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# Hotter is Smarter: The temperature-dependence of brain size in vertebrates

The tremendous variation in brain size among vertebrates has long been thought to be related to differences in species' metabolic rates. Species with higher metabolic rates can supply more energy to support the relatively high cost of brain tissue. And yet, while body temperature is known to be a major determinant of metabolic rate, the possible effects of temperature on brain size have scarcely been explored. Thus, here I explore the effects of temperature on brain size among diverse vertebrates (fishes, amphibians, reptiles, birds and mammals). I find that, after controlling for body size, brain size increases exponentially with temperature in much the same way as metabolic rate. These results suggest that temperature-dependent changes in aerobic capacity, which have long been known to affect physical performance, similarly affect brain size. The observed temperature-dependence of brain size may explain observed gradients in brain size among both ectotherms and endotherms across broad spatial and temporal scales.

2 **Hotter is Smarter: The temperature-dependence of brain size in vertebrates**

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James F. Gillooly

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Department of Biology, University of Florida

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Gainesville, FL 32611

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Email: [gillooly@ufl.edu](mailto:gillooly@ufl.edu)

## 7 1. INTRODUCTION

8           Among vertebrates, relatively larger brains are often thought to infer some form of greater  
9 cognitive ability (Jerison 1973; Dunbar & Shultz 2007; Sol & Price 2008; Kotrschal et al. 2013).  
10 But, the evolutionary costs and benefits that have led to several orders of magnitude variation in  
11 vertebrate brain size remain uncertain (Striedter 2005). In terms of evolutionary costs, many have  
12 suggested that the relatively high energetic cost of maintaining brain tissue may offset any  
13 positive selection for brain size (Aiello & Wheeler 1995).

14           The hypothesis that there are energetic constraints on brain size imposed by whole  
15 organism metabolism is supported by studies showing power law relationships of brain size with  
16 body size that are quite similar to those for metabolic rate (Jerison 1973; Martin 1981). These  
17 studies suggest an approximately linear relationship between metabolic rate and brain size within  
18 vertebrate taxonomic groups. Still, much uncertainty remains regarding to what extent metabolic  
19 rate may constrain brain size (Isler & van Schaik 2006). Most studies to date have focused on  
20 endotherms (Isler & van Schaik 2006), and do not address the approximately 10-fold difference  
21 in brain size between ectotherms and endotherms (Jerison 1973; Martin 1981).

22           Much overlooked in this debate are the well-established effects of body temperature on  
23 whole organism metabolic rate (Krogh 1916; Gillooly et al. 2001), and how such effects may  
24 influence brain size. If in fact brain size is constrained by metabolic rate, then one might expect  
25 brain size to increase exponentially with temperature in the same way as metabolic rate. In the  
26 case of ectotherms, this would mean that brain size would vary systematically across species  
27 living in different thermal environments.

28 Thus, here I explore whether relative brain size ( $RB_m$ ; % body mass) is temperature  
29 dependent after accounting for effects of body size. Specifically, I hypothesize that  $RB_m$  is related  
30 to body mass and temperature in the same way as mass-specific metabolic rate such that:

$$31 \quad RB_m \propto M^{-1/4} e^{-E/kT} \quad (\text{Eq. 1})$$

32 where  $M^{-1/4}$  describes the body-mass dependence of mass-specific metabolic rate, and  $e^{-E/kT}$   
33 describes the temperature dependence of metabolic rate. In the Boltzmann-Arrhenius term (i.e.,  
34  $e^{-E/kT}$ ),  $E$  is the average activation energy of the respiratory complex (-0.65 eV),  $k$  is Boltzmann's  
35 constant ( $8.62 \times 10^{-5}$  eV  $K^{-1}$ ) (Gillooly et al. 2005), and  $T$  is absolute temperature in degrees  
36 Kelvin. I acknowledge that that the mechanistic basis of this expression remains unclear (Price et  
37 al. 2012), and that significant variation in the proposed size and temperature dependencies have  
38 been shown (White et al. 2006). Nonetheless, this expression provides a useful point of departure  
39 for examining the combined effects of body size and temperature on relative brain size.

