- Paper I'm bringing up: Brain size in vertebrates, 1981, by Robert Martin, who was then at University College London.
- Became an important paper in allometry, the field of biological proportions
- The question Martin was interested in was:

What sets the brain size of a species?

He goes about this by looking at data across species and calling on a history of scaling in biology:

Scaling laws

$$Y = kX^{\boxed{a}}$$

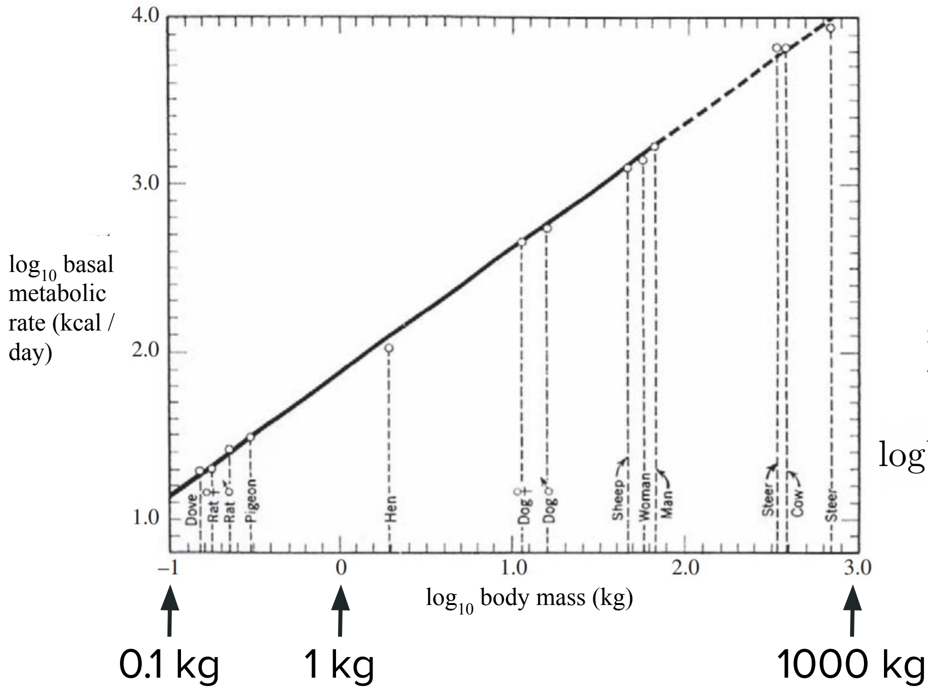
$$\log Y = \boxed{a} \cdot \log X + \log k$$

Metabolic rate | 3/4 | mass

Martin thinks about this in this scaling law kind of way.

Equivalently, we can think of it in the log-log form as a line.

The most common of these relationships was Kleiber's (Kly-burr) law, which related an animal's baseline metabolic rate with its mass, with a scaling exponent of 3/4.



metabolism vs body-mass, **3/4** scaling (Kleiber, 1932)

$$\log Y = \frac{3}{4}\log X + \log k$$

What we're looking at here

- log-body mass on the x axis
- log-basal metabolic rate, ie resting metabolic rate
- each point is an animal from Kleiber's analysis
- These axes are a bit confusing, so just for clarity, that 0 on the body mass scale = 1 kg, because we're in log units, -1 is 0.1kg, and 3 is 1000kg

Kleiber (Kly-burr) found this surprisingly good 3/4-fit slope on this log-log plot. Although this plot shows limited data, the correlation has been replicated with larger datasets. The 3/4 slope has been replicated in cold-blooded animals and protists.

The mechanistic explanation for Kleiber's 3/4 scaling is still debated, although a popular theory from 1997 relates it to branching networks in circulatory systems.

Okay, **back to the question of brains.**

- why focus on slope? ie what does the intercept actually represent?

Extra notes:

- "Explanations for 2⁄3-scaling tend to assume that metabolic rates scale to avoid heat exhaustion. Because bodies lose heat passively via their surface, but produce heat metabolically throughout their mass, the metabolic rate must

