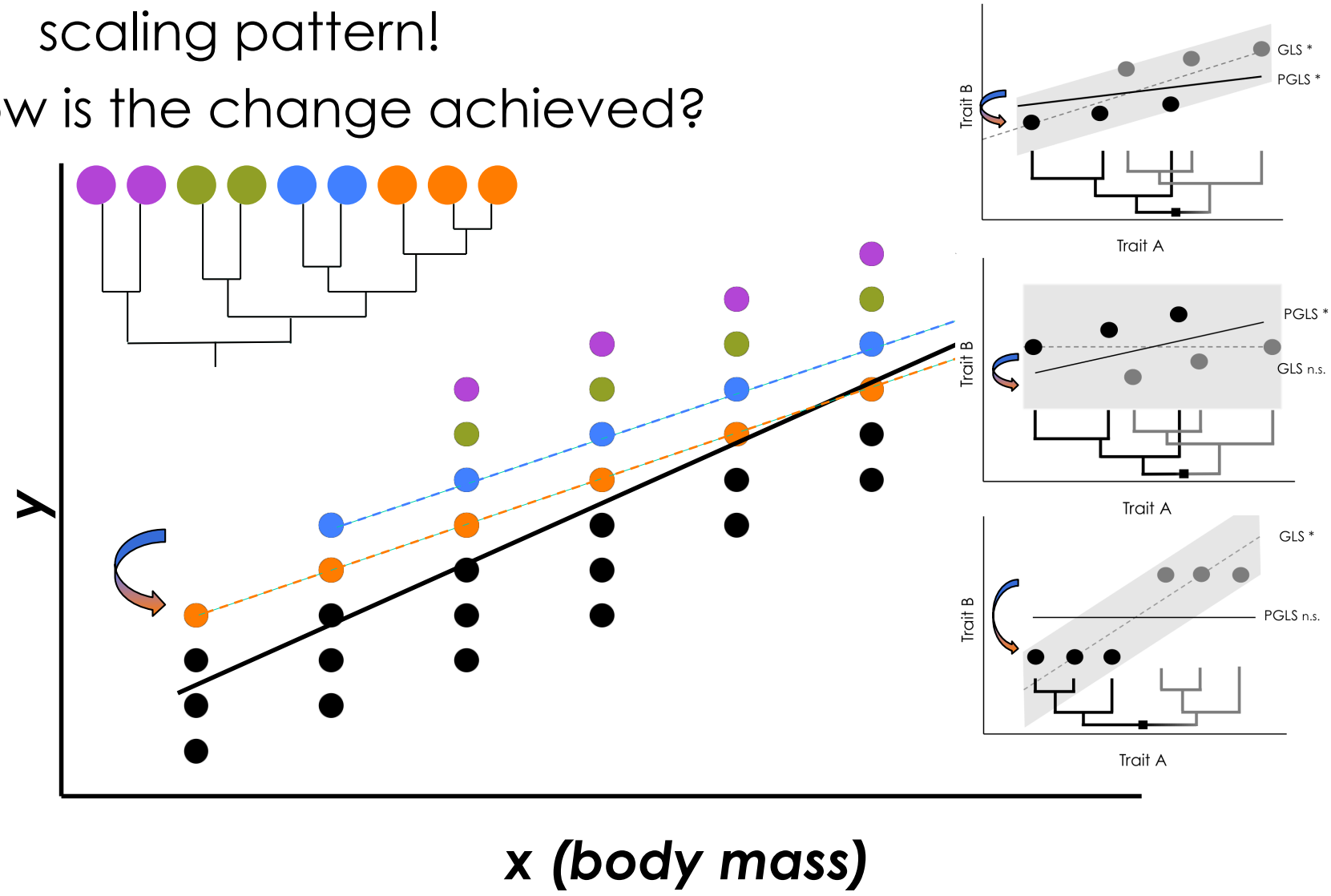
These changes are unrelated to the underlying scaling pattern!



Changing the intercept

These changes are unrelated to the underlying scaling pattern!

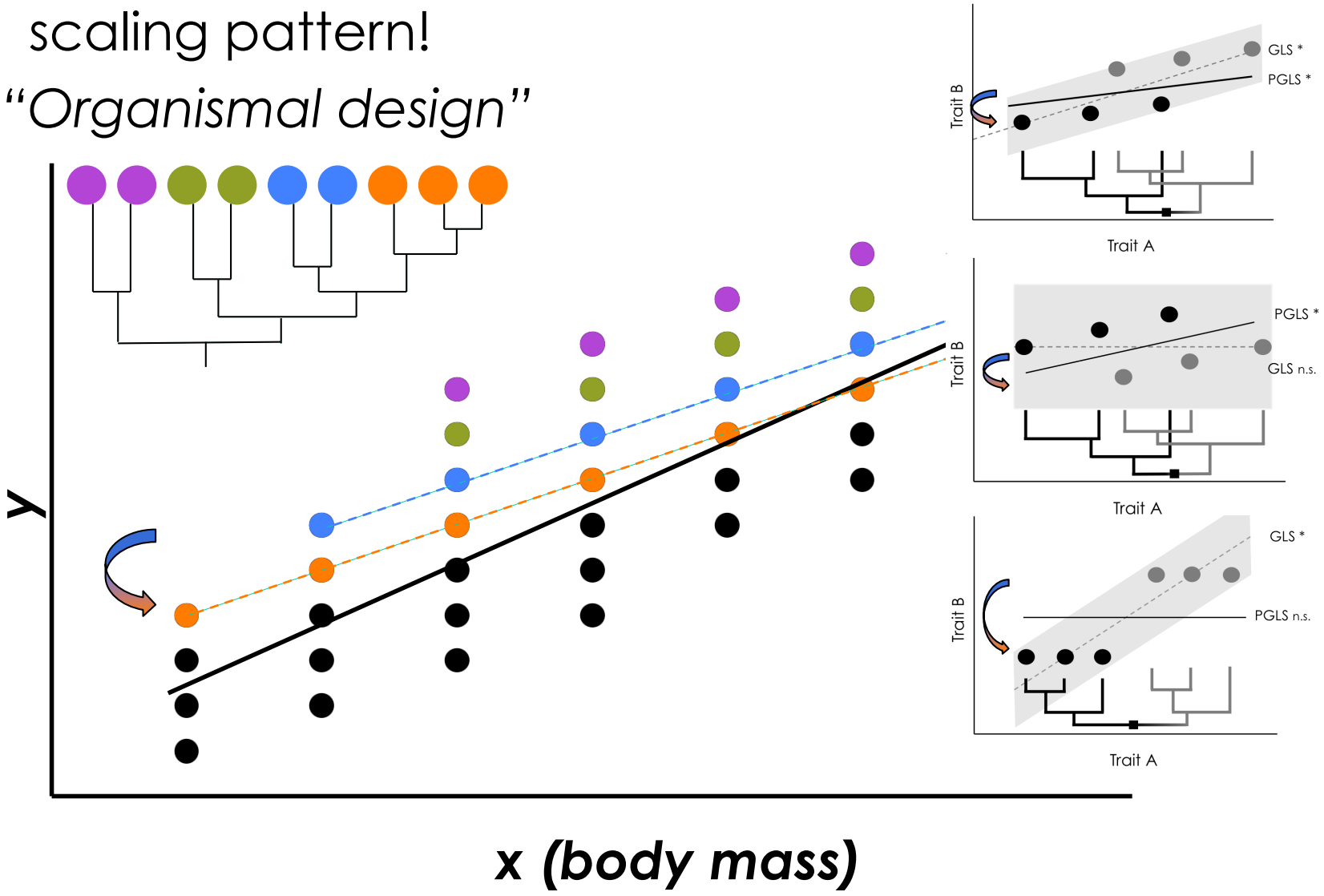
How is the change achieved?



Changing the intercept

These changes are unrelated to the underlying scaling pattern!

=> "*Organismal design*"



Changing the intercept

These changes are unrelated to the underlying scaling pattern!

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) CBP A

Changing the intercept

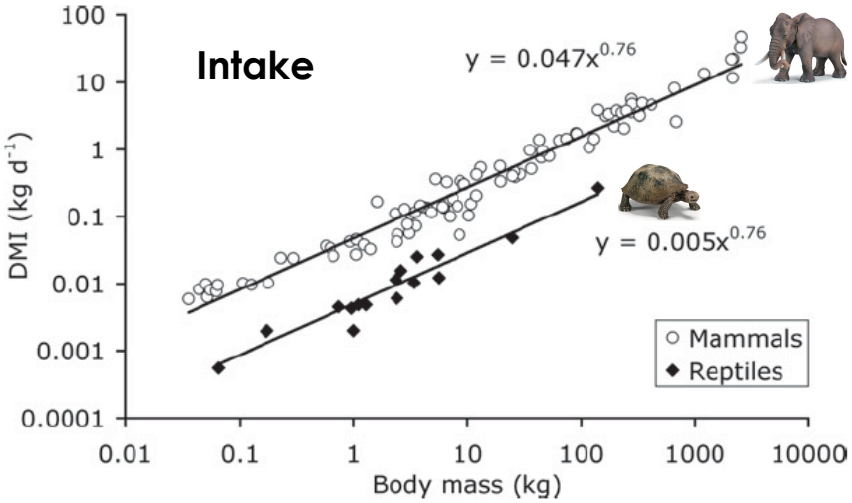
=> "*Organismal design*"

Easy to understand at high taxonomic level

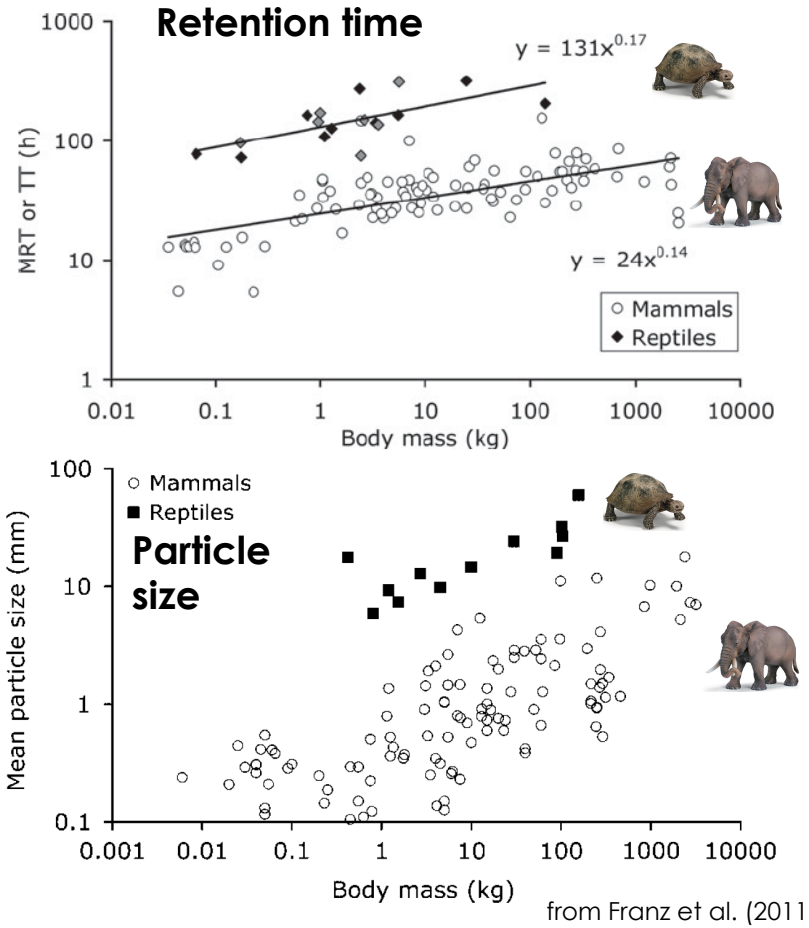
Changing the intercept

=> "*Organismal design*"