40 Eq. 1 indicates that the natural logarithm of temperature-corrected relative brain mass  
41 (i.e.,  $\ln(RB_m \times e^{E/kT})$ ) will scale linearly with the natural logarithm of body mass with a slope of  
42 about -1/4. Moreover, Eq. 1 indicates that the natural logarithm of body mass-corrected relative  
43 brain mass (i.e.  $\ln(RB_m \times M^{1/4})$ ) will be a linear function of inverse absolute temperature (i.e.,  
44  $1/kT$ ) with a slope of -0.65. In other words, after accounting for body mass, relative brain mass  
45 should increase about 2.5 fold for every 10 °C increase in temperature (i.e.,  $Q_{10}$  of 2.5; Gillooly et  
46 al. 2005) according to Eq. 1.

47 I examine the size and temperature dependence of relative brain size using a dataset of  
48 148 species from all major vertebrate groups (fishes,  $n=31$ ; amphibians,  $n=11$ ; reptiles,  $n=18$ ;  
49 birds,  $n=35$ ; and mammals,  $n=53$ ) over a body temperature range of about 40 °C. In the case of  
50 ectotherms, these temperatures equate to the environmental temperatures in which the species

51 naturally occur (see methods). The results point to an as yet unappreciated constraint on brain  
52 size in vertebrates-the effect of temperature.

## 53 **2. METHODS**

### 54 *(a) Data*

55 Data were collected from each taxonomic group in an effort to broadly represent the  
56 diversity present in habitat, taxonomy, life history, body size and body temperature present in  
57 each group (Supplementary Materials, Appendix 1). Data for mammals were restricted to  
58 terrestrial species, and data for birds were restricted to flying species, to facilitate comparisons  
59 within and between these groups.

60 Body temperatures were estimated using the resting body temperatures of endotherms  
61 (birds and mammals; Clarke & Rothery 2008), and the average body or environmental  
62 temperature of ectotherms (amphibians, reptiles, and fishes). Thus, average environmental  
63 temperature was assumed to be equivalent to the average body temperature in ectotherms. Any  
64 differences in species average body temperature due to differences in activity level or other  
65 factors was therefore assumed to be small relative to the roughly 40 °C range in temperature.  
66 Body mass and brain mass data were taken mainly from the classic data set of Crile & Quiring  
67 (1940). From this dataset, I included all species for which temperatures were available except for  
68 two species with values that appear to be in error (*Acinonyx jubatus* and *Osmerus mordax*). I  
69 supplemented this dataset with additional sources if a particular species group (e.g. amphibia) or  
70 temperature range was underrepresented in the dataset. In doing so, I occasionally estimated brain  
71 mass from brain volume assuming the density of water.

### 72 *(b) Analyses*

73 To evaluate the body size and temperature dependence of relative brain mass, I used least squares  
74 multiple regression. As the vertebrate phylogeny is currently undergoing major revision, and no  
75 well-supported phylogeny exists (Thomson & Shaffer 2010), performing phylogenetic analyses  
76 was not possible. However, I do consider the extent to which the relationships of individual  
77 taxonomic groups reflect the overall trend. I discuss this methodology below.

78 To graphically represent the observed temperature-dependence of relative brain mass, I  
79 divided relative brain mass by the observed mass dependence (i.e.  $\ln(RB_m/M^a)$ ) based on multiple  
80 regression, and then plotted this “body-mass-corrected” value against inverse temperature (i.e.,  
81  $1/kT$ ). Similarly, to represent the observed body mass-dependence of relative brain mass, I  
82 divided relative brain mass by the observed temperature dependence (i.e.,  $\ln(RB_m/e^{-E/kT})$ ), and  
83 then plotted this “temperature- corrected” value against the natural logarithm of body mass. Note  
84 that body-mass corrected relative brain mass used here is roughly equivalent to what is often  
85 described as the “encephalization quotient” (Jerison 1973).

