

We also tested whether the VD neuron inactivation might be due to a reduction in the electrical coupling between the VD neuron and the PD and anterior burster (AB) neurons of the pyloric network (Fig. 1), as this coupling is the only excitatory input the VD neuron receives from the pyloric network. The strength of this connection was identical for active and inactivated VD neurons.

Another reason for the VD neuron inactivation could be that the high-frequency VD neuron firing during CS network bursts induces a post-tetanic depression of the neuron. This hypothesis can be rejected because the VD neuron spike burst and inactivation can be experimentally dissociated. First, high-frequency VD neuron spike bursts induced either by injecting depolarizing current into the VD neuron or stimulating the IV neurons (Fig. 3B) do not inactivate the VD neuron. Second, curare blocks the VD neuron firing induced by lpln stimulation [by blocking the excitatory IV to VD neuron synapses (6)], but has no effect on VD neuron inactivation (Fig. 3C).

Finally, the VD neuron inactivation could be due to changes in the expression of regenerative membrane properties in the neuron itself. The rhythmic depolarization and firing of the pyloric network neurons depend on "plateau" or "oscillatory" membrane properties that are intrinsic to the neurons (11) but can be modified by extrinsic inputs (11, 12). A neuron expressing these properties responds to a brief depolarizing current injection sufficient to bring the membrane potential of the neuron beyond a certain threshold with a sustained depolarization (plateau) that long outlasts the current pulse (11). When the VD neuron fires with the pyloric network it always expresses these properties (Fig. 3D₁), but whenever it is inactivated [during CS network activity induced by tonic lpln stimulation (Fig. 3D₂), during spontaneous CS network activity, or after brief lpln stimulation (10)], the neuron shows only passive responses.

We have not identified the input that induces the VD neuron inactivation, but it is not the IV neurons, as their direct stimulation (Fig. 3B) does not cause VD neuron inactivation. This input is presumably neuromodulatory in nature, because brief lpln stimulation leading to a single CS network cycle inactivates the VD neuron for tens of seconds (Fig. 3A), and 10 to 20 min of continuous CS network activity (either spontaneous or induced by lpln stimulation) inactivates the VD neuron for several hours.

In summary, when the CS network is active, it always appropriates an otherwise integral member (the VD neuron) of the pyloric network. This work thus argues that

individual neurons can belong to more than one neural network. Switching of the VD neuron occurs when the CS network is activated by electrical stimulation of a sensory input or by mechanical stimulation of the stomach wall in semi-intact preparations (9); this switching may therefore be physiologically relevant. Our results are consistent with the VD neuron switch arising from a long-lasting neuromodulatory suppression of the intrinsic regenerative membrane properties of the neuron; changes in these properties may thus not only cause a single network to assume different configurations (2), but also switch neurons between different networks.

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Taxonomic Differences in the Scaling of Brain on Body Weight Among Mammals

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Theories for the evolution of brain weight in mammals suggest that closely related species have diverged largely as a result of selection for differences in body weight, but that differences among more distantly related species have arisen due to greater net directional selection on brain weight. This pattern of changing selection causes brain weight to evolve more slowly than body weight among closely related species, such as those in the same genus, than among more distantly related species, such as those from different families or orders; a phenomenon known as the "taxon-level effect." Thus, brain weight differs more for a given difference in body weight as the species compared are more distantly related. An alternative explanation for the taxon-level effect is proposed. Distantly related species are more likely to inhabit different ecological conditions than are more closely related species. Where the taxon-level effect occurs, brain weight appears to have evolved in response to the demands of these different ecological conditions. As a consequence, brain weight differs more among distantly related species, for any given difference in body weight, than among closely related species. This effect, rather than a progressive pattern of changing selection pressures, may account for the taxon-level effect in mammals.

