

# Environmental and Biological Determinants of Brain Mass

Kevin, Yunqin Zhang\*

Shanghai Foreign Language School Affiliated to SISU, China

**Abstract:** According to the expensive brain hypothesis, periodic energy level determines the brain mass. However, various environmental and biological factors directly or indirectly relevant to energy intake have not been well studied. Here, we systematically examined how body mass, hibernation, diurnally, substrate use, diet individually and synergistically determine brain mass in a large dataset of more than 1000 species. We found that body mass and hibernation are the major determinants of brain mass in most species. These findings will shed light on future studies of how evolutionary constraints acting on brain size.

## 1 INTRODUCTION

Though the “expensive-tissue trade-off” hypothesis is widely accepted, it lacks empirical evidence to support it. Researchers found that when fat-free body mass is controlled, there is no significant trade-off, or negative correlation, with mass of expensive tissues like digestive tract. However, there is a negative correlation between size of brains and adipose depots (Navarrete, 2011). Thus, a new hypothesis is derived: the unusually large brain size of human is a result of efficient energy usage: stable energy input, as well as a redirection of energy from locomotion to growth and reproduction. Though human brain is unusually large—three times larger than chimpanzee (Bruhn, 1936), relative whole-body energy consumption rates are about equal. According to the “expensive-tissue trade-off” theory, this phenomenon is a result of dietary shift (Aiello, 1995), as we can cope with a smaller digestive tract.

Researchers examined the sizes of visceral organs and their correlations with the brain while controlling body size. In this research, they used fat-free body mass as the best proxy of body size.

The results show that there is no negative correlation between brain size and digestive tract (Pond, 1998). However, adipose depots make up a large proportion of body mass in some mammals, and they have an energetic cost because of the extra work needed for locomotion (Pontzer, 2010). They also function as a physiological buffer against starvation. On the other hand, brains are cognitive buffers (Sol, 2009; van Woerden, 2012), helping us decide the best strategy, allowing quality food and lowering energetic costs of other life functions. They are complementary strategies. Consistently, there is indeed a negative correlation between brain size and fat storage mass.

If an animal can combine both strategies, they do not face an extra cost of every while transporting their mass,

as the correlated survival and metabolic rates are immense. (In this case, further studies are needed to investigate seasonal variation in body mass). Bigger brains are costly, as giving birth becomes very dangerous. The question, therefore, is how the large energy cost is overcome.

Refuting the expensive-tissue hypothesis, empirical evidence shows that a focus of energy on growing and maintaining brain tissue explains the variation in brain size. There is a positive correlation between basal metabolic rate (BMR) and brain (Isler, 2006). Indeed, human BMR/fat-free body mass is appreciably higher than chimpanzees or bonobos. This can be due to two possible pathways. The first one is on energy input and output: improved diet, reduced temporal fluctuations, and food sharing. Using tools and social interactions can all play a role in increased brain size (Wrangham, 2009). A keen acquisitiveness of energy rich resources is also a defining character of human. Another pathway is increased energy allocation to the brain, for example trade-off between locomotion and brain (Isler, 2006), or reproduction and brain—comprising both growth and reproductive effort (Isler, 2006; Cortex, 2001). Bipedal locomotion is more efficient, and humans invest a large amount of energy in offspring. Thus, due to all the changes in our surroundings, human lineage can have an extraordinary brain.

However, this research is not without flaws, the studied animals were captive animals, and does not truly represent primates in natural world.

Researchers compiled a broad data set on brain and body mass for 1104 mammalian species from 25 orders. To exclude sexual dimorphism, they used female values only. Hibernation is defined as hypometabolic state lasting for multiple consecutive days associated with low body temperature. Aquatic taxa were excluded because they cannot hibernate. Considering climate factors, researchers added the mid-latitude of the species ‘geographic distribution as covariate. Other characteristics that might correlate with brain size in mammals are

\* Corresponding author: [highschool\\_research@outlook.com](mailto:highschool_research@outlook.com)

considered and quantified. Using JMP 13.0, and log-transforming brain size and body mass to reduce skewness. In the present study, we systematically investigated the factors that affect brain mass.

## 2 MATERIALS AND METHODS

To study the factors affecting brain mass, we used 25 orders in 1104 mammalian species (only 12 orders were analyzed due to sample size). To reduce errors because of sexual dimorphism, we used female values if possible. Fully aquatic taxa were excluded also because they cannot hibernate.

Hibernation is defined as a hypometabolic state lasting for multiple consecutive days associated with low body temperature, profoundly reduced metabolic rate and cessation of normal foraging behavior (Ruf, 2015). Greater seasonality in temperature selects for larger body size and hibernation (Ashton, 2000; Meiri, 2003; VAN SCHAİK, 2005). The amplitude of seasonality decreases with increasing latitude. It is usually animals in seasonal regions that hibernate (Ruf, 2015). Thus, mid-latitude of geographical distribution was also included. Diet, substrate use, and diurnality contribute to brain mass, thus are also included.

These categorical factors were coded for further use in multiple variable regression tests and sorting. For diet, herbivore or folivore is coded as 1, frugivore/folivore or granivore as 2, frugivore/faunivore or omnivore as 3 and faunivore, piscivore, carnivore or insectivore as 4. For diurnality, with 0 is for nocturnal species while 1 is for diurnal species. For substrate use, each species was classified into five categories: semi-aquatic (1), fossorial or semi-fossorial (2), terrestrial or semi-arboreal (3), arboreal (4) and volant (5).

In statistical analysis, we ln transformed body mass to reduce skewness. Different factors were separately analyzed to study their significance on brain mass. Finally, we used multiple variable regression test to include all factors in the same model.