### 86 3. RESULTS

87 Across the 148 species, body mass and temperature explained 76 % of the variation in relative  
88 brain mass ( $RB_m$  range: 0.007-5.8 %) based on multiple regression of log-transformed data ( $F =$   
89  $226.5$ , 2 and 145 d. f.,  $P < 10^{-40}$ ). Both showed significant, independent effects on  $RB_m$  (both  $P <$   
90  $10^{-21}$ ). Across all species,  $RB_m$  decreased with increasing body mass,  $M$ , as  $RB_m \propto M^{-0.25}$  (95% CI:  
91  $-0.21$  to  $-0.30$ ) after accounting for temperature effects. Figure 1 shows a plot of the natural log of

92 temperature-corrected relative brain size vs. the logarithm of body mass. Clearly, there are  
93 differences in both the slopes and intercepts among groups. Within groups, for example, the body  
94 mass scaling exponents ranged from -0.20 in fish to -0.43 in birds. And, the exponents for  
95 mammals (-0.32), birds (-0.43) and reptiles (-0.40) were all significantly different from -0.25.  
96 Nonetheless, the overall relationship is in agreement with model predictions.

97         The multiple regression analysis also indicated a strong temperature dependence of  $RB_m$   
98 after accounting for the effects of body mass. Across all species, the natural logarithm of mass-  
99 corrected  $RB_m$  decreased with inverse temperature with a slope (-0.98; 95% CI: -0.88 to 0.109)  
100  $^{\circ}C^{-1}$ ) that was significantly different from the predicted value of -0.65. This indicates that, on  
101 average, there is a nearly 3-fold increase in relative brain mass with a 10  $^{\circ}C$  increase in  
102 temperature. Within ectothermic groups, both fishes and amphibians showed significant  
103 temperature dependencies of relative brain size that were weaker than the overall relationship,  
104 and not different from that predicted by the model (fishes: -0.42, 95% CI: -0.64 to -0.18;  
105 amphibians: -0.67, CI: 95% -0.18 to 1.16). Among the other three taxonomic groups (mammals,  
106 reptiles, birds), where the range of body temperatures was fairly limited, no statistically  
107 significant effect of temperature was observed.

#### 108 **4. DISCUSSION**

109 The results presented here provide support for the long-standing hypothesis that metabolic rate  
110 constrains brain size. While the observed body mass-dependence within groups varied somewhat,  
111 the overall dependence was similar to mass-specific metabolic rate, as previously described  
112 (Jerison 1973; Martin 1981). More surprisingly, relative brain size was shown to increase  
113 exponentially with temperature (Figure 2). Indeed, much of the variation in relative brain size

114 among taxonomic groups was removed after accounting for differences in temperature. The 10-  
115 fold difference cited in previous studies (Martin 1981) is reduced to a maximum of 4-fold  
116 between reptiles and mammals. And, the temperature-corrected relative brain size of fishes, for  
117 example, was roughly equivalent to that of mammals (Figure 1). This suggests that temperature-  
118 dependent changes in aerobic capacity, which have long been known to affect physical  
119 performance (Bennett & Ruben 1979), may similarly affect brain size and thus cognitive ability.

120         Still, there are many other factors not considered here that likely influence brain size-not  
121 just size and temperature. Taxon-specific differences in relative brain size are quite clear from  
122 these results (Figures 1 and 2), even after accounting for size and temperature. Moreover, fully  
123 accounting for phylogenetic relatedness would likely reduce somewhat the degrees of freedom  
124 and perhaps increase the variance in the relationships shown here. But, given the taxonomic  
125 breadth of the data, and the strength of the relationships, such an analysis would be unlikely to  
126 affect the overall results (Ricklefs & Starck 1996).

127         More generally, the relationship of brain size and temperature shown here could help  
128 explain broad-scale patterns in brain size across space and time for both endotherms and  
129 ectotherms. This is because environmental temperature affects not only the metabolic rate of  
130 ectotherms, but also that of endotherms, albeit to a lesser extent (Anderson & Jetz 2005). Thus,  
131 across space, one might expect gradients in brain size with elevation, latitude, or climate  
132 depending on the degree of temperature change and the taxonomic group in question.  
133 Interestingly, the latitudinal gradient in human brain volume is qualitatively consistent with the  
134 trend toward higher metabolic rates with latitude in endotherms (Anderson & Jetz 2005; Beals et  
135 al. 1984). And across time, one might expect changes brain size during the transition from water  
136 to land or the evolution of endothermy as these events involved changes in species' temperatures  
137 and aerobic capacity (Bennett & Ruben 1979). One could also speculate on the possibility of

138 phenotypic plasticity in brain size with respect to temperature. Indeed, the recognition that brain  
139 size is linked to environmental temperature through its effect on metabolic rate could provide a  
140 new vista on many questions of the topic of brain size evolution.