Easy to understand at high taxonomic level



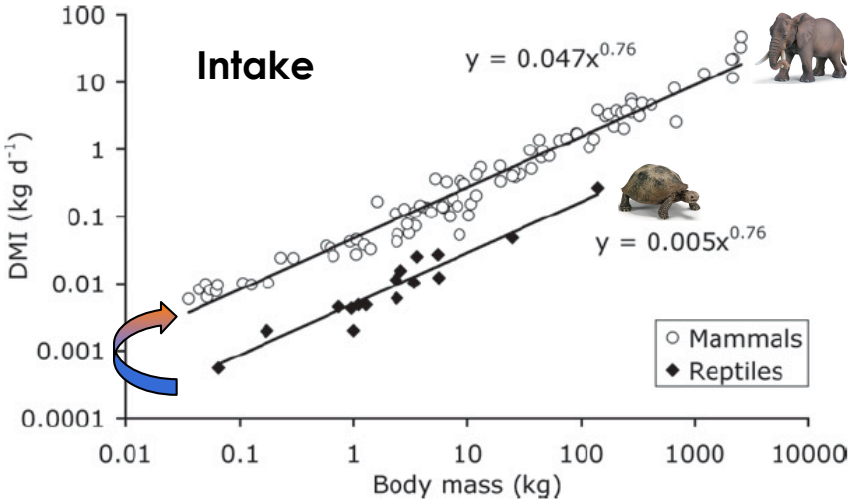
from Franz et al. (2011) CBP A



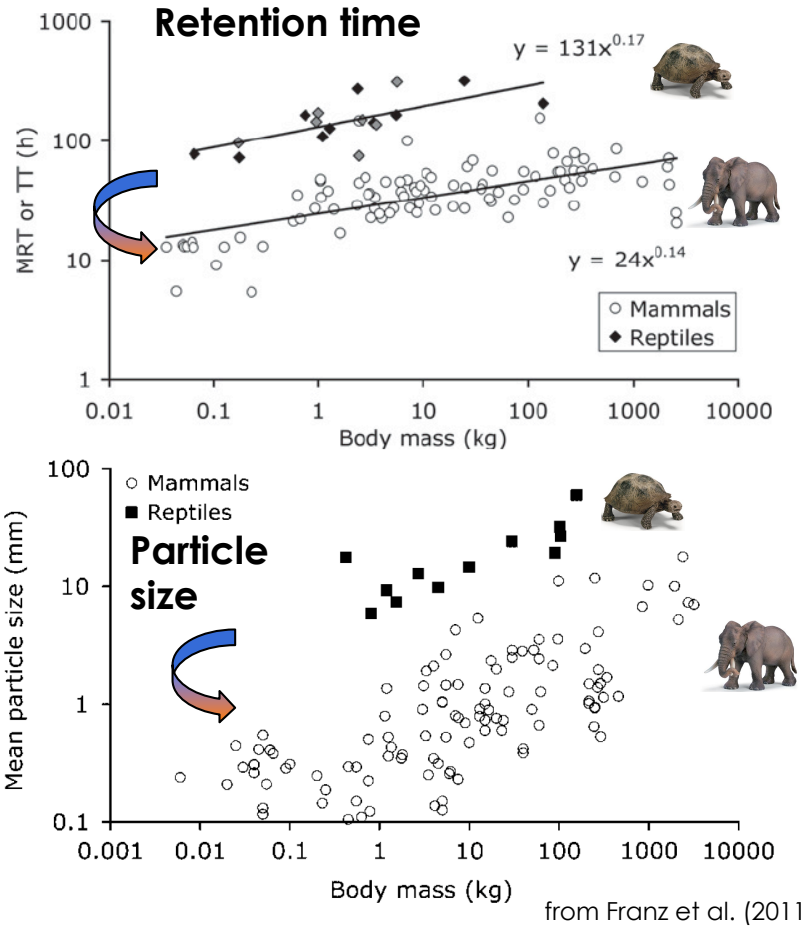
from Franz et al. (2011) CBP A and Fritz et al. (2010) JExpZool

Changing the intercept

Easy to understand at high 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

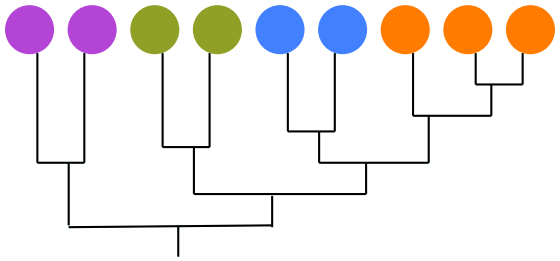
Easy to understand at high taxonomic level