## 3 RESULTS

### 3.1 Correlation Between Body Mass and Brain Mass

To study whether and how brain mass changes with body mass, and we plotted brain mass with body mass, with log transform applied to normalize the data set. We found that in Afrosoricida, the correlation is statistically significant ( $N = 11$ ,  $R^2 = 0.9097$ ,  $\ln(\text{brain mass}) = 0.5900 * \ln(\text{body mass}) - 2.705$ , slope:  $p < 0.0001$ , F test). In Artiodactyla, the correlation is statistically significant ( $N = 91$ ,  $R^2 = 0.912$ ,  $\ln(\text{brain mass}) = 0.5698 * \ln(\text{body mass}) - 1.173$ , slope:  $p < 0.0001$ , F test). In Carnivora, the correlation is statistically significant ( $N = 183$ ,  $R^2 = 0.9595$ ,  $\ln(\text{brain mass}) = 0.6632 * \ln(\text{body mass}) - 2.059$ , slope:  $p < 0.0001$ , F test). In Chiroptera, the correlation is statistically significant ( $N = 81$ ,  $R^2 = 0.964$ ,  $\ln(\text{brain mass}) = 0.8186 * \ln(\text{body mass}) - 3.123$ , slope:  $p <$

$0.0001$ , F test). In Dasyuromorphia, the correlation is statistically significant ( $N = 44$ ,  $R^2 = 0.9317$ ,  $\ln(\text{brain mass}) = 0.6329 * \ln(\text{body mass}) - 2.769$ , slope:  $p < 0.0001$ , F test). In Didelphimorphia, the correlation is statistically significant ( $N = 13$ ,  $R^2 = 0.9445$ ,  $\ln(\text{brain mass}) = 0.5698 * \ln(\text{body mass}) - 2.242$ , slope:  $p < 0.0001$ , F test). In Diprotodontia, the correlation is statistically significant ( $N = 87$ ,  $R^2 = 0.956$ ,  $\ln(\text{brain mass}) = 0.6511 * \ln(\text{body mass}) - 2.501$ , slope:  $p < 0.0001$ , F test). In Eulipotyphla, the correlation is statistically significant ( $N = 34$ ,  $R^2 = 0.9479$ ,  $\ln(\text{brain mass}) = 0.6217 * \ln(\text{body mass}) - 2.814$ , slope:  $p < 0.0001$ , F test). In Lagomorpha, the correlation is statistically significant ( $N = 30$ ,  $R^2 = 0.937$ ,  $\ln(\text{brain mass}) = 0.6037 * \ln(\text{body mass}) - 2.282$ , slope:  $p < 0.0001$ , F test). In Peramelemorphia, the correlation is statistically insignificant ( $N = 11$ ,  $R^2 = 0.1783$ ,  $\ln(\text{brain mass}) = 0.1316 * \ln(\text{body mass}) + 0.5591$ , slope:  $p = 0.1957$ , F test). In Primates, the correlation is statistically significant ( $N = 205$ ,  $R^2 = 0.9354$ ,  $\ln(\text{brain mass}) = 0.7944 * \ln(\text{body mass}) - 2.603$ , slope:  $p < 0.0001$ , F test). In Rodentia, the correlation is statistically significant ( $N = 287$ ,  $R^2 = 0.936$ ,  $\ln(\text{brain mass}) = 0.6498 * \ln(\text{body mass}) - 2.510$ , slope:  $p < 0.0001$ , F test) (Figure 1).

To sum up, out of 12 data sets, in Afrosoricida, Artiodactyla, Carnivora, Chiroptera, Dasyuromorphia, Didelphimorphia, Diprotodontia, Eulipotyphla, Lagomorpha, Primates, Rodentia  $\ln(\text{body mass})$  and  $\ln(\text{brain mass})$  are statistically significantly correlated, while in Peramelemorphia  $\ln(\text{body mass})$  and  $\ln(\text{brain mass})$  is not statistically significantly correlated.

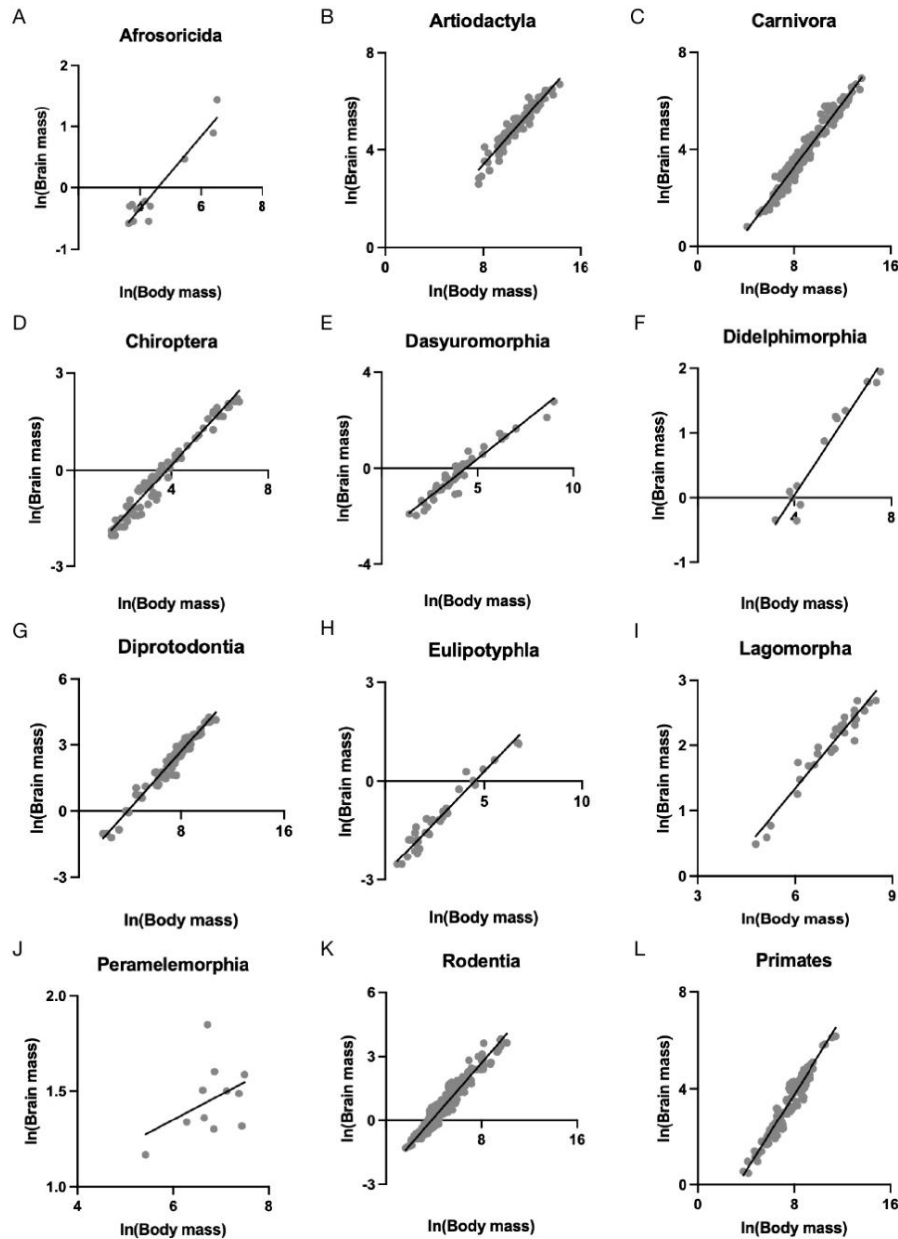
### 3.2 Comparisons Of Brain Mass in Species with and Without Hibernation