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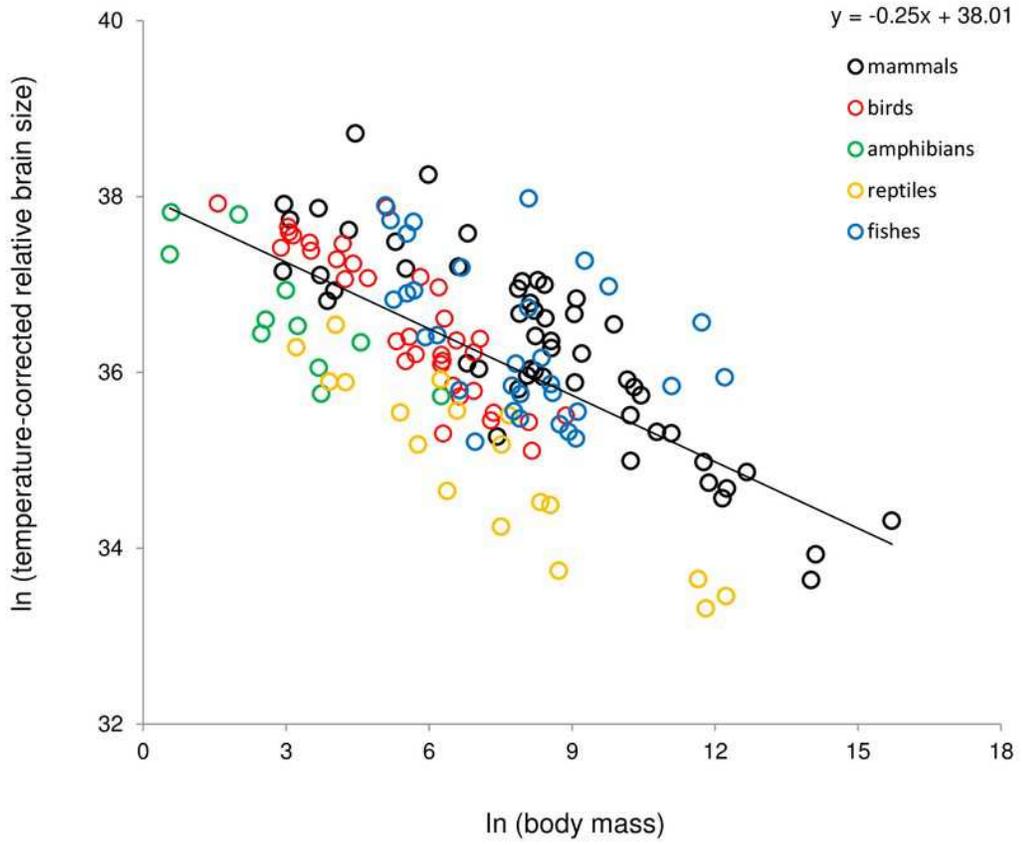
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# Figure 1

Figure 1: Relative brain mass vs. body mass in vertebrates.

**Figure 1** : The natural logarithm of temperature-corrected relative brain mass (i. e.,  $\ln (RB_m \times e^{E/kT})$ ) versus the natural logarithm of body mass for 148 vertebrate species. Temperature-correction was performed based on multiple regression analysis and following Eq. 1 (see methods). Data and sources are listed in the Appendix. Relative brain mass is expressed as a percentage of body mass.

JF Gillooly, Figure 1



# Figure 2

Figure 2: Relative brain mass vs. inverse absolute temperature in vertebrates.

**Figure 2** : The natural logarithm of body mass-corrected relative brain mass (i. e.,  $\ln (RB_m \times M^{1/4})$ ) versus inverse absolute temperature ( $1/kT$ ) for the data shown in Figure 1 ( $n = 148$ ). Temperature-correction was performed based on multiple regression analysis and following Eq. 1 (seemethods). Data and sources are listed in the Appendix. Relative brain mass is expressed as a percentage of body mass.

JF Gillooly, Figure 2