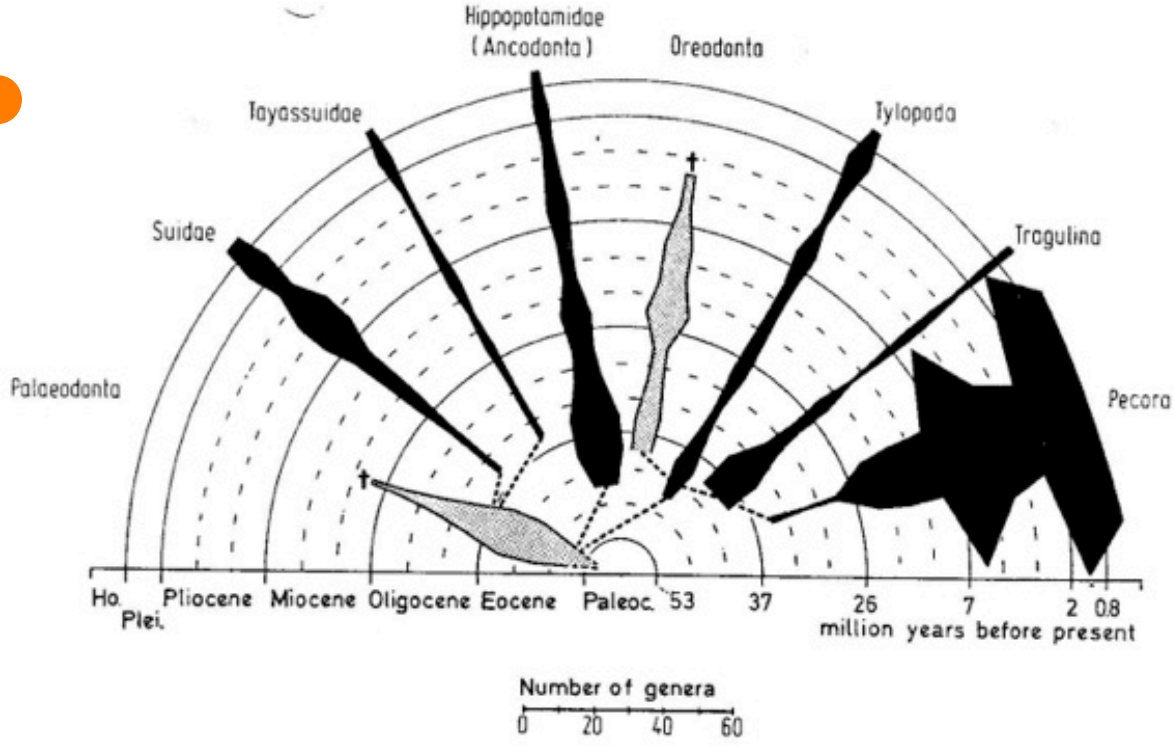
e.g. ectotherm vs. endotherm

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

Interpreting allometries

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

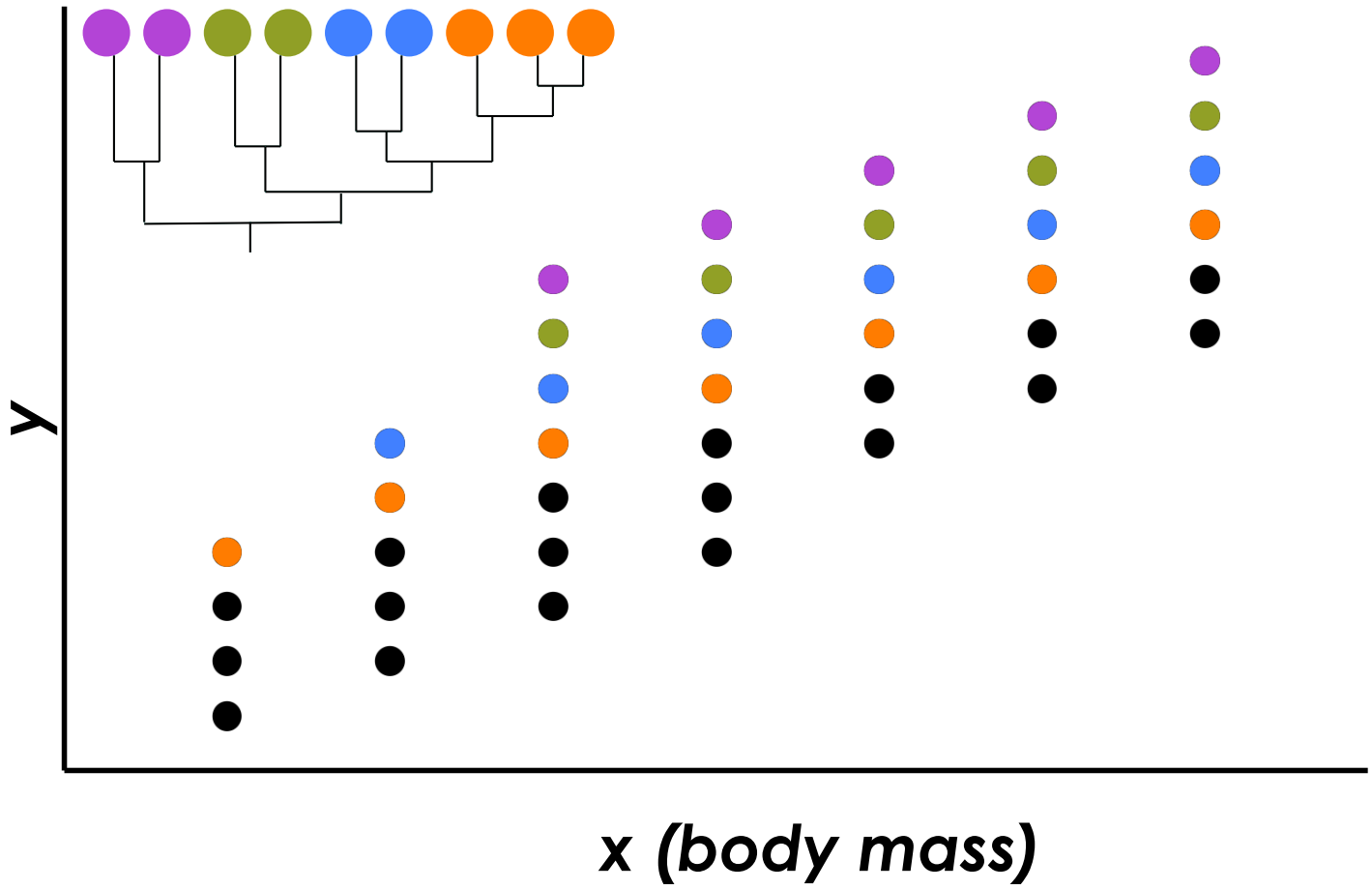




from Langer (1994)

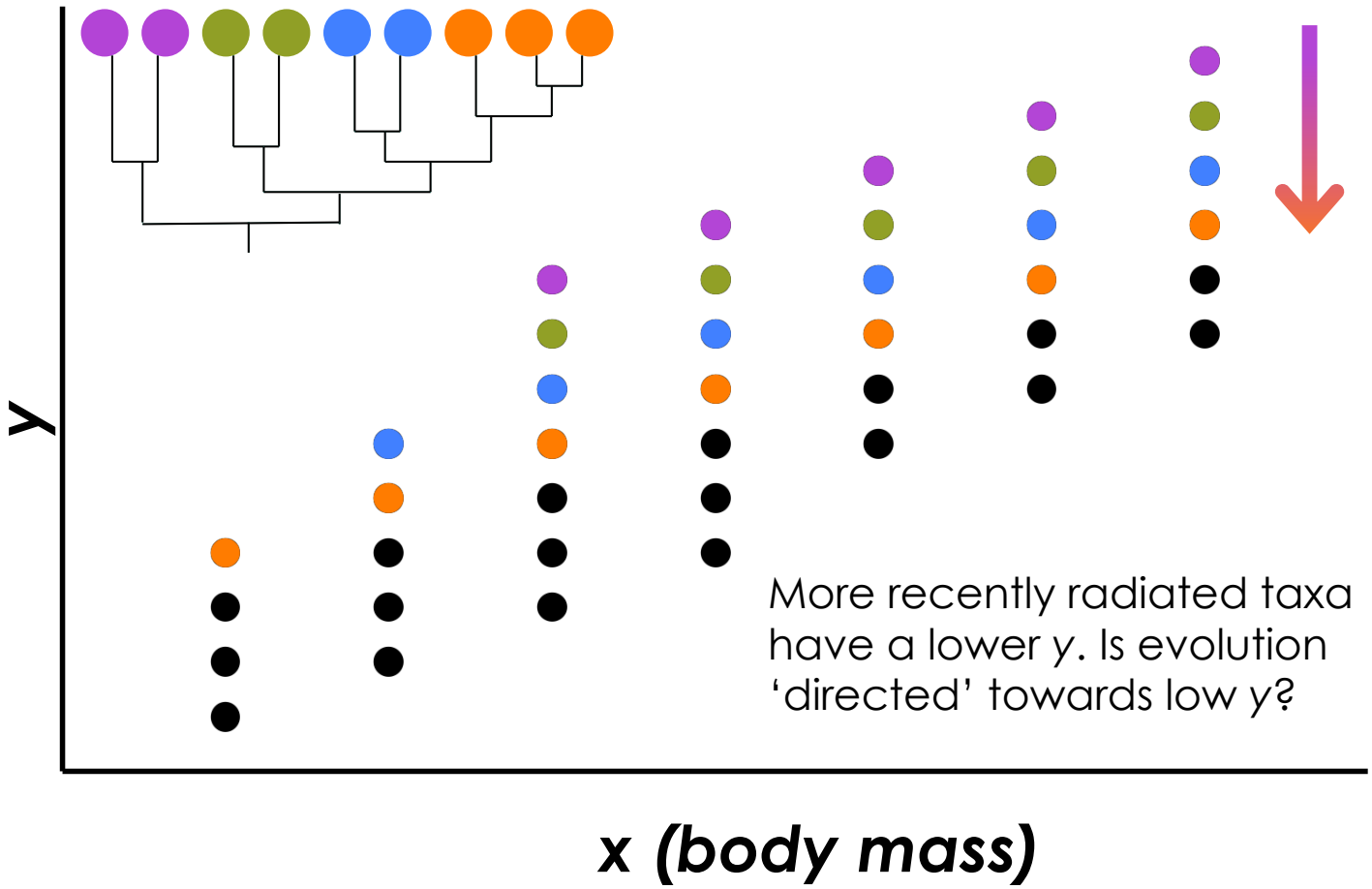
Interpreting allometries

Is there a systematic phylogenetic structure in the dataset?



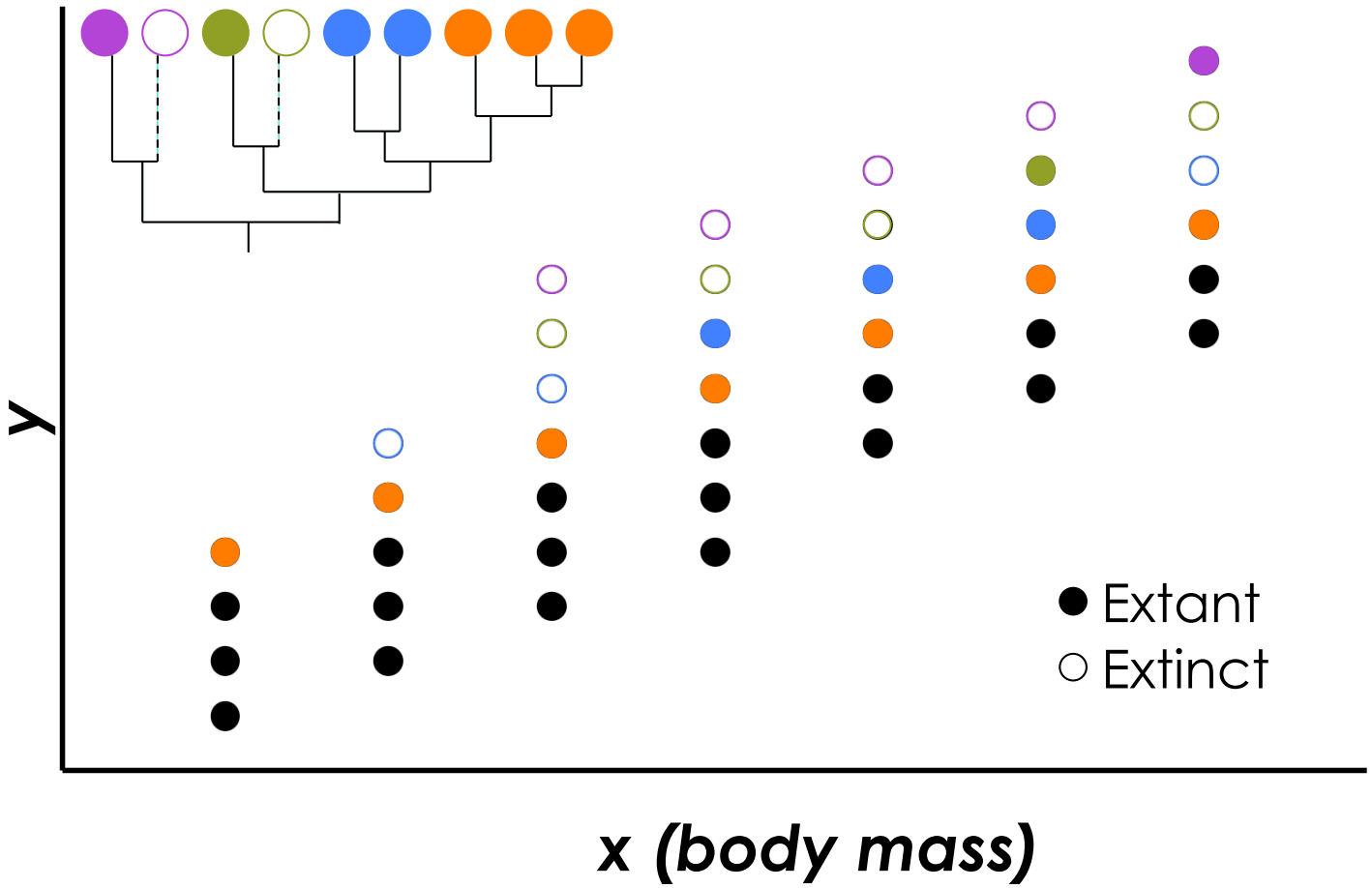
Interpreting allometries

Is there a systematic phylogenetic structure in the dataset?