To study whether and how brain mass changes with body mass, we compared brain mass in species with and without hibernation, and we used t-test to study whether the difference is significant. We found that in Afrosoricida, the difference in mean between the two groups is statistically insignificant ( $N = 8$ , 3, Hibernation (H) =  $1.141 \text{ g} \pm 1.259 \text{ g}$ , Non-hibernation (NH) =  $1.537 \text{ g} \pm 0.9311 \text{ g}$ ,  $p = 0.7969$ , unpaired t-test). In Carnivora, the difference in mean between the two groups is statistically insignificant ( $N = 176$ , 7, H =  $105.2 \text{ g} \pm 160.0 \text{ g}$ , NH =  $184 \text{ g} \pm 149.5 \text{ g}$ ,  $p = 0.9681$ , unpaired t-test). In Chiroptera, the difference in mean between the two groups is statistically significant ( $N = 58$ , 23, H =  $2.516 \text{ g} \pm 2.623 \text{ g}$ , NH =  $0.283 \text{ g} \pm 0.1477 \text{ g}$ ,  $p < 0.0001$ , unpaired t-test). In Diprotodontia, the difference in mean between the two groups is statistically significant ( $N = 83$ , 4, H =  $18.63 \text{ g} \pm 15.65 \text{ g}$ , NH =  $0.5225 \text{ g} \pm 0.3227 \text{ g}$ ,  $p < 0.0001$ , unpaired t-test). In Eulipotyphla, the difference in mean between the two groups is statistically significant ( $N = 31$ , 3, H =  $0.3606 \text{ g} \pm 0.3538 \text{ g}$ , NH =  $2.737 \text{ g} \pm 0.7260 \text{ g}$ ,  $p = 0.0489$ , unpaired t-test). In Primates, the difference in mean between the two groups is statistically significant ( $N = 200$ , 5, H =  $62.3 \text{ g} \pm 68.46 \text{ g}$ , NH =  $3.726 \text{ g} \pm 2.503 \text{ g}$ ,  $p < 0.0001$ , unpaired t-test). In Rodentia, the difference in mean between the two groups is statistically significant ( $N$

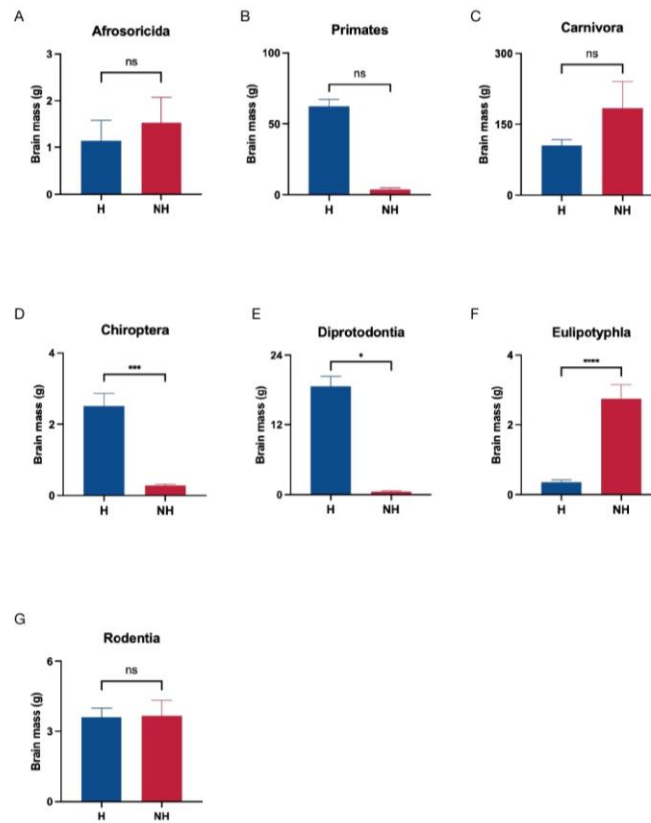
= 253, 33,  $H = 3.6 \text{ g} \pm 6.598$ ,  $NH = 3.665 \text{ g} \pm 3.897 \text{ g}$ ,  $p = 0.0007$ , unpaired t-test) (Figure 2).

