

Brain size varies with temperature in vertebrates

James F Gillooly

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.

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27 **1. INTRODUCTION**

28 The evolutionary costs and benefits that have led to several orders of magnitude variation
29 in vertebrate brain size remain uncertain (Striedter 2005). Relatively larger brains are often
30 thought to infer some form of evolutionary benefit (Jerison 1973; Dunbar & Shultz 2007; Sol &
31 Price 2008; Kotrschal et al. 2013), though any direct link between brain size and intelligence
32 remains in question. On the other hand, the relatively high energetic cost of maintaining brain
33 tissue may offset any such benefit (Aiello & Wheeler 1995).

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

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

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

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$$54 \quad \text{RB}_m \propto M^{-1/4} e^{-E/kT} \quad (\text{Eq. 1})$$

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56 where $M^{-1/4}$ describes the body-mass dependence of mass-specific metabolic rate, and $e^{-E/kT}$
57 describes the temperature dependence of metabolic rate. In the Boltzmann-Arrhenius term (i.e.,
58 $e^{-E/kT}$), E is the average activation energy of the respiratory complex (-0.65 eV), k is Boltzmann's
59 constant (8.62×10^{-5} eV K⁻¹ (Gillooly et al. 2005), and T is absolute temperature in degrees
60 Kelvin. I acknowledge that that the mechanistic basis of this expression remains unclear (Price et
61 al. 2012), and that significant variation in the proposed size and temperature dependencies have
62 been shown (White et al. 2006). Nonetheless, this expression provides a useful point of departure
63 for examining the combined effects of body size and temperature on relative brain size.

64 Eq. 1 indicates that the natural logarithm of temperature-corrected relative brain mass
65 (i.e., $\ln(\text{RB}_m \times e^{E/kT})$) will scale linearly with the natural logarithm of body mass with a slope of
66 about -1/4. Moreover, Eq. 1 indicates that the natural logarithm of body mass-corrected relative
67 brain mass (i.e. $\ln(\text{RB}_m \times M^{1/4})$) will be a linear function of inverse absolute temperature (i.e.,
68 $1/kT$) with a slope of -0.65. In other words, after accounting for body mass, relative brain mass
69 should increase about 2.5 fold for every 10 °C increase in temperature (i.e., Q₁₀ of 2.5; Gillooly
70 et al. 2005) according to Eq. 1.

71 I examine the size and temperature dependence of relative brain size using a dataset of
72 148 species from all major vertebrate groups (fishes, n=31; amphibians, n=11; reptiles, n=18;
73 birds, n =35; and mammals, n=53) over a body temperature range of about 40 °C. In the case of
74 ectotherms, these temperatures equate to the environmental temperatures in which the species
75 naturally occur (see methods). The results point to an as yet unappreciated constraint on brain
76 size in vertebrates-the effect of temperature.

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78 **2. METHODS**

79 *(a) Data*

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

85 Body temperatures were estimated using the resting body temperatures of endotherms
86 (birds and mammals; Clarke & Rothery 2008), and the average body or environmental temperature
87 of ectotherms (amphibians, reptiles, and fishes). Thus, average environmental temperature was
88 assumed to be equivalent to the average body temperature in ectotherms. Any differences in
89 species average body temperature due to differences in activity level or other factors was therefore
90 assumed to be small relative to the roughly 40 °C range in temperature. Body mass and brain mass
91 data were taken mainly from the classic data set of Crile & Quiring (1940). From this dataset, I
92 included all species for which temperatures were available except for two species with values that

93 appear to be in error (*Acinonyx jubatus* and *Osmerus mordax*). I supplemented this dataset with
94 additional sources if a particular species group (e.g. amphibia) or temperature range was
95 underrepresented in the dataset. In doing so, I occasionally estimated brain mass from brain
96 volume assuming the density of water.

97 *(b) Analyses*

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

103 To graphically represent the observed temperature-dependence of relative brain mass, I
104 divided relative brain mass by the observed mass dependence (i.e. $\ln(RB_m/M^a)$) based on multiple
105 regression, and then plotted this “body-mass-corrected” value against inverse temperature (i.e.,
106 $1/kT$). Similarly, to represent the observed body mass-dependence of relative brain mass, I divided
107 relative brain mass by the observed temperature dependence (i.e., $\ln(RB_m/e^{-E/kT})$), and then plotted
108 this “temperature- corrected” value against the natural logarithm of body mass. Note that body-
109 mass corrected relative brain mass used here is roughly equivalent to what is often described as
110 the “encephalization quotient” (Jerison 1973).