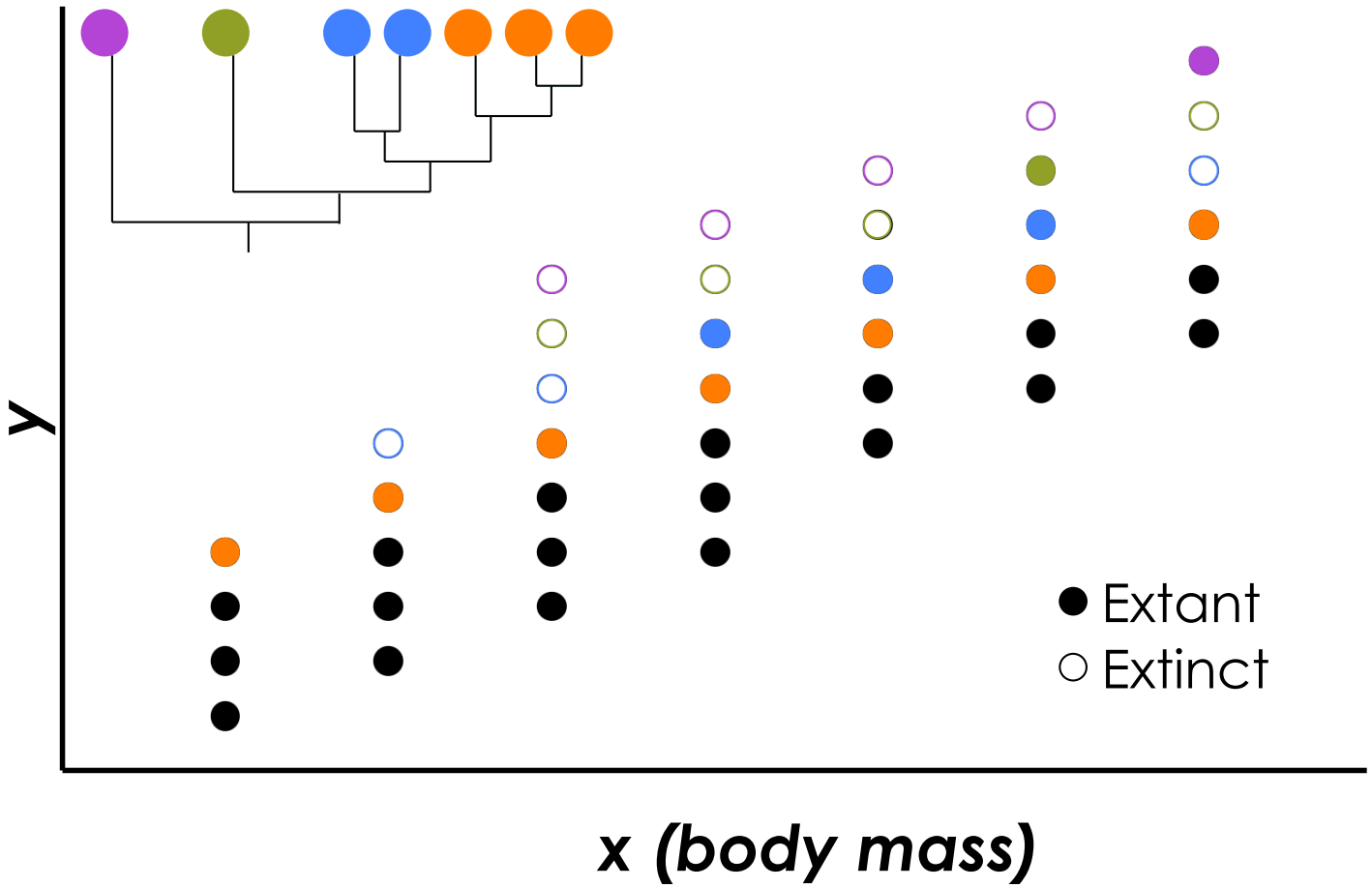
Interpreting allometries

Is there a systematic phylogenetic structure in the dataset?



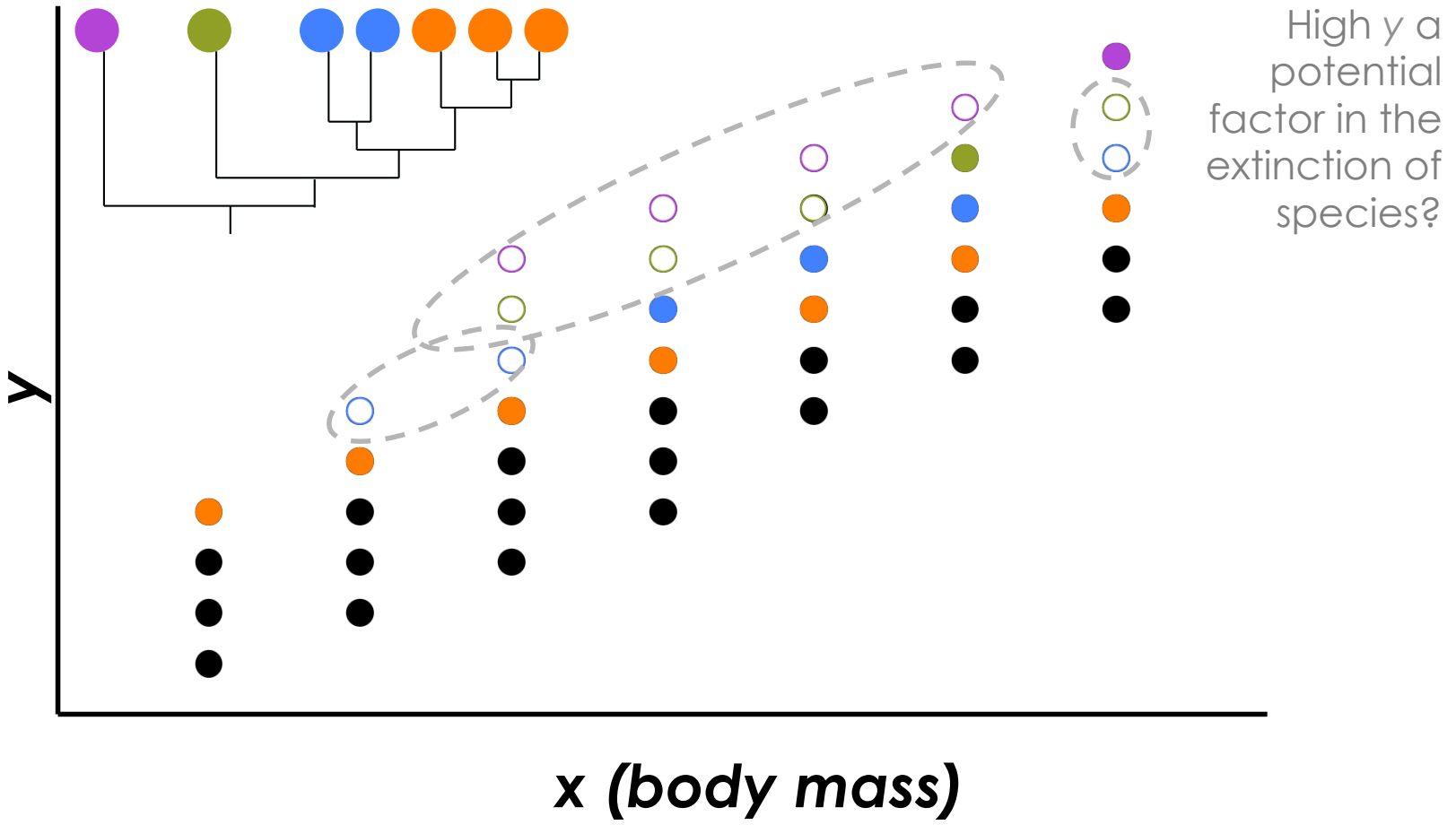
Interpreting allometries

Is there a systematic phylogenetic structure in the dataset?



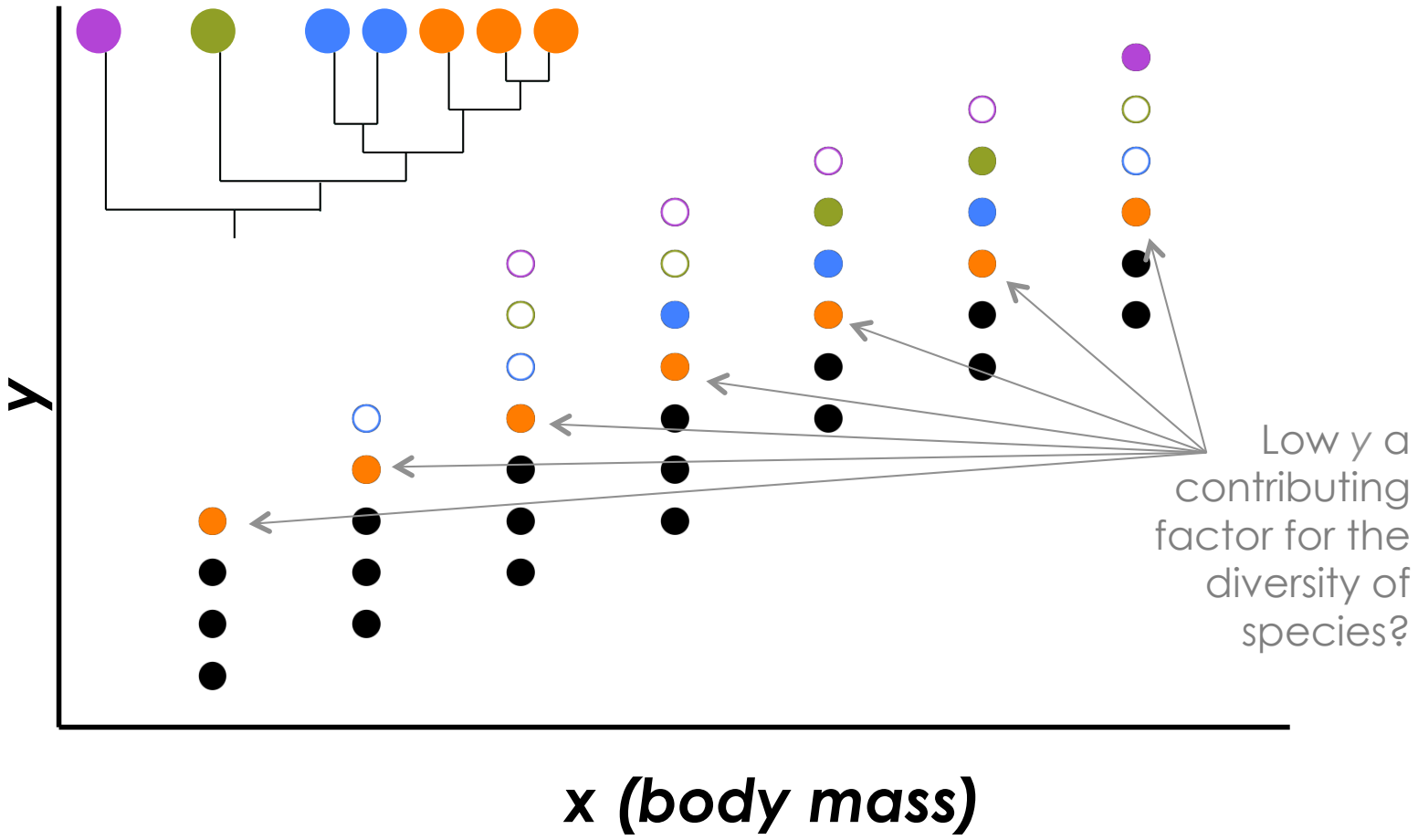
Interpreting allometries

Is there a systematic phylogenetic structure in the dataset?