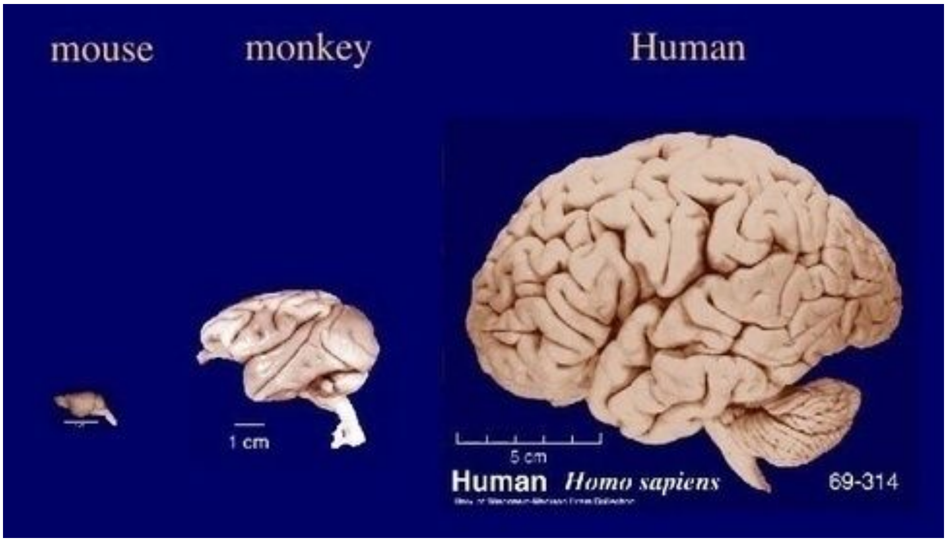
- scale in such a way as to counteract the square–cube law. The precise exponent to do so is 2⁄3"
- BMR = basal here. "metabolic rate without moving"
- 3/4 exponent: circulatory branching system (nutrient flow), blood volume. proposed by West Enquist Brown 1997

Suggested that it is

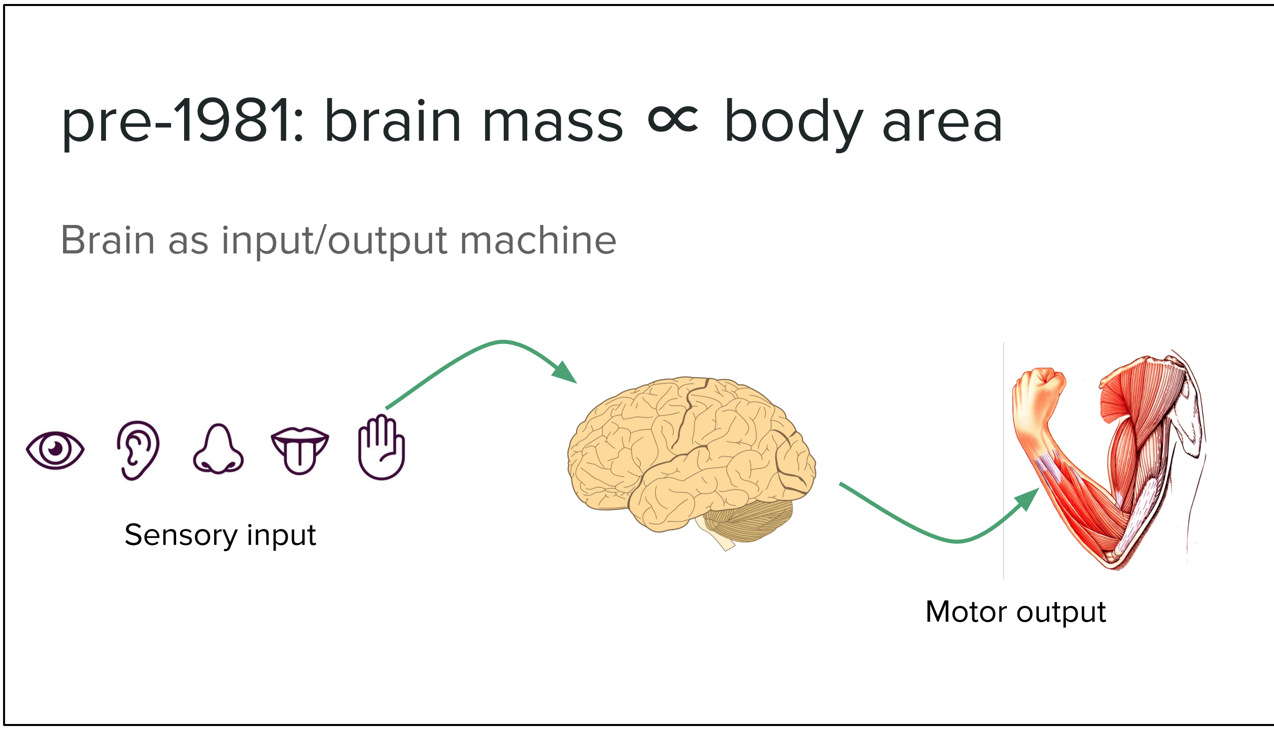
- Hints at physical limits / principles.
  - A straw-man / reasonable argument = energy / mass?
  - power = mass

y-axis = calories

Does the brain scale? With what exponent?



We're interested in whether brains scale, and with what exponent:



Before this paper came out in 1981, a popular argument was that brain mass scaled with body area, supported by a limited study of 40 animals.