THE RELATIONSHIP OF BRAIN weight to body weight in mammals can be described by an allometric power formula, brain weight $\approx a(\text{body weight})^b$, which becomes linear when both variables are expressed in logarithmic form: $\log(\text{brain weight}) \approx \log(a) + b \log(\text{body weight})$. The taxon-level problem in the evolution of mammalian brain weight refers to the finding that the slope b of the logarithmic relation depends upon the taxonom-

ic level within which it is estimated (1–4). Slopes fitted to species of the same genus are reported to be typically about 0.2 to 0.4, but if a slope is fitted across species from different orders it ranges up to around 0.75 (1–4). This means that brain weight differs more for a given difference in body weight among more distantly related taxa (Fig. 1).

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Theories advanced to explain the taxon-level effect hold that closely related species typically have diverged as a result of selection on body weight, with brain weight changing as a secondary correlated response (2-4). Direct selection on body weight is estimated to bring about a correlated response in brain weight that would produce an allometric slope of about 0.2 to 0.4 (3, 4). The evolutionary forces differentiating more distantly related taxa are supposed to have acted more strongly on brain weight (3), or on genes that control both brain and body growth (4). These forces cause brain weight to evolve more rapidly with evolutionary changes in body weight, leading to steeper slopes among more distantly related taxa.

We considered two ways that the taxon-level effect could arise. First, the increase in slope with taxonomic level may be a general phenomenon caused either by different selection regimes or by different responses to selection, with higher taxa in each case differing from lower taxa (2-4). For example, one theory explains the taxon-level effect as a by-product of the length of the fetal and early postnatal growth periods that are required to produce species of different body weights (4). Larger body size may require a longer period of prenatal and early postnatal growth in addition to the period of juvenile growth (4). However, an individual's brain weight increases more rapidly for a given increase in its body weight during fetal and early postnatal growth ("early growth"), compared to the period of juvenile growth. Higher taxa, spanning a greater range of body weight, may differ characteristically in the length of the early growth period, whereas the length of the juvenile growth period may be more characteristic of differences among closely related species (2, 4). Consequently, smaller differences in brain weight for a given difference in body weight (and therefore shallower slopes) will be found among species from lower taxonomic levels (Fig. 2).

A second explanation for the taxon-level effect assumes that steeper slopes found in higher level taxa may not reflect a general trend. Rather, the steeper slopes may be caused by only one or a few subtaxa that have become highly encephalized (or poorly encephalized) and which have thus diverged from the shallower slope describing the other subtaxa. Relatively large or small brain weight for a given body weight may occur in response to the demands of particular ecological conditions (5-8). Since the ecologies of more distantly related taxa differ more than those of closely related taxa, this kind of adaptive difference in brain weight would be more likely among distantly related taxa.

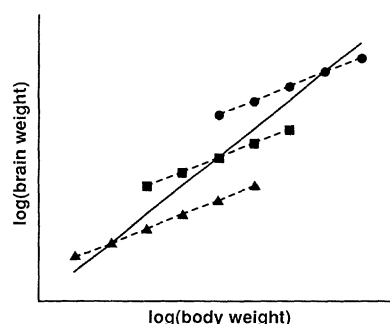


Fig. 1. Hypothetical plot of the logarithm of brain weight versus that of body weight showing the taxon-level effect. The three dashed lines represent the relation between brain weight and body weight for the species within each of three genera. Points with the same symbol are species belonging to the same genus. The solid line is the steeper slope found when the line is fitted across the three genera within the family. Thus, brain weight differs more for a given difference in body weight when the taxa compared are more distantly related. Similar increases in slope are found for higher level taxa.

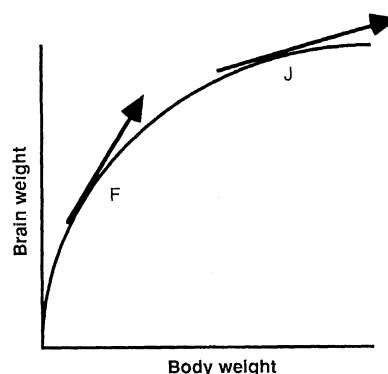


Fig. 2. Curve showing the increase in brain and body weight through time during the development of an individual mammal. Early in development, during fetal and early postnatal life, the brain grows faster in relation to the body than it does later in development. The evolution of a prolonged period of fetal growth (along the trajectory shown by the left-hand arrow, the tangent to the line at point F) would lead to an adult with a relatively larger brain weight for its body weight than would the evolution of a period of prolonged juvenile growth (the right-hand arrow at point J).