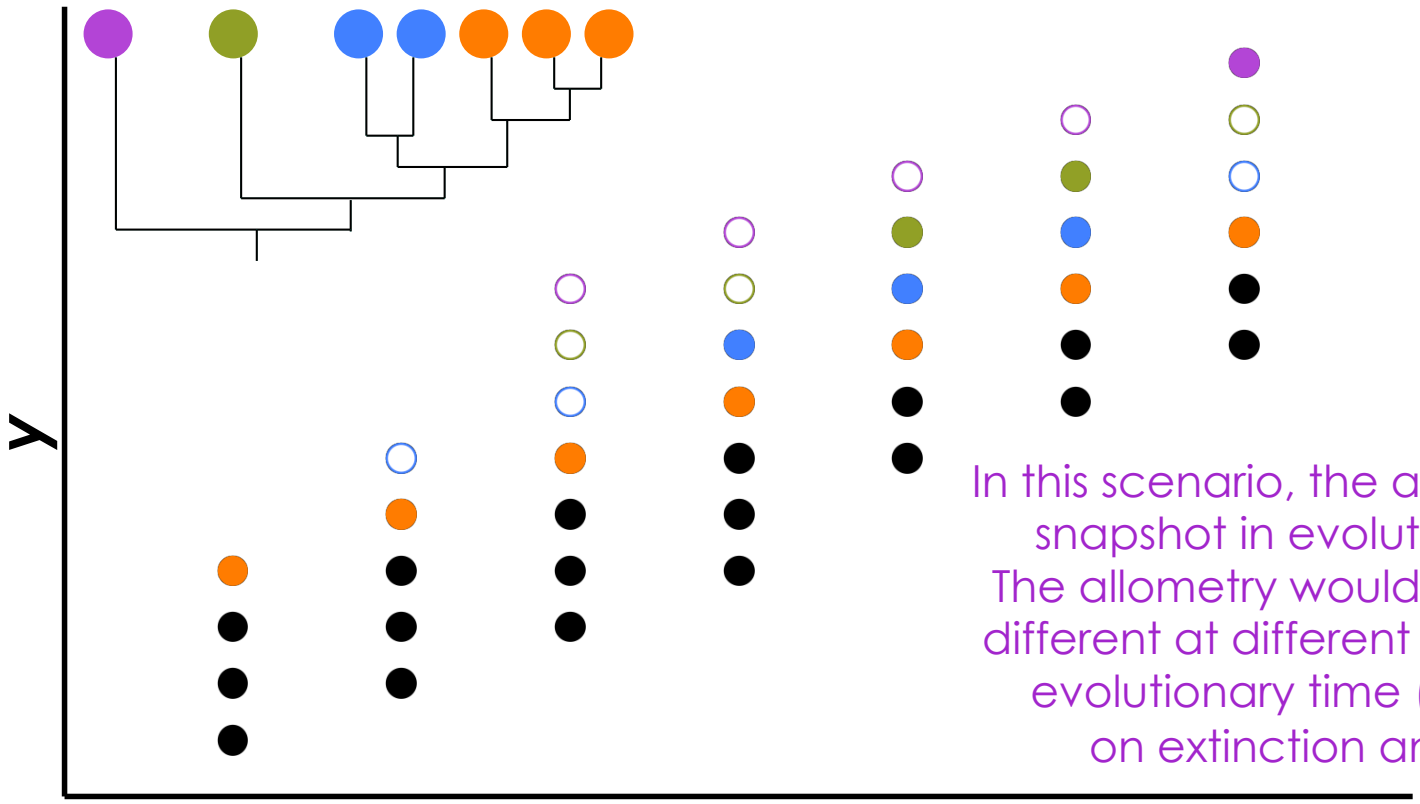
Interpreting allometries

Is there a systematic phylogenetic structure in the dataset?



Interpreting allometries

Is there a systematic phylogenetic structure in the dataset?



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)

‘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.

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™

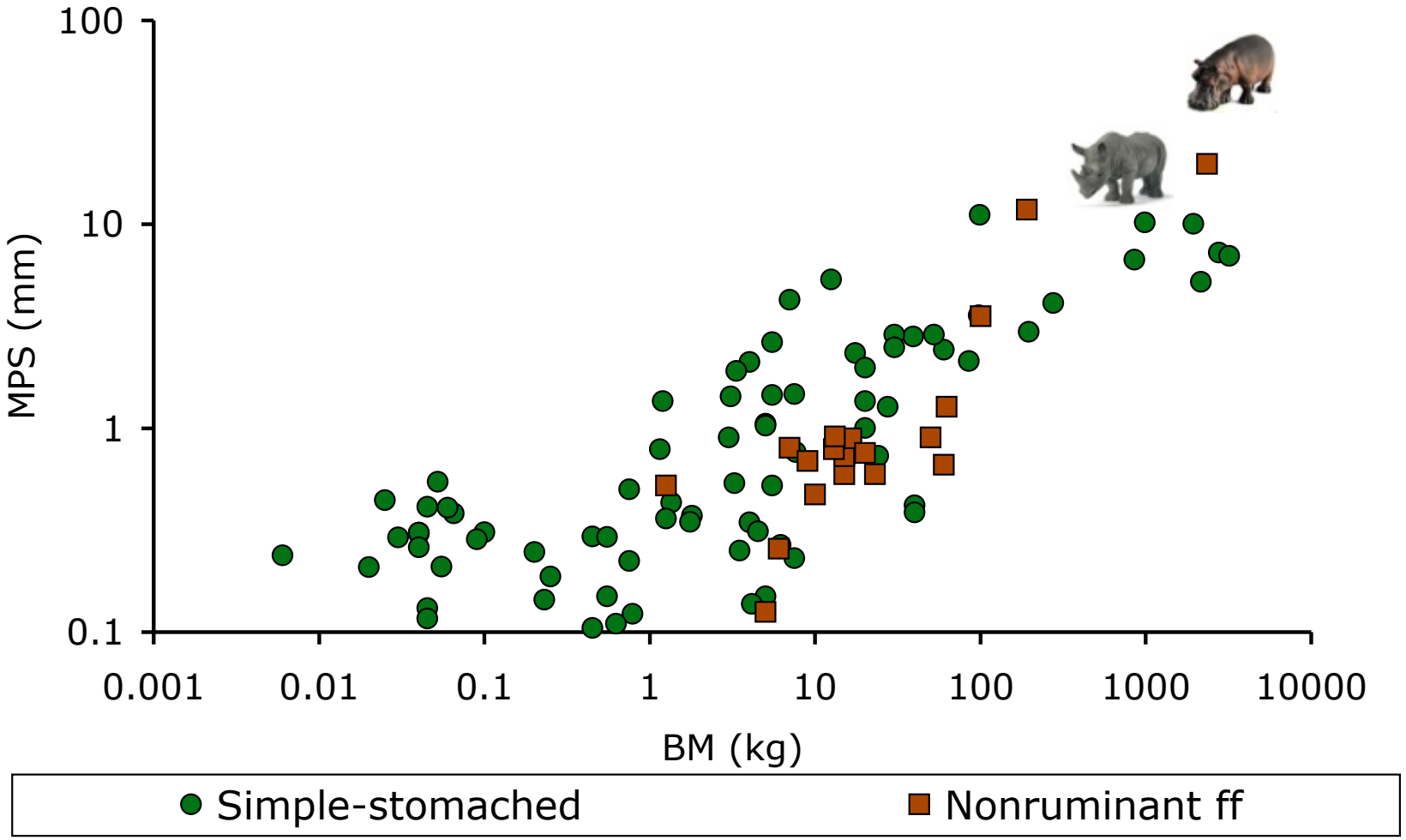
Herbivore ultimate™

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).

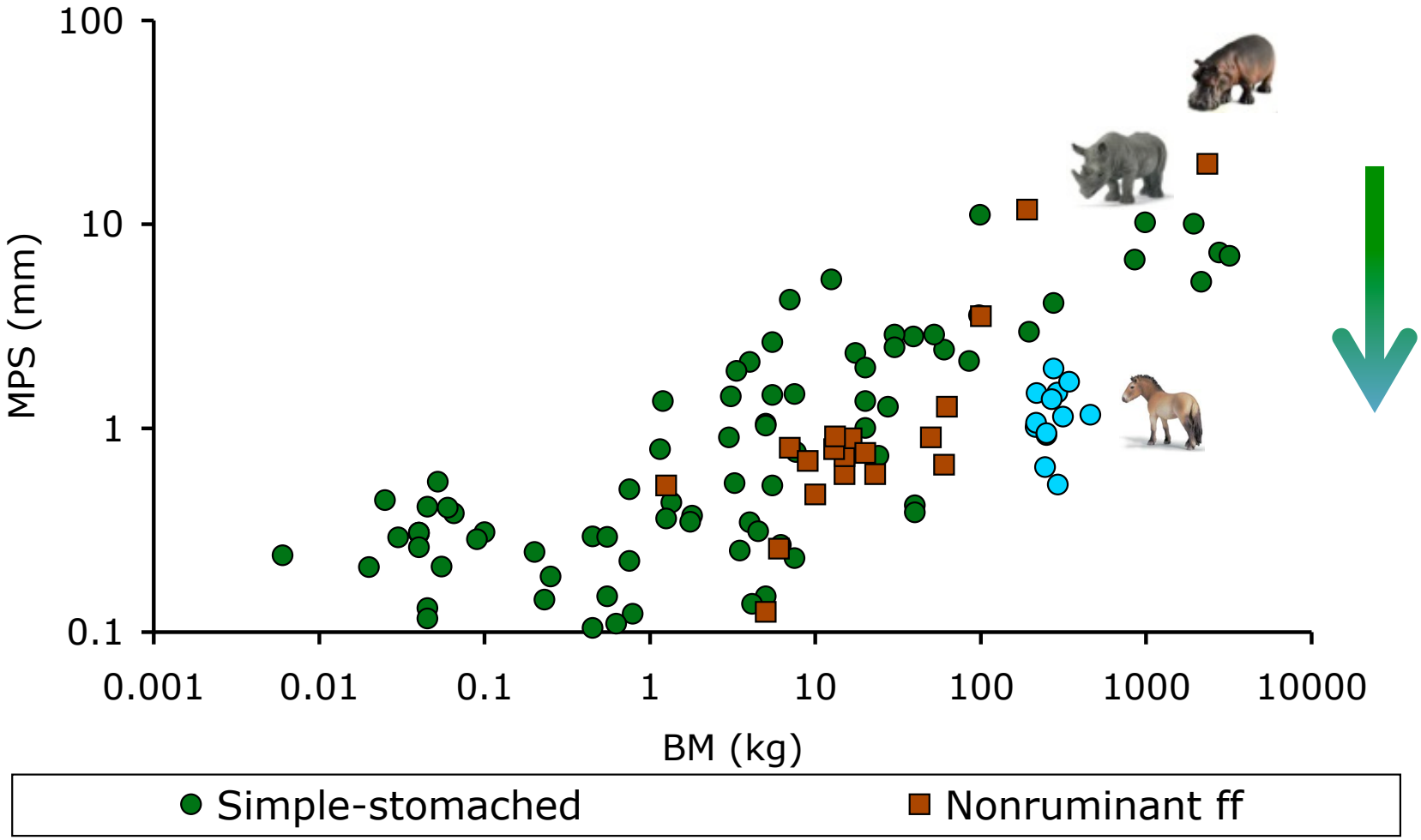
We would predict that herbivore group with the highest chewing efficiency should be particularly 'successful' (e.g. in terms of species diversity).