To sum up, out of seven data sets, in Chiroptera, Diprotodontia, Eulipotyphla, Primates, Rodentia the

differences between hibernating and non-hibernating species are statistically significant, while in Afrosoricida and Carnivora the differences are statistically insignificant.



**Figure 1.** Correlation between body mass and brain mass. (A) Scatter plot of ln(body mass) with ln(brain mass) in Afrosoricida with best fit line of linear regression (black). (B) Similar as (A), but for Artiodactyla. (C) Similar as (A), but for Carnivora. (D) Similar as (A), but for Chiroptera. (E) Similar as (A), but for Dasyuromorphia. (F) Similar as (A), but for Didelphimorphia. (G) Similar as (A), but for Diprotodontia. (H) Similar as (A), but for Eulipotyphla. (I) Similar as (A), but for Lagomorpha. (J) Similar as (A), but for Peramelemorphia. (K) Similar as (A), but for Primates. (L) Similar as (A), but for Rodentia.



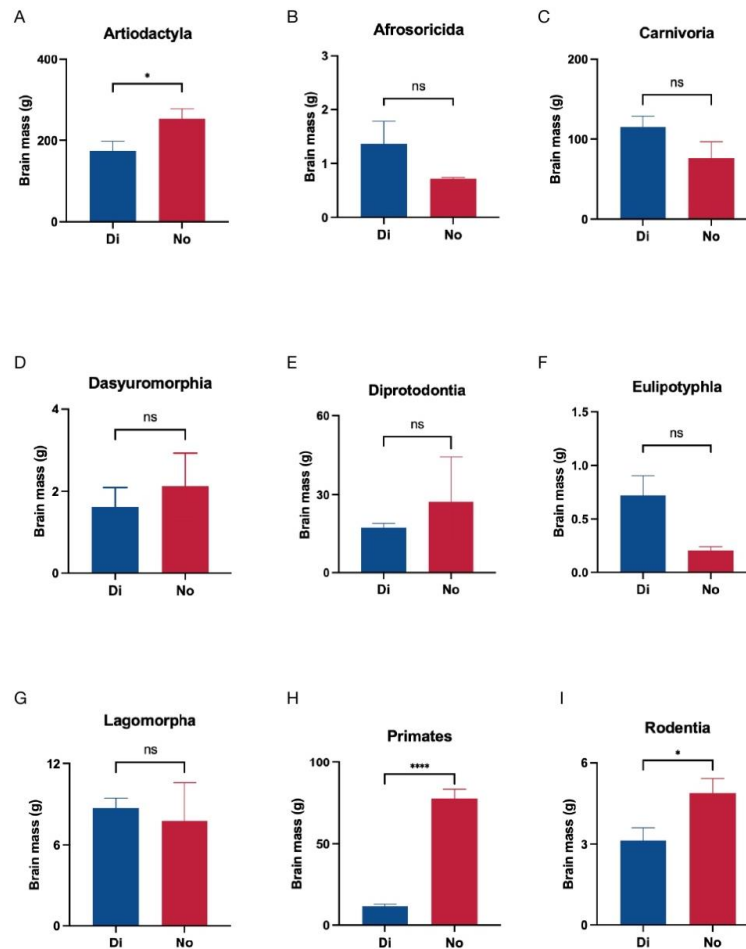
**Figure 2.** Comparisons of brain mass in species with and without hibernation. (A) Bar graph of brain mass in hibernation (H) and non-hibernation (NH) species in Afrosoricida. (B) Similar as (A), but for Carnivora. (C) Similar as (A), but for Chiroptera. (A) Similar as (A), but for Diprotodontia. (B) Similar as (A), but for Eulipotyphla. (C) Similar as (A), but for Primates. (D) Similar as (A), but for Rodentia. Error bar = SEM. \*,  $P < 0.05$ ; \*\*\*,  $P < 0.001$ ; \*\*\*\*,  $P < 0.0001$ ; n.s., not significant.

### 3.3 Comparisons of Brain Mass in Diurnal Versus Nocturnal Species

To study whether and how brain mass changes with diurnality, we compared brain mass in diurnal versus nocturnal species, respectively, and we used t-test to study whether the difference is significant. We found that in Afrosoricida, the difference in mean brain mass between the two groups is statistically insignificant ( $N = 9, 2$ , Diurnal (Di) =  $1.367 \text{ g} \pm 1.249 \text{ g}$ , Nocturnal (No) =  $0.72 \text{ g} \pm 0.02828 \text{ g}$ ,  $p = 0.5003$ , unpaired t-test). In Artiodactyla, the difference in mean brain mass between the two groups is statistically insignificant ( $N = 53, 38$ , Di =  $173.8 \text{ g} \pm 173.6 \text{ g}$ , No =  $253.1 \text{ g} \pm 149.5 \text{ g}$ ,  $p = 0.3426$ , unpaired t-test). In Carnivora, the difference in mean brain mass between the two groups is statistically significant ( $N = 151, 32$ , Di =  $115 \text{ g} \pm 167.5 \text{ g}$ , No =  $76.35 \text{ g} \pm 114.2 \text{ g}$ ,  $p = 0.0143$ , unpaired t-test). In Dasyuromorphia, the difference in mean brain mass between the two groups is statistically insignificant ( $N = 40, 3$ , Di =  $1.609 \text{ g} \pm 2.901 \text{ g}$ , No =  $2.023 \text{ g} \pm 1.116 \text{ g}$ ,  $p = 0.7108$ , unpaired t-test). In