The suggested mechanism went something like this: the brain is an input/output machine. It takes sensory input, and converts it into motor output.

Because sensors and effectors are often distributed over surfaces, more body area => more sensors / effectors, and thus you need more brain mass to do that computation from input to output.

5. Jerison, H. J. Evolution of the Brain and Intelligence (Academic, New York, 1973).
6. Bauchot, R. Brain Behav. EooL 15, 1-18 (1978).

pre-1981: brain mass ∝ body area → 2/3

$$A_{body} \propto L_{body}^{2}$$

$$M_{body} \propto V_{body} \propto L_{body}^{3}$$

$$M_{brain} \propto A_{body} \propto M_{body}^{\boxed{\frac{2}{3}}}$$

body area is a bit difficult, so researchers measured mass and made further approximations:

Take, for example, a spherical cow:

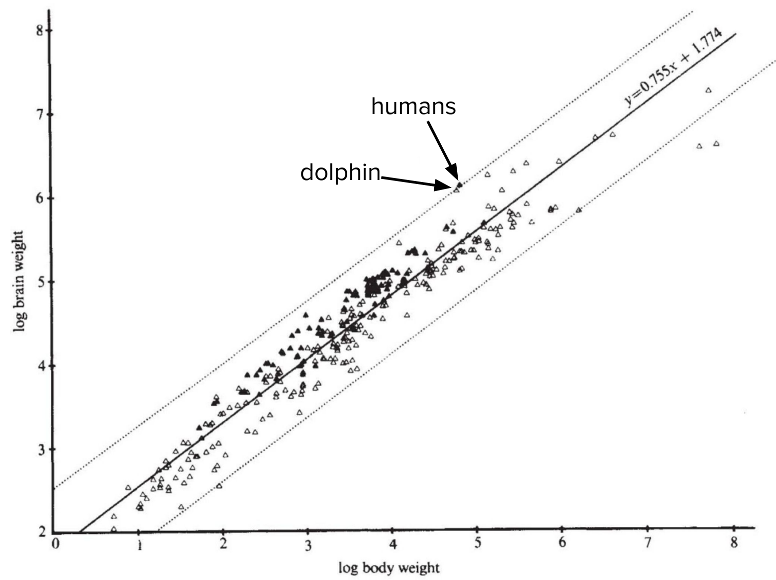
- Area roughly proportional to length-squared
- Mass is proportional to volume, proportional to length-cubed
- So if you assume that brain mass proportional to body area
- Assuming that the mass of the brain is proportional to body area, you get that mass_brain proportional to this 2/3 exponent mass

Although there are many leaps in this argument, this was seem as plausible at the time. Or at the very least, the empirical 2/3 relationship.

In the paper I picked for this week, the authors take issue that the previous studies used only 40 animals, so he bumps up the data to 300 species:

Analysis: 40 ➔ 300 mammals (Martin, 1981)

In the paper I picked for this week, the authors take issue that the previous studies used only 40 animals, so he bumps up the data to 300 species:



$$\underset{(\mathrm{mg})}{\log_{10} E_M} = 0.76 \underset{(\mathrm{g})}{\log_{10} P} + 1.77$$

2/3 $\notin$ [0.73, 0.78] (95% CI)

Brain size vs body size: (placental) mammals, 0.76-scaling

And the author finds a scaling exponent of 0.76.

This figure plots the brain weight and body weight of 300 extant mammals on a log-log scale. Each triangle is a different species, with shaded triangles indicating primates. Dotted lines are 5x variation above / below.

- Again, Martin finds a different relationship slope: about **0.76.**
- Importantly, the authors state, the 95% confidence interval is [0.73, 0.78], and this precludes the previously proposed 2/3-scaling factor. Formally disproving the brain-size-body-area hypothesis.

When I first saw this graph, I immediately had 2 thoughts:

1. This is a pretty good fit over 6 orders of magnitude.
2. I wonder what the outliers are:
    a. Up here are humans, so good, we can pat ourselves on the back for having big brains
    b. Next to us is not another primate, but rather a dolphin.

This hints at some interesting questions on variations within this trend. Do social animals like humans and dolphins have bigger brains? What effect do gestational period, social structure, or ecology have on brain size?