Example I: Mammal chewing efficiency



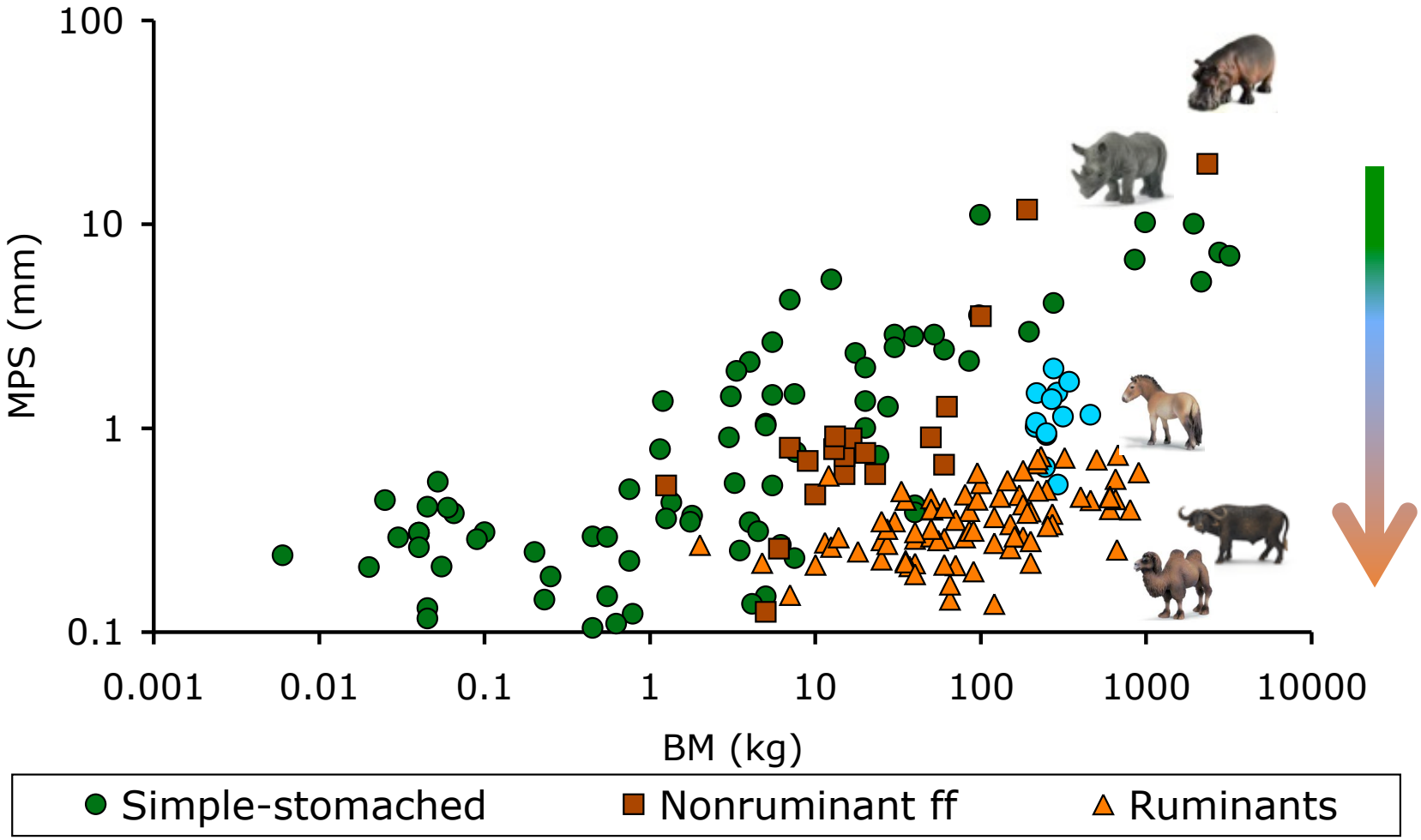
from Fritz et al. (2009)

Example I: Mammal chewing efficiency



from Fritz et al. (2009)

Example I: Mammal chewing efficiency



from Fritz et al. (2009)

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).

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).

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

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).

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!

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).

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

nearly extinct in a very limited geographical range

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).

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

only in extreme, resource-poor habitats

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).

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

rule the world !!

Example II: (Precocial) Mammal gestation period

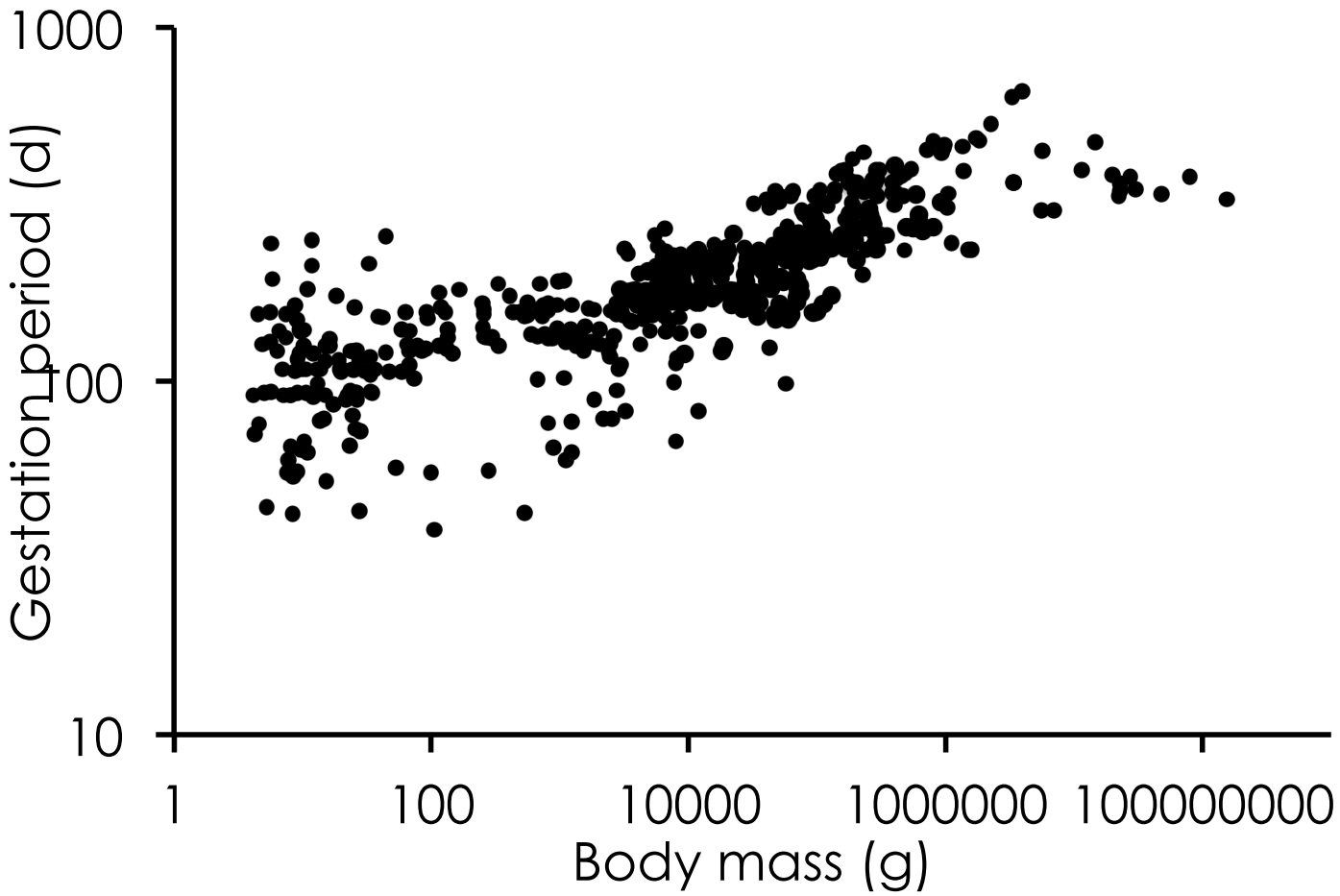
For any mammal, achieving the same degree of neonatal development in a shorter gestation period – if not associated with higher costs – should be advantageous (higher fecundity due to shorter generation times).

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

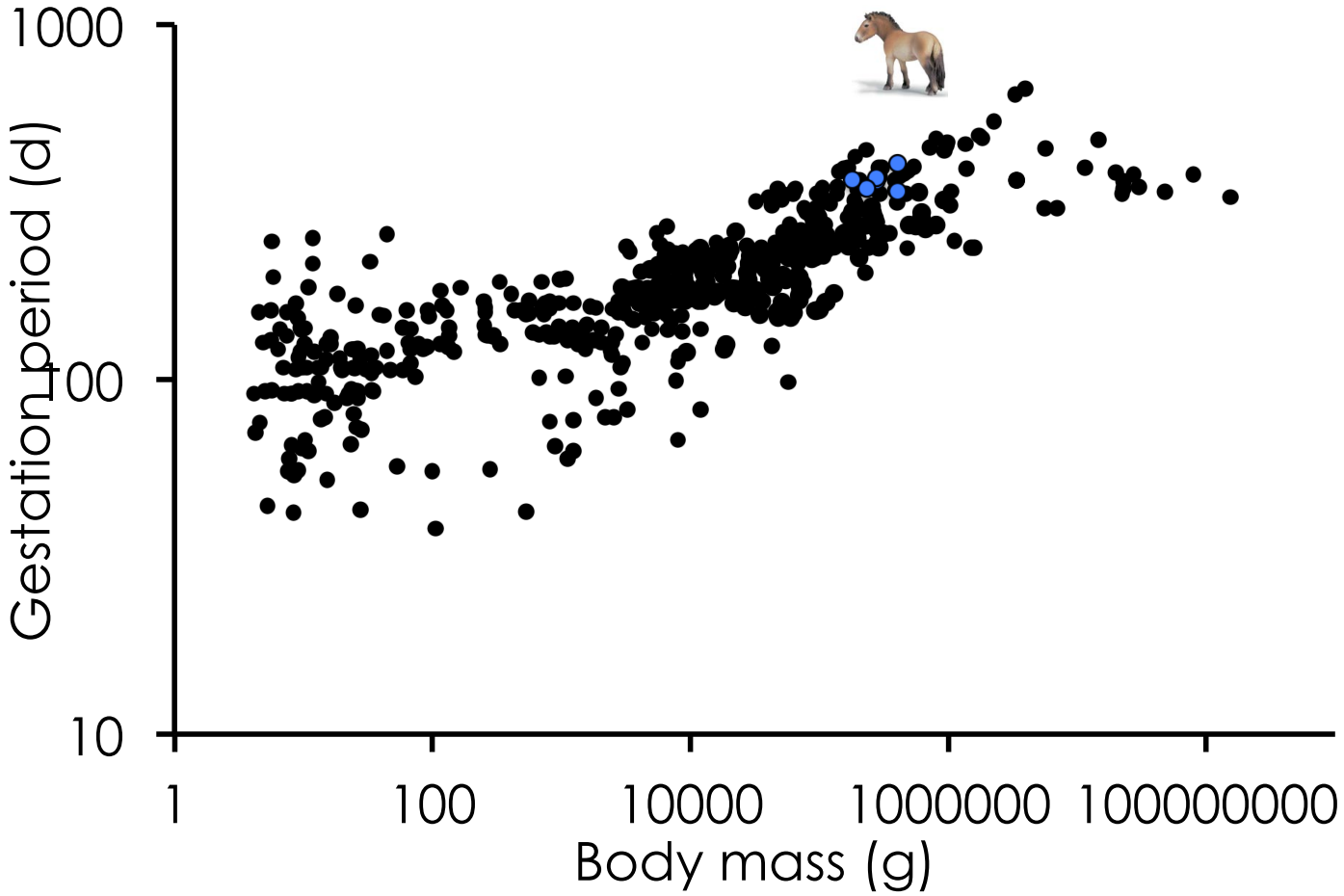
We would predict that animals with a shorter gestation period should be particularly 'successful' (e.g. in terms of species diversity).