Diprotodontia, the difference in mean brain mass between the two groups is statistically insignificant ( $N = 84, 3$ , Di =  $17.45 \text{ g} \pm 15.24 \text{ g}$ , No =  $27.27 \text{ g} \pm 29.64 \text{ g}$ ,  $p = 0.0537$ , unpaired t-test). In Eulipotyphla, the difference in mean brain mass between the two groups is statistically significant ( $N = 24, 10$ , Di =  $0.7217 \text{ g} \pm 0.8913 \text{ g}$ , No =  $0.207 \text{ g} \pm 0.1104 \text{ g}$ ,  $p < 0.0001$ , unpaired t-test). In Lagomorpha, the difference in mean brain mass between the two groups is statistically insignificant ( $N = 27, 3$ , Di =  $8.724 \text{ g} \pm 3.755 \text{ g}$ , No =  $7.763 \text{ g} \pm 4.885 \text{ g}$ ,  $p = 0.4075$ , unpaired t-test). In Primates, the difference in mean brain mass between the two groups is statistically significant ( $N = 52, 153$ , Di =  $11.74 \text{ g} \pm 8.952 \text{ g}$ , No =  $77.57 \text{ g} \pm 71.51 \text{ g}$ ,  $p < 0.0001$ , unpaired t-test). In Rodentia, the difference in mean brain mass between the two groups is statistically significant ( $N = 209, 77$ , Di =  $3.135 \text{ g} \pm 6.804 \text{ g}$ , No =  $4.888 \text{ g} \pm 4.668 \text{ g}$ ,  $p = 0.0002$ , unpaired t-test) (Figure 3).

To sum up, out of nine data sets, for Carnivora, Eulipotyphla, Primates, Rodentia, brain mass differences in diurnal versus nocturnal species are statistically significant.



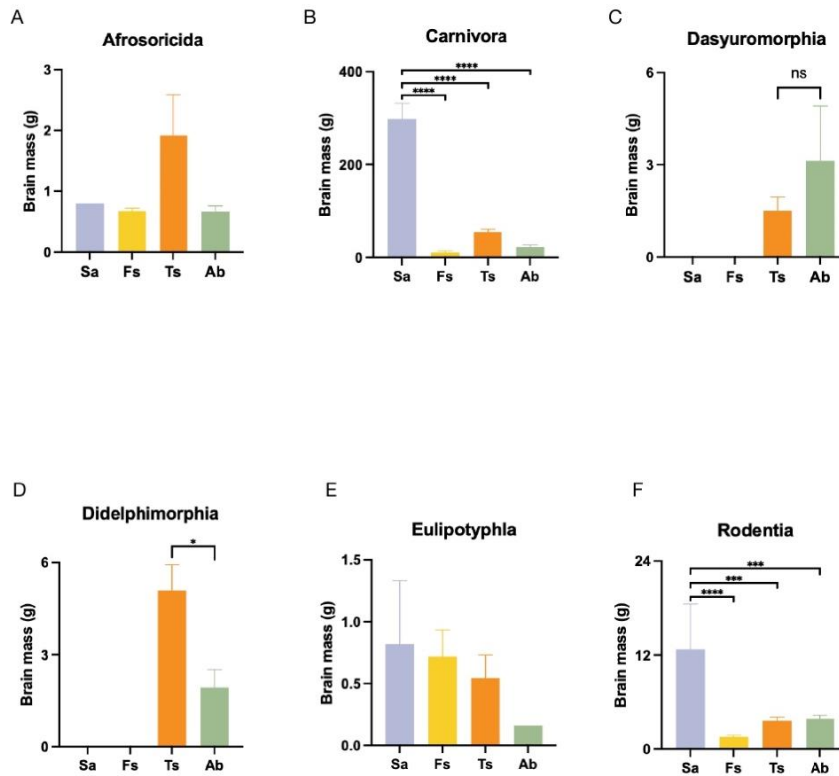
**Figure 3.** Comparisons of brain mass in species with and without hibernation. (A) Bar graph of brain mass in hibernation (H) and non-hibernation (NH) species in Afrosoricida. (B) Similar as (A), but for Carnivora. (C) Similar as (A), but for Chiroptera. (A) Similar as (A), but for Diprotodontia. (B) Similar as (A), but for Eulipotyphla. (C) Similar as (A), but for Primates. (D) Similar as (A), but for Rodentia. Error bar = SEM. \*,  $P < 0.05$ ; \*\*\*,  $P < 0.001$ ; \*\*\*\*,  $P < 0.0001$ ; n.s., not significant.

### 3.4 Comparisons of brain mass in species with different substrate uses

To study whether and how brain mass changes with substrate use, we compared brain mass in species with different substrate uses, and we used ANOVA and post hoc multiple comparison test to study whether the differences are significant; for species with only two kinds of substrate uses, we used t-test to study whether the difference is significant. We found that in Afrosoricida, the differences in mean brain mass between groups are statistically insignificant (ANOVA:  $N = 1, 3, 5, 2$ , Semi-aquatic (Sa) =  $0.8000$ , Fossorial or semi-fossorial (Fs) =  $0.6733 \pm 0.08327$ , Terrestrial or semi-arboreal (Ts) =  $1.916 \pm 1.504$ , Arboreal (Ab) =  $0.6700 \pm 0.1273$ ,  $p = 0.4279$ , F test). In Carnivora, the differences in mean brain mass between groups are statistically significant (ANOVA:  $N = 42, 4, 130, 7$ , Sa =  $297.8 \pm 223.6$ , Fs =  $11.09 \pm 7.009$ , Ts =  $54.59 \pm 69.90$ , Ab =  $22.71 \pm 11.61$ ,  $p < 0.0001$ , F test. Sa vs. Fs,  $p < 0.0001$ , Sa vs. Ts,  $p <$

