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Reply to: Comparisons of static brain–body allometries across vertebrates must distinguish between indeterminate and determinate growth

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REPLYING TO T. Froese & R. Froese *Nature Ecology & Evolution* https://doi.org/10.1038/s41559-019-0984-1 (2019).

In the accompanying piece, Froese and Froese[1] challenge our hypothesis[2] that the reduction of allometric constraints in birds and mammals may have allowed their dramatic encephalization. Here we contest their claims.

Froese and Froese[1] make a valid point that there are several reasons to doubt that static allometries may not be comparable across lineages exhibiting determinate and indeterminate growth. One aspect of this issue was validated in our paper by demonstrating that

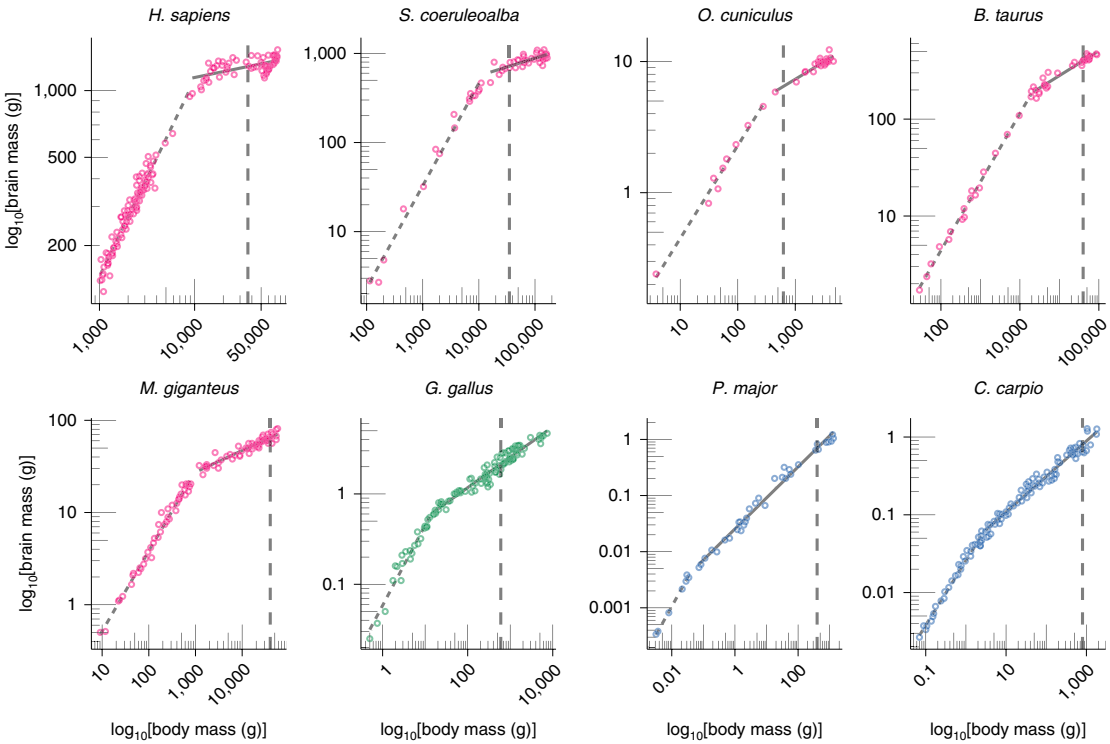

Fig. 1 | Ontogenetic brain–body allometry in eight species of vertebrates and their adult body mass. Brain and body mass growth in humans (*Homo sapiens*, the minimum adult body mass: 36.3 kg), striped dolphins (*Stenella coeruleoalba*, 35 kg), European rabbits (*Oryctolagus cuniculus*, 622 g), cows (*Bos taurus*, 400 kg), eastern grey kangaroos (*Macropus giganteus*, 40 kg), chickens (*Gallus gallus*, 600 g), red seabream (*Pagrus major*, 400 g) and common carp (*Cyprinus carpio*, 800 g) are shown. The colours designate the class: magenta, mammals; green, birds; blue, fishes. The unbroken lines and broken lines show the ontogenetic allometry during the slow- and rapid-growth phases, respectively. The dashed vertical lines indicate adult body mass.