Example II: (Precocial) Mammal gestation period



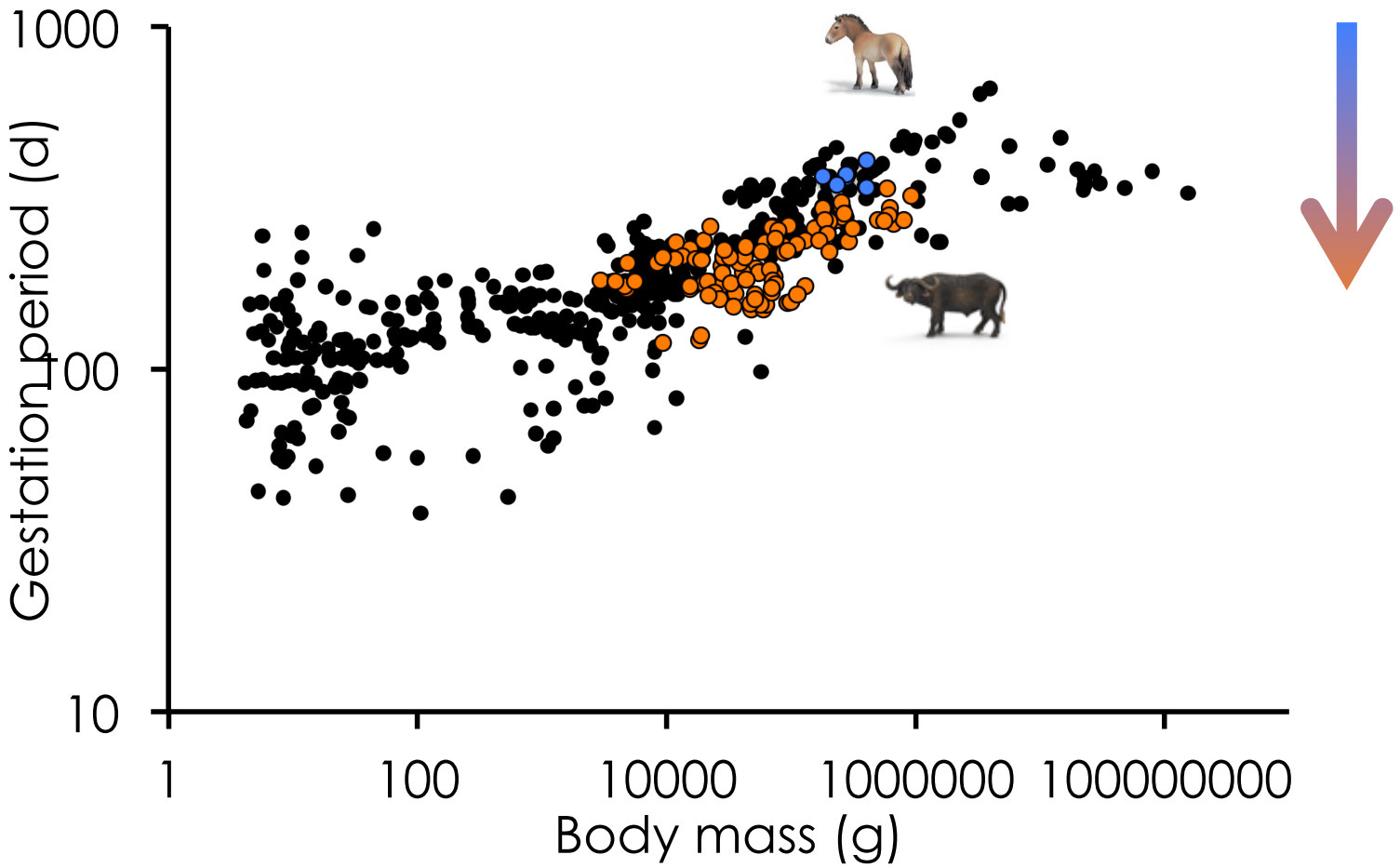
from Clauss et al. (2013)

Example II: (Precocial) Mammal gestation period



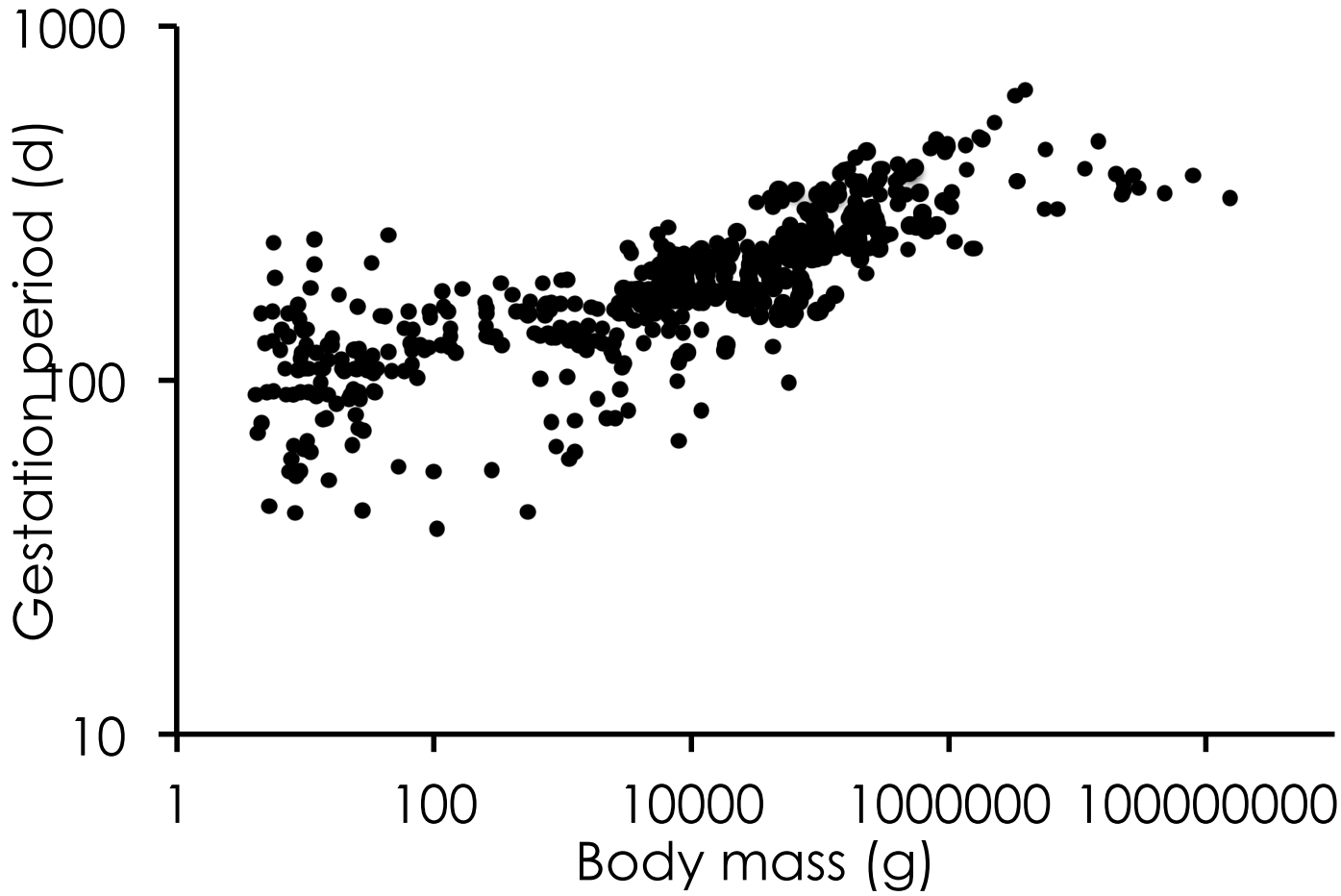
from Clauss et al. (2013)

