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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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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 (8.62×10^{-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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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

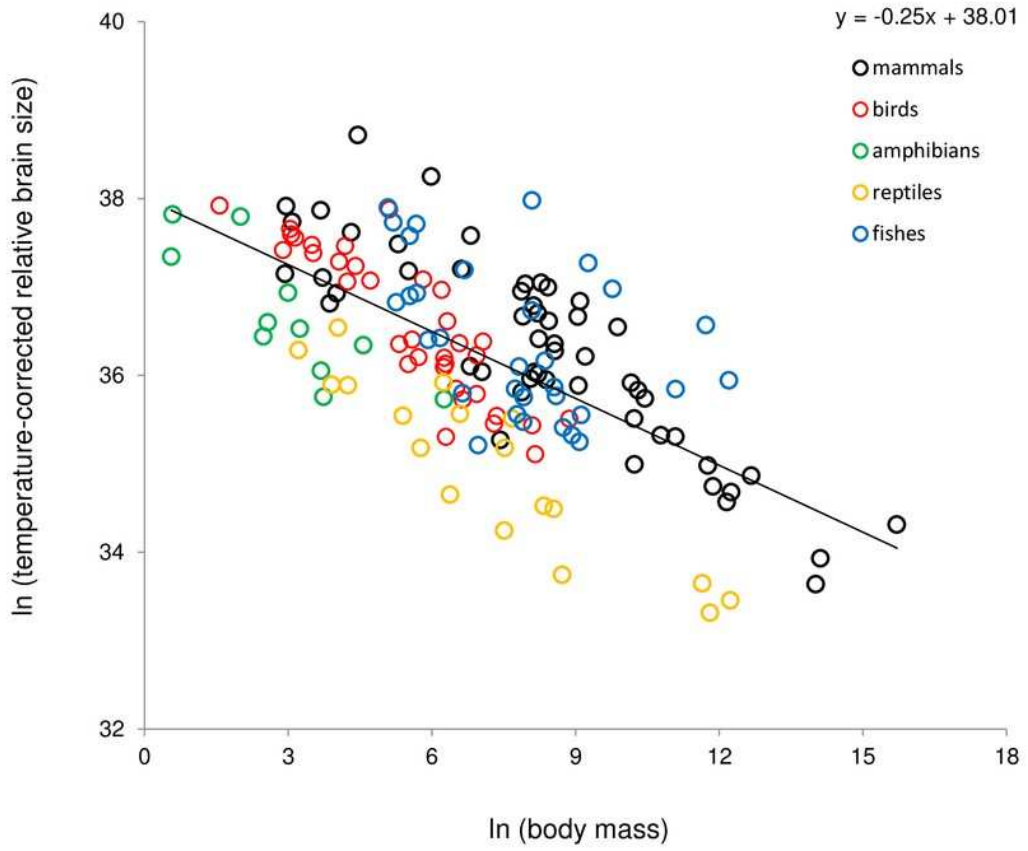


Figure 2

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