But I think it's more interesting to think about this large-scale trend. And that's what the author also focuses in on. When we see a pattern like this in nature, we should ask a few questions:

Notes on figures:

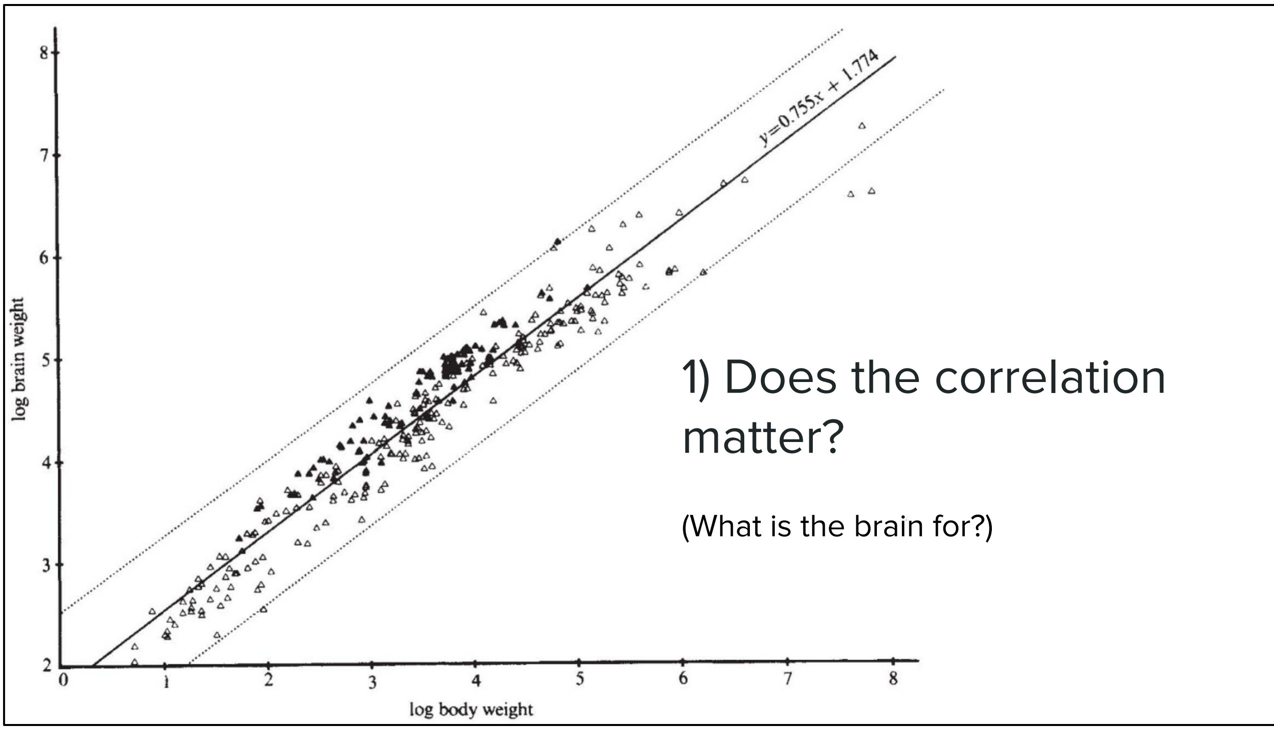
- shaded in = primates
- not shaded in = others
- Dashed lines

Questions

1. Does the correlation matter?
2. What would explain the correlation?
3. Does the pattern generalize to other groups?

There are 2 questions

1. When you find a pattern out in nature, you have to ask yourself: does this pattern matter?
2. What would explain the pattern? Finally,
3. Does the pattern generalize to other groups?



First question: does the observed correlation matter?

Caveats:

- Not a causal explanation
- data availability bias, focused on big-brain species
    - Further studies affirm slope value
- but: within-taxon fitting?
- Not 100% explanation
- Does brain size matter?
    - implicitly: what is the brain for
    - Seems like a funny question to ask a bunch of people who have been in school for 17+ years

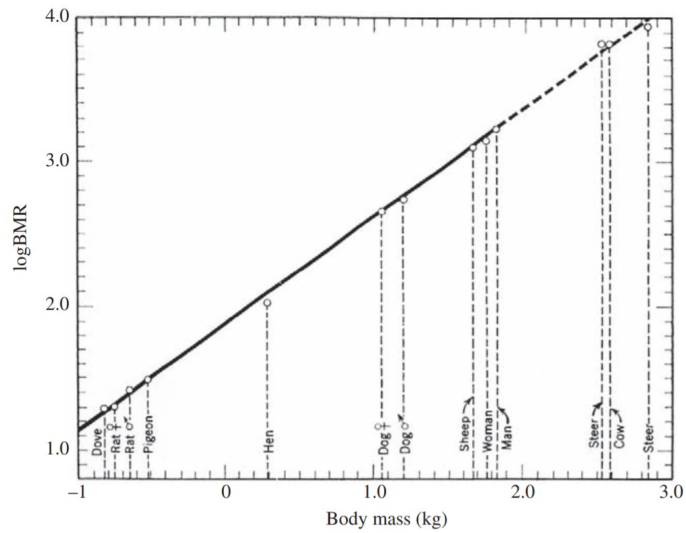
Pros:

- We're interested in principles that are true across biology, in part why we focus so much on the building blocks in this seminar: DNA, RNA, and proteins
- this kind of relationship is the effect of long-term evolution and can hint at biological principles that are worth investigating.
- that it holds across many orders of magnitude does seem relevant.
- challenges the popular the body area hypothesis (as Dave mentioned)

Extra notes:

- energy consumption scales linearly with # neurons: highly correlated with brain mass
- **Recent 2018 study extends to 1500 species:**
- **Coefficient values confirmed by recent 2018 study.**
- **Lack of brain size data for 70% of species:**
- strong bias in representation from Primates, Carnivores

2) What could explain the ~0.76 scaling exponent?