Example II: (Precocial) Mammal gestation period



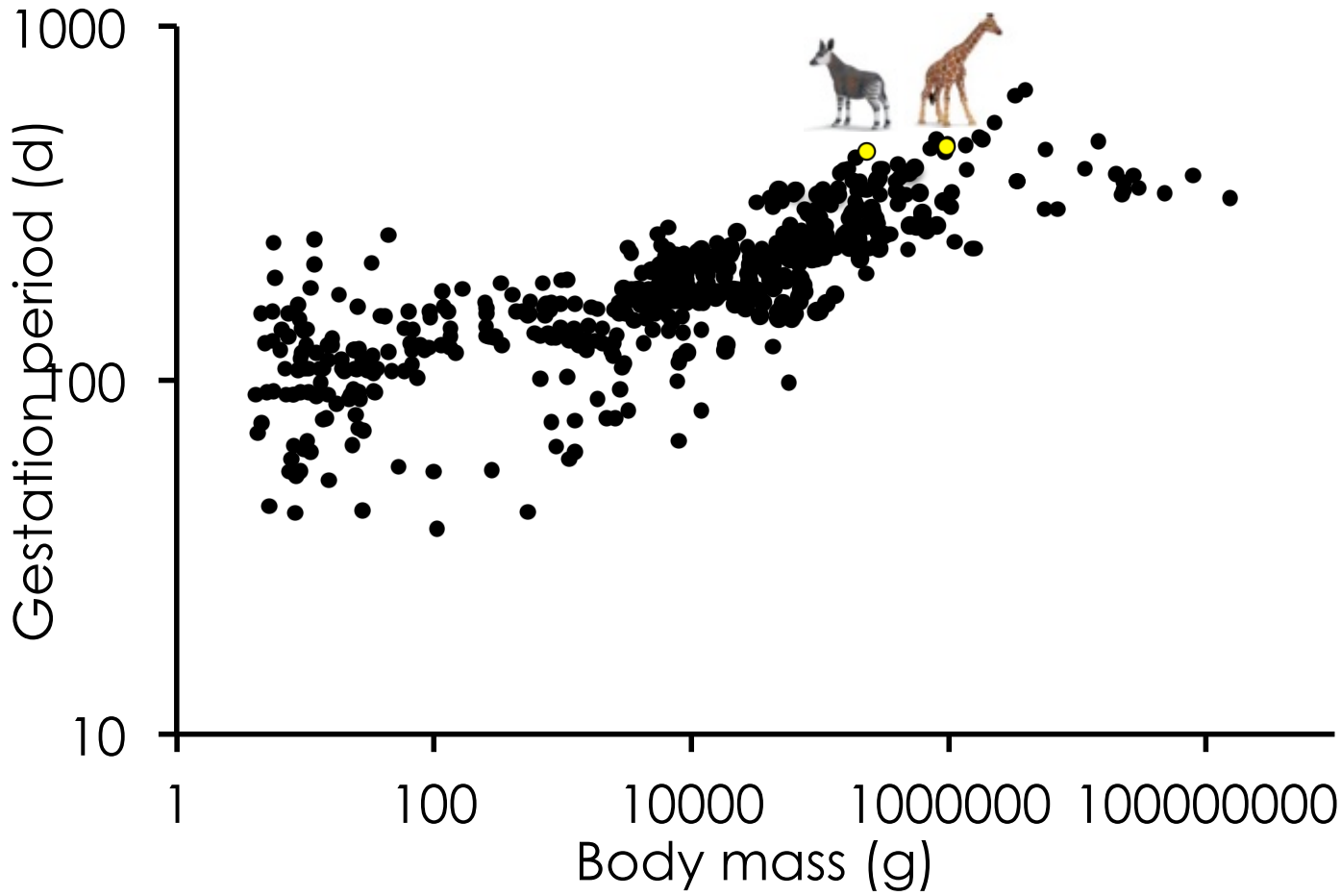
from Clauss et al. (2013)

Example II: (Precocial) Mammal gestation period



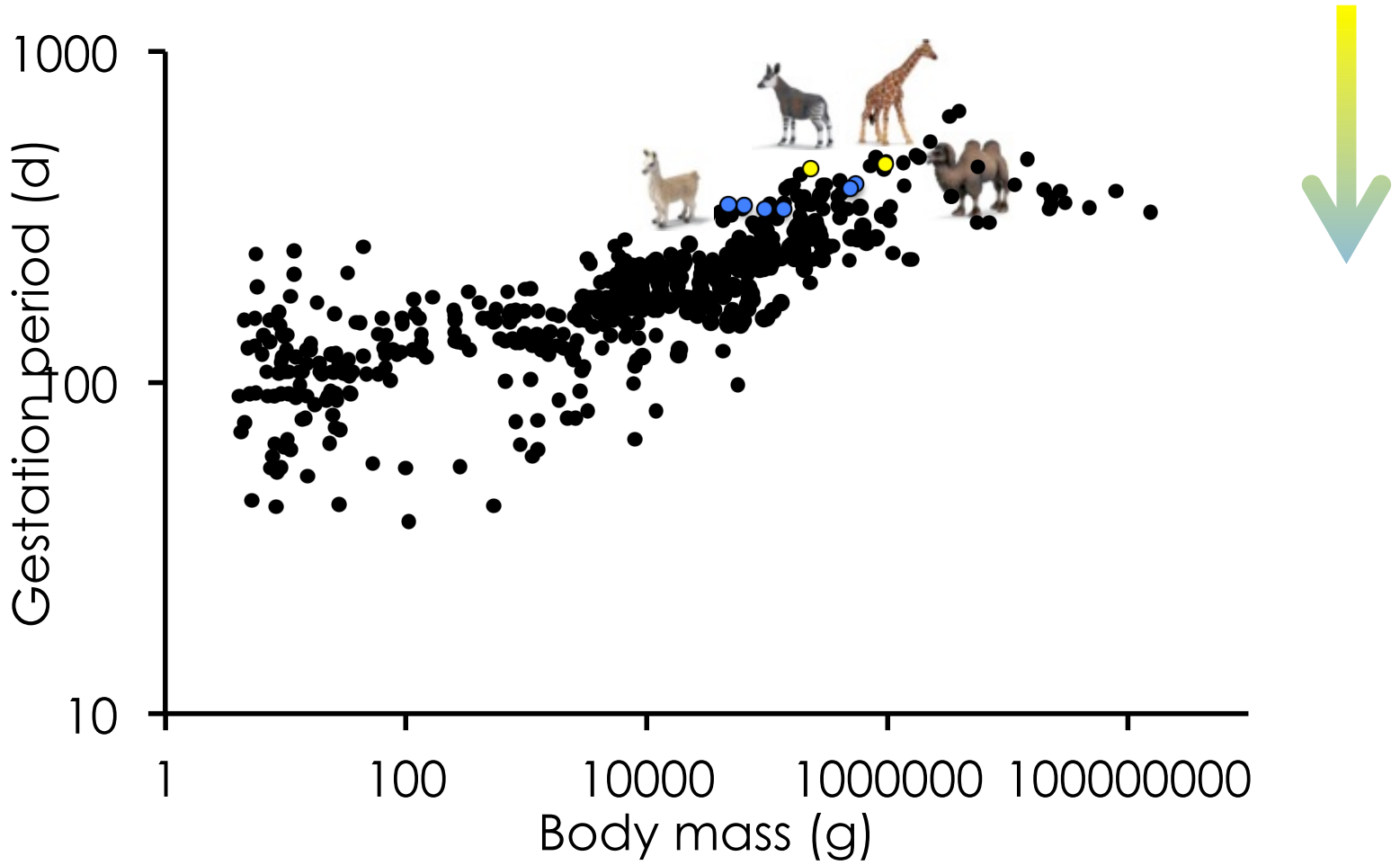
from Clauss et al. (2013)

Example II: (Precocial) Mammal gestation period



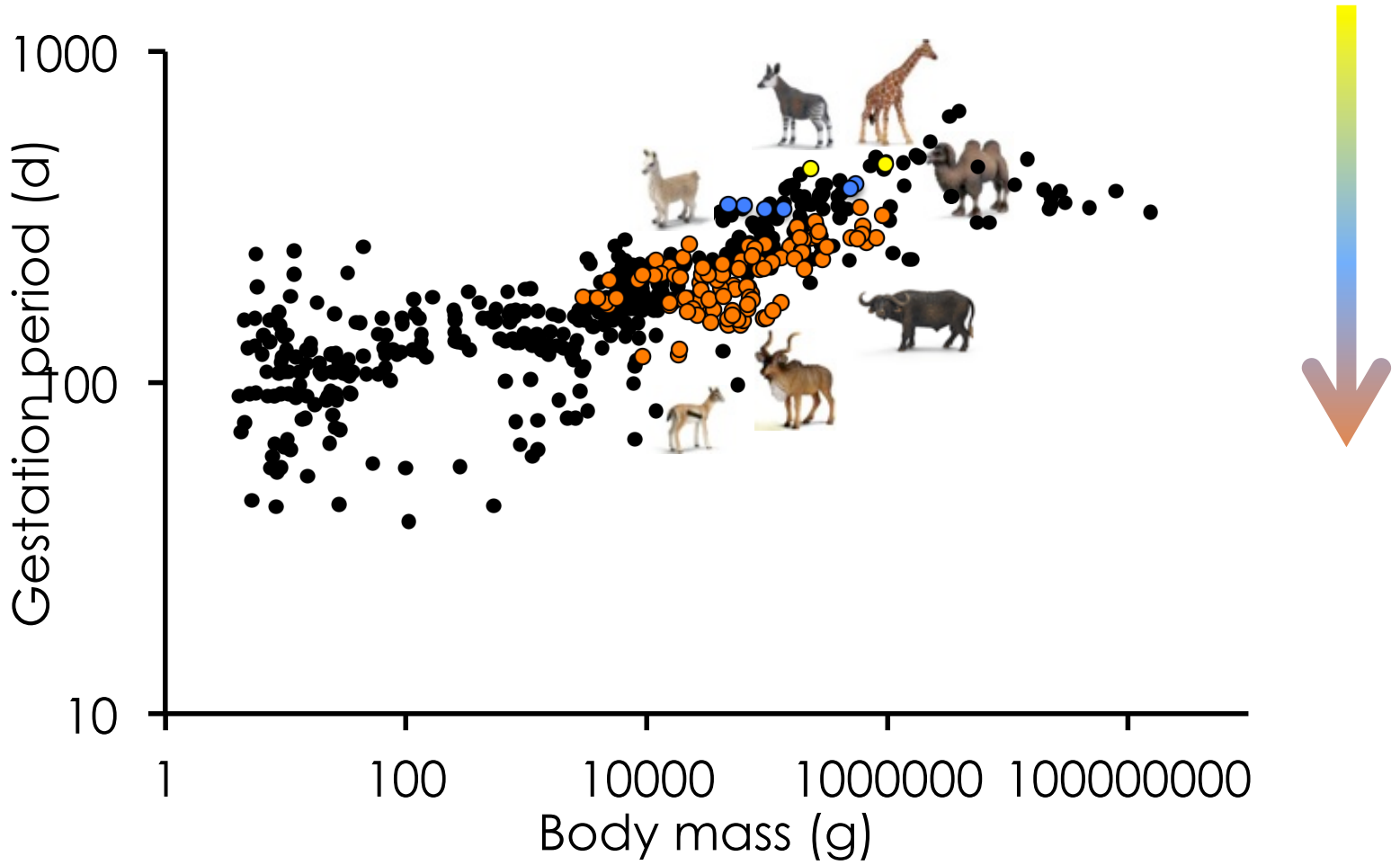
from Clauss et al. (2013)

Example II: (Precocial) Mammal gestation period



from Clauss et al. (2013)

Example II: (Precocial) Mammal gestation period



from Clauss et al. (2013)

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.

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' (for which then physiological mechanisms would have to be identified that could be innovations, constraints, and parts of evolutionary cascades).