$0.0001$ , Sa vs. Ab,  $p < 0.0001$  post hoc multiple comparison test). In Dasyuromorphia, the differences in mean brain mass between groups are statistically insignificant ( $N = 39, 4$ , Ts =  $1.509 \pm 2.757$ , Ab =  $3.128 \pm 3.583$ ,  $p = 0.3711$ ). In Didelphimorphia, the differences in mean brain mass between groups are statistically significant ( $N = 4, 9$ , Ts =  $5.083 \pm 1.692$ , Ab =  $1.926 \pm 1.748$ ,  $p = 0.0114$ ). In Eulipotyphla, the differences in mean brain mass between groups are statistically insignificant ( $N = 2, 6, 23, 1$ , Sa =  $0.8200 \pm 0.7212$ , Fs =  $0.7200 \pm 0.5284$ , Ts =  $0.5448 \pm 0.8998$ , Ab =  $0.1600$ ,  $p = 0.8907$ ). In Rodentia, the differences in mean brain mass between groups are statistically significant ( $N = 9, 42, 177, 55$ , Sa =  $12.74 \pm 17.38$ , Fs =  $1.545 \pm 1.308$ , Ts =  $3.589 \pm 6.486$ , Ab =  $3.831 \pm 3.394$ ,  $p < 0.0001$ , ANOVA; Sa vs. Fs,  $p < 0.0001$ , Sa vs. Ts,  $p < 0.0001$ , Sa vs. Ab,  $p < 0.0001$ , post hoc multiple comparison test) (Figure 4).

To sum up, out of six data sets, the brain mass difference between different substrate uses in Carnivora, Didelphimorphia, Rodentia are statistically significant, while 3 are statistically insignificant.



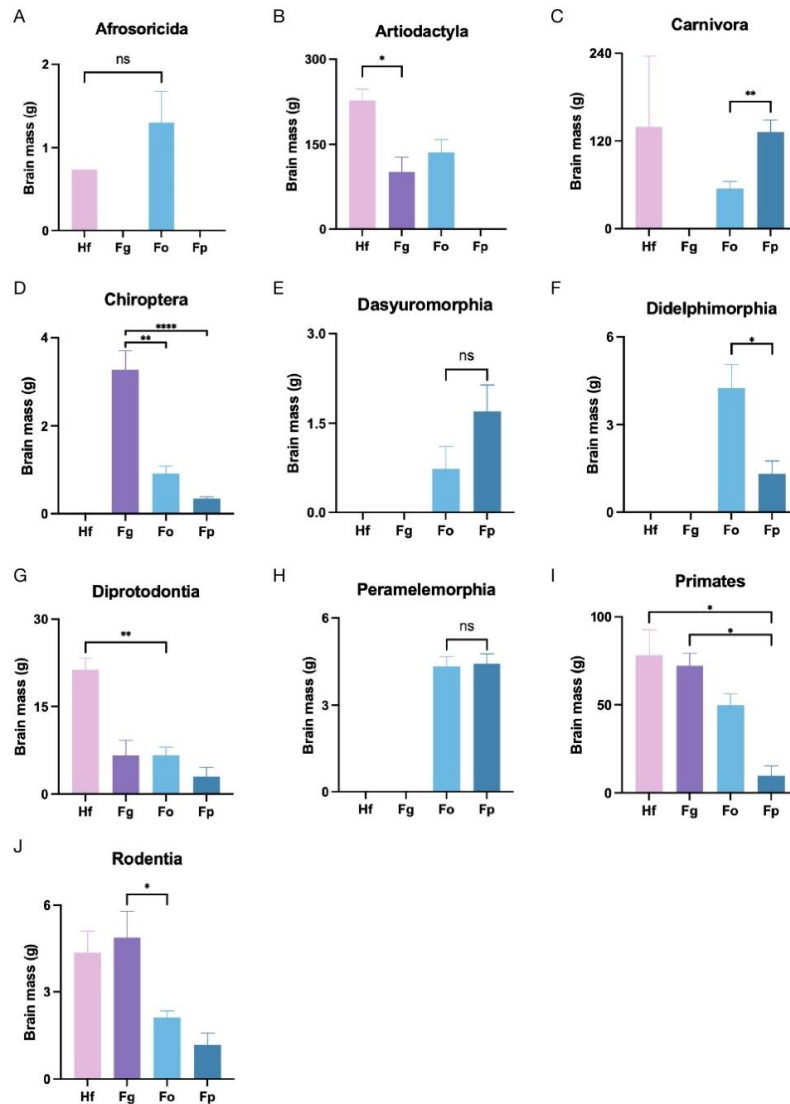
**Figure 4.** Comparisons of brain mass in species with different substrate uses. (A) Bar graph of brain mass in Semi-aquatic (Sa), Fossorial or semi-fossorial (Fs), Terrestrial or semi-arboreal (Ts), Arboreal (Ab) species in Afrosoricida. (B) Similar as (A), but for Carnivora. (C) Similar as (A), but for Dasyuromorphia. (D) Similar as (A), but for Didelphimorphia (E) Similar as (A), but for Eulipotyphla. (F) Similar as (A), but for Rodentia. Error bar = SEM. \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ ; \*\*\*\*,  $P < 0.0001$ ; n.s., not significant.