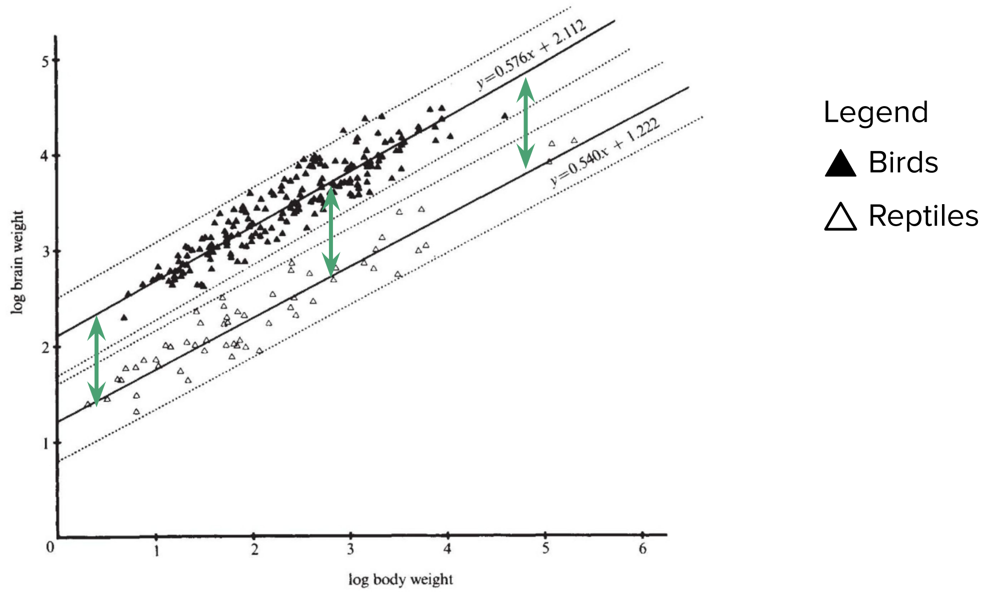
(Kleiber, 1932) 3/4-scaling metabolic rate

Second question: 0.76 scaling exponent

So it's not body area. There could be many complex explanations for 0.76, but I'll focus on what the author proposes: the author notes that it calls to mind metabolic rate: 3/4 scaling.

Seems reasonable: brains consume a large of energy, we might expect it to be related:

Extra notes:
Hypotheses to explain
brain–body evolutionary allometric exponents fall into two broad categories: those based on physiological scaling and those based on developmental constraints



3) 0.76-scaling does not generalize to Birds and Reptiles. Slope ≅ **0.56**

But when you look at birds and reptiles, they have a much shallower scaling exponent, around 0.56

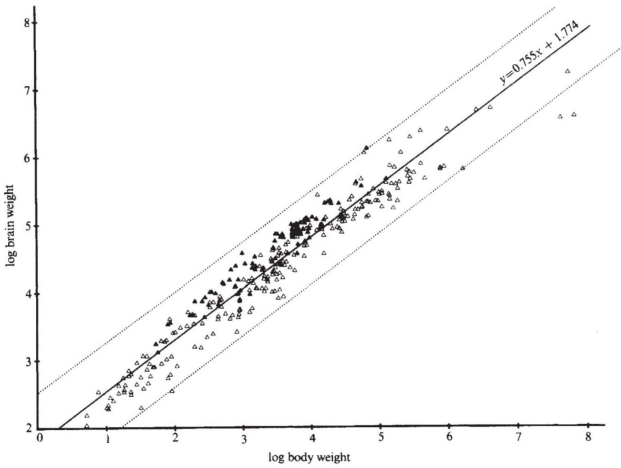
Figure description:

- log-body weight on x-axis, log-brain weight on y-axis
- birds = shaded triangles
- reptiles = hollow triangles