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114 3. RESULTS

115 Across the 148 species, body mass and temperature explained 76 % of the variation in relative
116 brain mass (RB_m range: 0.007-5.8 %) based on multiple regression of log-transformed data (F =
117 226.5, 2 and 145 d. f., P < 10⁻⁴⁰). Both showed significant, independent effects on RB_m (both P <
118 10⁻²¹). Across all species, RB_m decreased with increasing body mass, *M*, as RB_m ∝ *M*^{-0.25} (95%
119 CI: -0.21 to -0.30) after accounting for temperature effects. Figure 1 shows a plot of the natural
120 log of temperature-corrected relative brain size vs. the logarithm of body mass. Clearly, there are
121 differences in both the slopes and intercepts among groups. Within groups, for example, the
122 body mass scaling exponents ranged from -0.20 in fish to -0.43 in birds. And, the exponents for
123 mammals (-0.32), birds (-0.43) and reptiles (-0.40) were all significantly different from -0.25.
124 Nonetheless, the overall relationship is in agreement with model predictions.

125 The multiple regression analysis also indicated a strong temperature dependence of RB_m
126 after accounting for the effects of body mass. Across all species, the natural logarithm of mass-
127 corrected RB_m decreased with inverse temperature with a slope (-0.98; 95% CI: -0.88 to -0.109)
128 °C⁻¹) that was significantly different from the predicted value of -0.65. This indicates that, on
129 average, there is a nearly 3-fold increase in relative brain mass with a 10 °C increase in
130 temperature. Within ectothermic groups, both fishes and amphibians showed significant
131 temperature dependencies of relative brain size that were weaker than the overall relationship,
132 and not different from that predicted by the model (fishes: -0.42, 95% CI: -0.64 to -0.18;
133 amphibians: -0.67, CI: 95% -0.18 to -1.16). Among the other three taxonomic groups (mammals,
134 reptiles, birds), where the range of body temperatures was fairly limited, no statistically
135 significant effect of temperature was observed.

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137 4. DISCUSSION

138 The results presented here provide support for the long-standing hypothesis that metabolic rate
139 constrains brain size. While the observed body mass-dependence within groups varied
140 somewhat, the overall dependence was similar to mass-specific metabolic rate, as previously
141 described (Jerison 1973; Martin 1981). More surprisingly, relative brain size was shown to
142 increase exponentially with temperature (Figure 2). Indeed, much of the variation in relative
143 brain size among taxonomic groups was removed after accounting for differences in temperature.
144 The 10-fold difference cited in previous studies (Martin 1981) is reduced to a maximum of 4-
145 fold between reptiles and mammals. And, the temperature-corrected relative brain size of fishes,
146 for example, was roughly equivalent to that of mammals (Figure 1). This suggests that
147 temperature-dependent changes in aerobic capacity, which have long been known to affect
148 physical performance (Bennett & Ruben 1979), may similarly affect brain size.

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

156 More generally, the relationship of brain size and temperature shown here could help
157 explain broad-scale patterns in brain size across space and time for both endotherms and

158 ectotherms. This is because environmental temperature affects not only the metabolic rate of
159 ectotherms, but also that of endotherms, albeit to a lesser extent (Anderson & Jetz 2005). Thus,
160 across space, one might expect gradients in brain size with elevation, latitude, or climate
161 depending on the degree of temperature change and the taxonomic group in question.
162 Interestingly, the latitudinal gradient in human brain volume is qualitatively consistent with the
163 trend toward higher metabolic rates with latitude in endotherms (Anderson & Jetz 2005; Beals et
164 al. 1984). And across time, one might expect changes brain size during the transition from water
165 to land or the evolution of endothermy as these events involved changes in species' temperatures
166 and aerobic capacity (Bennett & Ruben 1979). One could also speculate on the possibility of
167 phenotypic plasticity in brain size with respect to temperature. Indeed, the recognition that brain
168 size is linked to environmental temperature through its effect on metabolic rate could provide a
169 new vista on many questions of the topic of brain size evolution.

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