### 3.5 Comparisons of brain mass in species with different diets

To study whether and how brain mass changes with different diets, we compared brain mass in species with different diets, and we used ANOVA and post hoc multiple comparison test to study whether the differences are significant; for species with only two kinds of diets, we used t-test to study whether the difference is significant. We found that in Afrosoricida, the differences are statistically insignificant ( $N = 1,10$ , Herbivore or folivore (Hf) =  $0.7400$ , Frugivore/faunivore or omnivore (Fo) =  $1.300 \pm 1.197$ ,  $p = 0.666$ , F test). In Artiodactyla, the differences are statistically significant ( $N = 75, 12, 4$ , Hf =  $227.5 \pm 174.5$ , Frugivore/folivore or granivore (Fg) =  $101.9 \pm 88.31$ , Fo =  $135.6 \pm 46.70$ ,  $p = 0.0359$ ; Hf vs. Fg,  $p = 0.0403$ , post hoc multiple comparison test). In Carnivora, the differences are statistically significant ( $N = 2, 57, 124$ , Hf =  $139.3 \pm 136.8$ , Fo =  $54.61 \pm 74.42$ , Faunivore, piscivore, carnivore or insectivore (Fp) =  $132.4 \pm 182.3$ ,  $p = 0.0088$ , ANOVA; Fo vs. Fp,  $p = 0.0063$ , post hoc multiple comparison test). In Chiroptera, the differences are statistically significant ( $N = 41, 8, 32$ , Fg =  $3.271 \pm 2.780$ , Fo =  $0.9200 \pm 0.4614$ , Fp =  $0.3428 \pm 0.2428$ ,  $p < 0.0001$ , ANOVA; Fg vs Fo,  $p = 0.0089$ , Fg

vs. Fp,  $p < 0.0001$ , post hoc multiple comparison test). In Dasyuromorphia, the differences are statistically insignificant ( $N = 2, 42$ , Fo =  $0.7350 \pm 0.5303$ , Fp =  $1.700 \pm 2.858$ ,  $p = 0.6393$ , unpaired t-test). In Didelphimorphia, the differences are statistically significant ( $N = 7, 6$ , Fo =  $4.250 \pm 2.123$ , Fp =  $1.318 \pm 1.080$ ,  $p = 0.0111$ , unpaired t-test). In Diprotodontia, the differences are statistically significant ( $N = 67, 5, 13, 3$ , Hf =  $21.29 \pm 16.20$ , Fg =  $6.610 \pm 5.205$ , Fo =  $6.630 \pm 5.061$ , Fp =  $2.993 \pm 2.768$ ,  $p = 0.0015$ , ANOVA; H vs. O,  $p = 0.0074$ , post hoc multiple comparison test). In Peramelemorphia, the differences are statistically insignificant ( $N = 8, 3$ , Fo =  $4.326 \pm 0.9693$ , Fp =  $4.423 \pm 0.5788$ ,  $p = 0.8766$ ). In Primates, the differences are statistically significant ( $N = 42, 66, 87, 10$ , Hf =  $78.18 \pm 94.12$ , Fg =  $72.13 \pm 58.32$ , Fo =  $49.84 \pm 59.55$ , Fp =  $9.889 \pm 17.46$ ,  $p = 0.0056$ , ANOVA; Hf vs. Fp,  $p = 0.0206$ , Fg vs. Fp,  $p = 0.0324$ , post hoc multiple comparison test). In Rodentia, the differences are statistically significant ( $N = 92, 83, 102, 9$ , Hf =  $4.353 \pm 7.301$ , Fg =  $4.889 \pm 8.245$ , Fo =  $2.107 \pm 2.333$ , Fp =  $1.173 \pm 1.218$ ,  $p = 0.0079$ , ANOVA; Fg vs. Fo,  $p = 0.0079$ , post hoc multiple comparison test) (Figure 5).

To sum up, out of ten data sets, brain mass differences between different diets are significant in Artiodactyla, Carnivora and Chiroptera.



**Figure 5.** Comparisons of brain mass in species with different diets. (A) Bar graph of brain mass in Herbivore or folivore (Hf), Frugivore/faunivore or omnivore (Fo), Frugivore/folivore or granivore (Fg), Faunivore, piscivore, carnivore or insectivore (Fp) species in Afrosoricida. (B) Similar as (A), but for Artiodactyla. (C) Similar as (A), but for Carnivora. (D) Similar as (A), but for Chiroptera. (E) Similar as (A), but for Dasyuromorphia. (F) Similar as (A), but for Didelphimorphia. (G) Similar as (A), but for Diprotodontia. (H) Similar as (A), but for Peramelemorphia. (I) Similar as (A), but for Primates. (J) Similar as (A), but for Rodentia. Error bar = SEM. \*,  $P < 0.05$ ; \*\*,  $P < 0.001$ ; \*\*\*,  $P < 0.0001$ ; \*\*\*\*,  $P < 0.0001$ ; n.s., not significant.

### 3.6 Comparisons of brain mass in species with different diets

To study whether and how brain mass changes with body mass, geographic distribution, diurnally, substrate use and diet, and we plotted brain mass with body mass, with log transform applied to body mass and brain mass to normalize the data set. We found that in Afrosoricida, the regression is statistically significant ( $N = 11$ ,  $R^2 = 0.9872$ , F test; coefficient of  $\ln(\text{body mass})$ :  $p = 0.0161$ , F test). In Artiodactyla, the regression is statistically significant ( $N = 91$ ,  $R^2 = 0.9200$ , F test; coefficient of  $\ln(\text{body mass})$ :  $P < 0.0001$ , coefficient of mid-latitude of geographical distribution,  $p = 0.0323$ , F test). In Carnivora, the regression is statistically significant ( $N = 183$ ,  $R^2 = 0.9635$ , F test; coefficient of  $\ln(\text{body mass})$ :  $< 0.0001$ , coefficient of substrate use:  $p = 0.0368$ ,