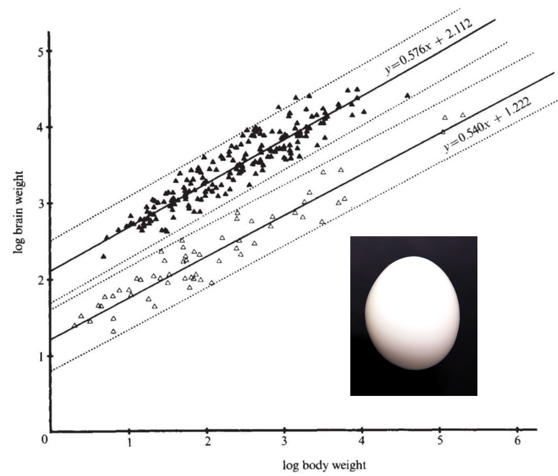
Offset:

- We focus on shared scaling exponent, instead of this offset. This seems common practice, although I couldn't find a good explanation.
- possible approach is: structure of brain different, but metabolic scaling constraints still hold.

Brain size relationship: not **self** metabolic rate



Mammals

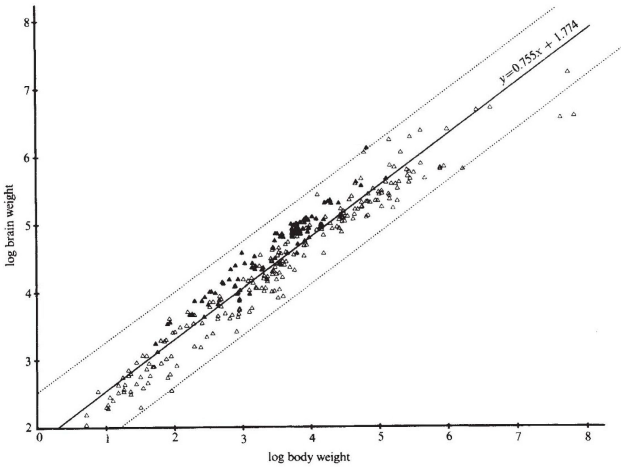


Birds and reptiles

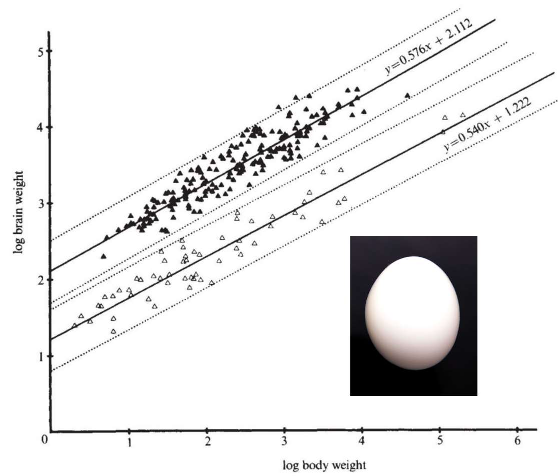
ie, so it's not adult brain size and their own BMR.
A key difference: egg-laying.

Perhaps, instead has to do with **maternal** metabolic rate

Brain size relationship: **maternal** metabolic rate



Mammals



Birds and reptiles

ie, so it's not adult brain size and their own BMR.
A key difference: egg-laying.

Perhaps, instead has to do with **maternal** metabolic rate

What explain the ~0.56 bird/reptile exponent?

$$M_M = k_1 P^{\frac{3}{4}}$$

$$W = k_5 M_M = k_5 k_1 P^{\frac{3}{4}}$$

$$M_E = k_6 W^{\frac{3}{4}}$$

$$E_H = k_7 M_E$$

$$E_A = k_8 E_H$$

$$E_A = k_9 (P^{\frac{3}{4}})^{\frac{3}{4}} \approx k_9 P^{0.56}$$

$$\begin{aligned} P &= \text{maternal mass} \\ M_M &= \text{maternal metabolic rate} \\ W &= \text{egg weight} \\ M_E &= \text{egg's metabolic rate} \\ E_H &= \text{hatchling brain weight} \\ E_A &= \text{adult brain weight} \end{aligned}$$

There are a lot of assumptions being made here, I'm going to gloss over some of them, although the authors provide some very preliminary data to support these equations.

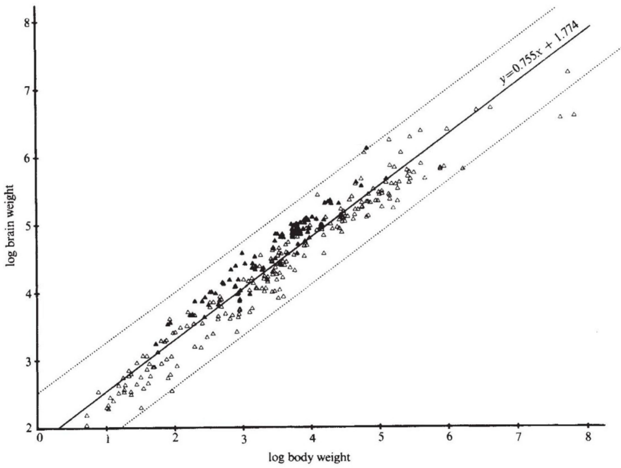
The high-level idea is that there are 2 steps of mass -> metabolic output.