If this explanation for the taxon-level effect is correct, slopes calculated after controlling for such adaptive differences in brain weight will resemble those at lower taxonomic levels where ecological conditions are more uniform.

We examined slopes calculated at successive taxonomic levels and tested for ecological conditions associated with steeper slopes in higher taxa. If we are to distinguish between the two explanations that we have described, it is essential that the statistical procedures used have realistic assumptions. At least some of the increase in slope with taxonomic level reported in the literature

may be an artifact of statistical models that have used unrealistic assumptions about the distribution of statistical error in brain and body weight measurements (9). We used a maximum-likelihood regression model (10) in preference to the usual regression models, which are special cases of the one we used but which make unrealistic assumptions about the error variances in brain and body weight.

Data on brain and body weight were collected from the literature for 927 mammal species from 16 orders (1). Taxonomic classification followed Corbet and Hill (11), and Eisenberg (12), giving priority to classifying taxa into monophyletic groups. The data were logarithmically transformed before analysis. This makes the variances at different body weights roughly equal and transforms the power relation into a linear one. Allometric slopes were estimated as the slopes (b) of the logarithmically transformed data, separately within successive taxonomic levels. At each successive level, mean values of the logarithmically transformed values from the next lowest level were employed. Analyses within successive taxonomic levels were conducted separately for each order, and a slope was calculated across the order means within the class.

The slope relating brain and body weight across the 16 order points was 0.74 [95% confidence interval (C.I.), 0.69, 0.79], similar to that found in previous analyses (1, 13). Sufficient data were available for seven orders to analyze slopes separately within successive taxonomic levels (Table 1). Two broad features of the results are noteworthy. First, with the exception of the Rodentia (1), the slopes calculated among species within genera are usually well above the 0.2 to 0.4 range often thought to characterize closely related species that have diverged due to selection on body weight alone. The mean within-genus (that is, across species within genera) slope was 0.55 ($n = 116$) (14), which was significantly greater than 0.40 [$t(115) = 5.75$, $P < 0.0001$, two-tailed test]. In fact, average within-genus slopes ranged to levels approaching those previously thought to be attained only by distantly related taxa. This difference from previous reports is due partly to the inclusion of a wider range of taxa and partly to the statistical line-fitting model used (9, 10).

The relationship of brain weight to body weight among adults within a single species may also help explain why the average within-genus slope (Table 1) is significantly steeper than the commonly quoted range of 0.20 to 0.40. It has long been thought that the slope relating brain to body weight within species is about 0.20 (15) and that low slopes among closely related species

represent an extrapolation of within-species trends (2). However, many intraspecific slopes are not different from zero when juveniles are excluded and sex differences in weight are controlled for (1). If this low phenotypic covariance is representative of the genetic covariance between brain and body weight among adults, then selection may change brain or body weight independently of constraints imposed by a genetic covariance with the other.

The second major pattern is the absence of a uniform tendency for slopes to increase with taxonomic level. Combining subfamily, family, superfamily, and suborder slopes, a seven (orders) by three (taxonomic levels: genus, subfamily-suborder, order) ANOVA showed that there is not a significant overall trend for slopes to increase [$F(1,179) = 3.18, P < 0.10$ (16)]. In the Artiodactyla, Carnivora, Insectivora, and the Marsupialia the average slope within genera does not differ significantly from the value of the slope calculated within the order (all t tests, $P > 0.25$). However, confining the analysis to the slopes for the Chiroptera, Primates, and Rodentia, the trend is significant [$F(1,118) = 4.70, P < 0.05$]. The average within-genus slope is significantly lower than the value of the slope within the order for each of these three orders (all t tests, $P < 0.001$).