coefficient of diet:  $p = 0.0154$ , F test). In Chiroptera, the regression is statistically significant ( $N = 81$ ,  $R^2 = 0.7383$ , F test; coefficient of  $\ln(\text{body mass})$ :  $P < 0.0001$ , coefficient of hibernation:  $P = 0.0059$ , coefficient of diet:  $P = 0.0104$ , F test). In Dasyuromorphia, the regression is statistically significant ( $N = 44$ ,  $R^2 = 0.9401$ , F test; coefficient of  $\ln(\text{body mass})$ :  $P < 0.0001$ , F test). In Didelphimorphia, the regression is statistically significant ( $N = 13$ ,  $R^2 = 0.9576$ , F test; coefficient of  $\ln(\text{body mass})$ :  $P = 0.0004$ , F test). In Diprotodontia, the regression is statistically significant ( $N = 87$ ,  $R^2 = 0.9632$ , F test; coefficient of  $\ln(\text{body mass})$ :  $P < 0.0001$ , coefficient of hibernation:  $P = 0.0268$ , F test). In Eulipotyphla, the regression is statistically significant ( $N = 32$ ,  $R^2 = 0.9585$ , F test; coefficient of  $\ln(\text{body mass})$ :  $P < 0.0001$ , F test). In Lagomorpha, the regression is statistically significant ( $N = 30$ ,  $R^2 = 0.9444$ , F test; coefficient of  $\ln(\text{body mass})$ :  $P < 0.0001$ , F test). In Peramelemorphia, the regression is

statistically insignificant ( $N = 11$ ,  $R^2 = 0.2155$ ,  $P = 0.6125$ ,  $F$  test). In Primates, the regression is statistically significant ( $N = 205$ ,  $R^2 = 0.9609$ ,  $F$  test; coefficient of  $\ln$  (body mass):  $P < 0.0001$ , coefficient of diurnality:  $P < 0.0001$ , coefficient of diet:  $P = 0.0011$ , coefficient of diurnality:  $P < 0.0001$ ,  $F$  test).

To sum up, out of twelve data sets, the regressions of Afrosoricida, Artiodactyla, Carnivora, Chiroptera, Dasyuromorphia, Didelphimorphia, Diprotodontia, Eulipotyphla, Lagomorpha, Primates and Rodentia are statistically significant. For  $\ln$ (body mass), the coefficients of Afrosoricida, Artiodactyla, Carnivora, Chiroptera, Dasyuromorphia, Didelphimorphia, Diprotodontia, Eulipotyphla, Lagomorpha and Primates are significantly non-zero. For diet, the coefficients of Carnivora, Chiroptera and Primates are significantly non-zero. For substrate use, the coefficient of Carnivora is significantly non-zero. For hibernation, the coefficient of Chiroptera is significantly non-zero. For diurnality, the coefficient of Primates is significantly non-zero. For mid-latitude of geographical distribution, the coefficient of Artiodactyla is significantly non-zero.

## 4 DISCUSSION

Hibernation is observed from the arctic to the tropics. Thus, for mammals, they hibernate to overcome seasonal periods of food shortage instead of the temperature. (Lyman, 2013) During hibernation, it is determined that fat, including ketone bodies, is metabolized to sustain the brain energy intake, which is of lower amount and of lower efficiency (Owen, 1967; Zhang, 2013). This result supports the expensive brain framework—hibernation limits the energy intake and thus hibernation animals evolve a lower brain mass. During these periods of starvation, hibernation can be a successful strategy, but on balance it is less efficient. (Knott, 1998; Sokoloff, 1973; Berry, 2001) Therefore, hibernators can only drastically downregulate energy expenditure (Ruf, 2015). In the end, individuals may not be able to supply a large brain. Thus, natural selection would select individuals with smaller brain mass. Big mass is only evolutionarily advantageous when individuals can use their brain continuously for more flexible foraging movements and a broader diet (van Woerden, 2012; Heldstab, 2016; Navarrete, 2011).

The correlation between hibernation and brain mass is also reinforced by evidence within the hibernation species: the longer they hibernate, the smaller their brain mass are (Jiang, 2015). Hibernation affects the memory. A smaller brain might also be the result of inactivity of brain cells and tissue during hibernation, which can be shown by the reduced cognitive ability. In the same species, Hibernating European ground squirrels (*Spermophilus citellus*), hibernating and non-hibernating individuals show significant cognitive difference. Hibernating ones show lower memory abilities and even some behaviors required relearning. The reasons are the neural connectivity and inactivity during hibernation (Millesi, 2001). A reduction in neuronal connectivity was observed in Arctic ground squirrels (*Urocitellus parryi*) (Popov, 1992; Popov, 1992) and Golden-mantled

ground squirrels (*Spermophilus lateralis*) (Christina, 2006). Furthermore, EEG used on torpid animals show no activity present. These negative effects put constraints on their cognition (Walker, 1977; Krilowicz, 1988; Daan, 1991). Though these effects were not observed in greater mouse-eared bats, this might be since their hibernation period is too short. Thus, the effect of hibernation impairing memory makes complex problem solving impossible, posing constraints on animals.

The hibernation effect holds true except for two species in our analysis: Afrosoricida and Carnivora. But other studies report seeing exceptions in Eulipotyphla and Primates. For Afrosoricida and Carnivora, this might be the fact that non-hibernating genera are too rare (3 and 7, to be specific), with reasons unknown. Similarly, in primates the cases seem like the sample number being too small. The only three primate genera known to hibernate (*Cheirogaleus*, *Microcebus*, and *Nycticebus*) (Ruf, 2015; Schülke, 2007) are among the smallest-brained primates (Isler et al., 2008), thus, the non-significance is due to the unbalanced sample. A possible explanation for the rare occurrence of hibernation might be that adverse effects of hibernation are experienced as more severe in primates because in general, primates are relatively large-brained mammals (Isler, 2006; VAN SCHAIK, 2005). Furthermore, the costs of transporting additional body fat are especially high in arboreal species such as primates, making such fat deposits and thus hibernation a less profitable strategy to survive seasonally lean periods in this order (Heldstab, 2016).

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