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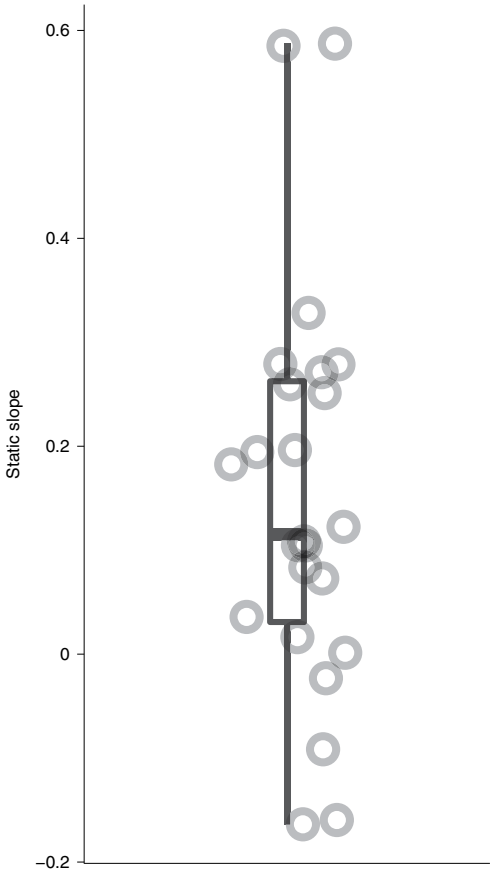

Fig. 2 | The static allometric slope of 24 species of birds based on tarsus length. The box plot shows the median (black line) of the static allometric slopes in log[brain mass (g)] against log[cube of tarsus length (mm)] with the lower and upper limits representing the 25th and 75th percentiles. The overlaid points show estimates.

the difference in adult body size range between determinate and indeterminate growers is unlikely to explain the observed difference in the static allometric slopes among vertebrate classes. Froese and Froese[1] raise two additional concerns. First, they question whether the static allometric slope of lineages exhibiting determinate growth reflects their underlying growth trajectory. Second, they point out that the static allometric slopes of determinate growers may be downwardly biased due to variation in body condition.

To verify that static allometric slopes of determinate growers capture their ontogenetic trajectory, we plot the ontogenetic allometry in eight species of vertebrates with the typical adult body mass of each species overlaid (Fig. 1). This reveals that the brain–body allometric slopes are unchanged before and after the size at sexual maturity in all species examined here. Hence, the static allometric slope indeed represents underlying ontogenetic processes regardless of whether growth is determinate or indeterminate. Although additional data are necessary for generalization over a wider range of taxa, currently available evidence suggests that the static slopes reflect underlying developmental trajectories similarly for determinate and indeterminate growers.

Concerning the second question of biases caused by body condition, we see no inherent reasons for why this bias should influence species with determinate growth more than species with indeterminate growth, because variation in non-size-related components of body mass, such as fat deposits, should be similar across taxa. Even so, we explored whether the shallow static allometries in birds and mammals may have resulted from the effect of body condition by assessing static allometries in 24 species of birds using tarsus length, a condition-independent proxy for avian body size. This analysis reveals a static brain–body allometric slope of log[brain mass] against log[cube of tarsus length] of 0.15 ± 0.04 (mean ± s.e.m., Fig. 2), which matches our original observation based on body mass (0.14 ± 0.05). Therefore, variation in body condition is unlikely to explain why birds and mammals have substantially shallower static slopes than other lineages.

Evolution requires genetic variation, but the question of whether genetic variation is available for adaptation has often been overlooked[3–7]. The chief novelty of our study is that it shows that the variation in available genetic variation may arise from the variability of ontogenetic processes. This idea is partly contingent on our surprising discovery that the biphasic brain growth seems to be conserved across Gnathostomata. Here, we provide evidence that the arising two issues of concern (the developmental difference between indeterminate and determinate growers; and the bias in the estimation of the static allometric slope due to body condition) are unlikely to downplay our findings. However, our argument is based on a handful of observations owing to the paucity of relevant data. We agree with Froese and Froese[1] that additional ontogenetic allometric data, especially those at the very beginning of life, are crucial to examine our findings further. We hope that our correspondence will encourage future investigation on the causes and consequences of genetic constraints in vertebrate brain size evolution.

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Author contributions

M.T. conceived the idea of the study and wrote the manuscript. All authors provided input to the manuscript.

Competing interests

The authors declare no competing interests.

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