Do the steeper slopes seen within some higher level taxa describe a general characteristic of the members of those taxa? Or, are the steeper slopes brought about by one or a few taxa in which brain weight diverges from a more general and shallower brain weight-body weight trend in the remaining taxa? We examined ecological correlates of brain weight in the higher taxa of the Chiroptera, Primates, and Rodentia (17) to distinguish between these two explanations.

First, in the Rodentia the average slopes across families within suborders and across suborders within the order are steeper than those at lower levels (Table 1). Both effects result from the influence of one group, the families of the suborder Hystricomorpha. The average slope for families within the other two suborders (Sciuromorpha and Myomorpha) is 0.46 (95% C.I., 0.34, 0.69), similar to lower taxonomic levels. The Hystricomorph families all lie above the line describing the other two suborders. Unlike other rodents, the Hystricomorphs [which may not be a monophyletic group (12)] give birth to precocial offspring (12, 18). The slope within the suborder of Hystricomorph rodents is 0.62 (95% C.I., 0.49, 0.84). The higher slope calculated across the three suborders within the order (Table 1), then, results from the increased encephalization of the Hystricomorphs compared to the

other two suborders: when Hystricomorphs are removed, the slope declines to 0.46 (two suborders).

The increases in slope at the suborder and order levels in the Chiroptera (Table 1) are associated with variation in encephalization between frugivorous and insectivorous bats (7). Eisenberg and Wilson (7) speculate that larger brain weight in frugivorous bats is a response to the foraging demands associated with frugivory. The suborder Megachiroptera comprises a single family of fruit-eating bats, the Pteropidae. The slope across genera in the Megachiroptera is 0.70 (95% C.I., 0.64, 0.77). The suborder Microchiroptera contains a variety of diet types including several families of insectivores and one subfamily of frugivores, the Stenoderminae. The slope across families in the Microchir-

optera is 0.85 (95% C.I., 0.64, 1.22). Differences in brain weight associated with diet (diet treated as a dichotomous category of frugivorous or nonfrugivorous) in the Microchiroptera were controlled for by multiple regression. The slope controlling for diet this way decreases to 0.75 (95% C.I., 0.66, 0.87). The slopes within both suborders are similar to those at lower taxonomic levels and to those reported by Eisenberg and Wilson (7) who analyzed the relationships separately within diet categories. The steep slope across the two Chiropteran suborders results from the increased relative brain weight of the Pteropidae family of fruit-eating bats that make up the suborder Megachiroptera. Controlling for diet, the slope fitted across families from these two suborders is 0.75 (95% C.I., 0.65, 0.88).

Table 1. Slopes relating brain weight to body weight within taxonomic levels in mammals. Values of the slopes are derived from the structural model (10) and estimate b in the relationship $\log(y) = \log(a) + b \log(x)$ linking brain weight (y) to body weight (x). The values for the slopes are averages for their taxonomic level. "Taxonomic level" is the level within which slopes were estimated. "Number of taxa" refers to the number of groups at that level within which sufficient data were available to calculate slopes. Thus, the average slope within genera for Artiodactyla was calculated from 12 different genera. The confidence intervals were calculated according to Rayner (10) and may only be approximate for some taxa with small sample sizes. The slopes and confidence intervals obtained after adjusting for ecological influences are shown in parentheses. The taxonomic levels used differ among orders because of taxonomic practice (for example, not all orders contain suborders) and the distribution of the data (for example, analyses of superfamilies within suborders would not have been possible if a suborder contained only one superfamily). Genera with only one species do not contribute a slope but do contribute a mean to the next highest level. The same is true for families with only one genus and so on. The value of 0.205 for λ (10) was used at each taxonomic level. Error has a relatively small effect at higher taxonomic levels and regression models employing other values of λ produced a similar pattern of results.