1. Mother -> egg
2. Egg -> hatchling

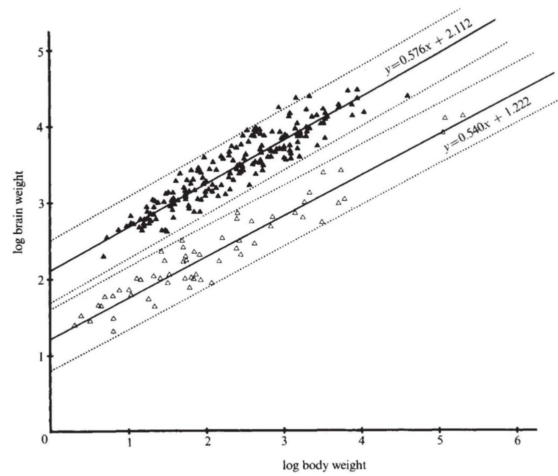
Equations:

- maternal metabolic rate -> species adult mass, 3/4 comes from Kleiber's 3/4 scaling
- egg weight -> maternal metabolic rate
- egg metabolic rate -> mass, Kleiber's scaling
- hatchling brain -> egg metabolic rate
- adult brain -> hatchling brain
- Put it all together: 0.56 exponent

Brain size ∝ **maternal** metabolic rate (-squared)



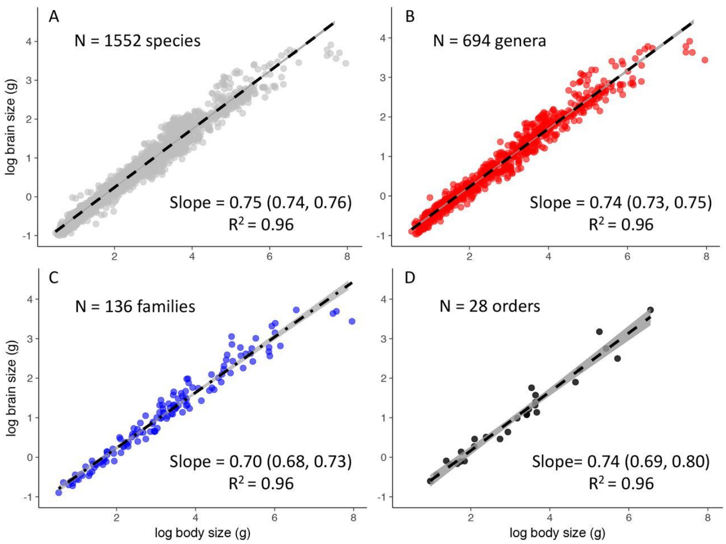
Mammals



Birds and reptiles

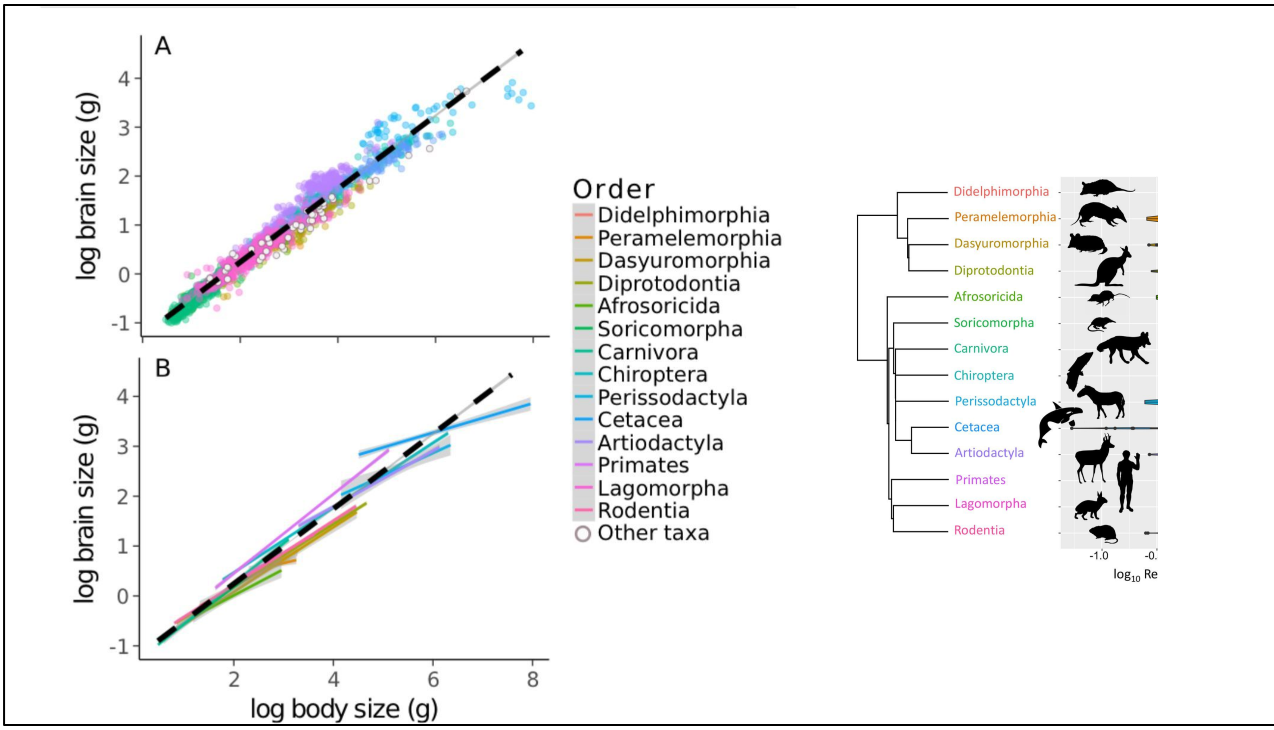
The authors take this as evidence that maternal metabolic is still the explanatory factor in these 2 cases:

Updated mammal data (Burger et al., 2019)



Mentioned earlier: additional data supports the 0.75 slope

- Includes split by species, genera, families, orders
- Seems that this may be a long-term evolutionary constraint, bc within-taxa, we find smaller slopes



Top is similar similar plot to before, color-coded by class order: (shown on right)

- Bottom plot shows shallower slopes within most taxa, even though their medians lie on this 0.75 slope major axis.

Extra notes:

- Explanation by authors for : "evolutionary histories impose limits to how quickly traits can evolve resulting in non-independence among closely related species (Felsenstein 1985)."
- Perhaps this is a constraint only at higher taxa levels, although not 100% clear to me.

Summary

- Power scaling between brain mass and body mass, across **6** orders of magnitude
  - Mammals: ~0.75
  - Reptiles / birds: ~0.56
- Proposed mechanism: constrained by maternal resources channelled to embryo
- <0.75 within-Order slope

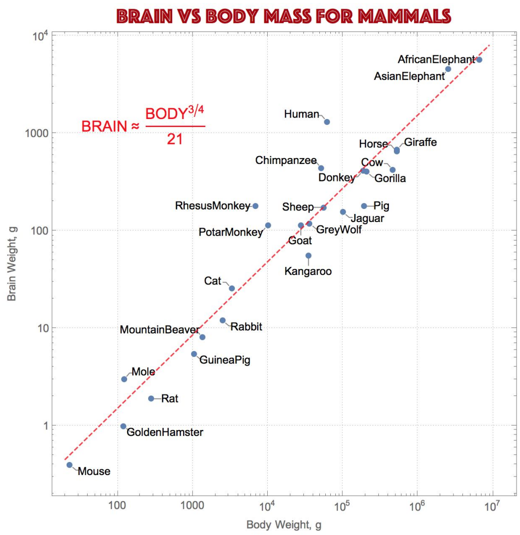
- Some sampling bias still, but an interesting pattern across many orders of magnitude
- Proposed mechanism that is very clean but requires a lot of assumptions.

Thanks!

Appendix: Datasets

- 41 primate species
- 4,587 of amphibians, birds, cartilaginous fishes, mammals, reptiles, and teleost fishes
- UW Brain sizes

Appendix: common mammals plot



https://community.wolfram.com/groups/-/m/t/946991

Appendix: mammalian scaling

$$E_N = k_2\, M_M = k_2 k_1\, P^{\frac{3}{4}} \tag{10}$$

Further, because brain tissue growth is generally restricted to expansion of existing neurones and addition of glial cells following birth, one might expect that adult brain weight (E_A) would be directly proportional to (that is, isometric with) neonatal brain weight

$$E_A = k_3\, E_N \tag{11}$$

Equations (10) and (11) combined yield the overall relationship

$$E_A = k_4\, P^{\frac{3}{4}} \tag{12}$$

ie BMR in the mother (end of page 2).
Not much neonatal data, so Martin uses a proxy

Appendix: notes on dinosaurs

- Theropods seemed to have a brain size in between the expected ranges for birds and reptiles. (Larsson, Sereno, and Wilson, 2000)
- Some difficulty in analyzing brain-body relationships because we lack live species, and dinosaur sizes were highly variable even within species.

Martin 1981: Most dinosaurs fall within the expected reptile ranges: Archaeopteryx, Allosaurus, Stenonychosaurus potentially more bird-like