Order	Taxonomic level	Number of taxa	Slope	95% C.I.
Artiodactyla	Genus	12	0.55	0.32, 1.37
	Subfamily	12	0.59	0.39, 1.14
	Family	2	0.48	0.39, 0.61
	Order	1	0.49	0.29, 1.12
Carnivora	Genus	15	0.57	0.34, 1.42
	Family	8	0.63	0.45, 0.98
	Superfamily	2	0.63	0.52, 0.77
	Order*	1	0.65	0.56, 0.81
Chiroptera	Genus	31	0.70	0.51, 1.10
	Family	9	0.71	0.56, 0.96
	Suborder*	2	0.78 (0.73)	0.64, 0.99 (0.60, 0.92)
	Order*	1	0.92 (0.75)	0.75, 1.16 (0.60, 0.94)
Insectivora	Genus	6	0.66	0.43, 1.09
	Family	4	0.64	0.44, 1.14
	Order	1	0.63	0.44, 1.05
Marsupialia	Genus	4	0.65	0.49, 0.94
	Family	4	0.51	0.34, 0.91
	Order	1	0.67	0.58, 0.81
Primates	Genus	18	0.47	0.23, 2.13
	Subfamily	12	0.67	0.49, 1.02
	Superfamily	4	0.69	0.50, 1.05
	Suborder	3	0.77 (0.73)	0.55, 1.25 (0.57, 0.99)
	Order	1	0.83 (0.83)	0.60, 1.29 (0.60, 1.29)
Rodentia	Genus	30	0.40	0.22, 1.06
	Subfamily	10	0.45	0.35, 0.63
	Family	3	0.40	0.23, 0.97
	Suborder	3	0.51 (0.46)	0.38, 0.75 (0.34, 0.69)
	Order†	1	0.58 (0.46)	0.54, 0.63

*Because there were too few data points to calculate the slope from means at the level immediately below, means from two levels below were used. †The estimate of the adjusted slope is based on two points and thus confidence intervals could not be calculated.

Slopes gradually increase with taxonomic level in the Primates (Table 1). Significant associations of diet with encephalization occur in this order: within families, frugivorous and insectivorous primates are significantly more encephalized than folivores (5). Diet does not account for the lower slopes within genera [diets from (5)]. However, confidence intervals around the slopes for primate genera are wide compared to genera from other orders. This suggests that primate congeneric species have not diverged strictly along lines of shallower slope, but rather that brain weight has been relatively free to vary.

Steeper slopes within the three primate suborders (Prosimii, Platyrrhini, and Catarrhini) may be associated with dietary differences, however. The slope within the Prosimii (Prosimians) is 0.74 (95% C.I., 0.53, 1.17) based on seven subfamilies. The species *Daubentonia madagascariensis* (only member of the Daubentoniidae) is the only insectivore, the other six subfamilies being frugivorous and folivorous. *Daubentonia madagascariensis* has a particularly large brain weight for its body weight (5, 19–21) and an enlarged olfactory bulb (20), which may be an adaptation for locating insect larvae in bark (20). It has also been suggested that *D. madagascariensis* is a phyletic dwarf, whose brain weight is more appropriate to its larger ancestor (21). Removing *D. madagascariensis*, the slope for the Prosimii declines from 0.74 to 0.60 (95% C.I., 0.47, 0.81). Within the Catarrhini (Old World Monkeys) the slope is 0.78 (95% C.I., 0.52, 1.37). Removing the only folivorous subfamily from the group, the Colobinae, the slope decreases to 0.67 (95% C.I., 0.54, 0.87). The slope within the Platyrrhini (New World Monkeys) is 0.84 (95% C.I., 0.58, 1.37). Of the seven subfamilies in the Platyrrhini for which we have data, six are frugivores. Removing the folivorous subfamily Alouattinae whose members have large bodies but small brains, the slope increases to 0.93 (95% C.I., 0.67, 1.41); New World frugivorous monkeys may have diverged with a steeper slope. Thus, each of the within-suborder slopes is strongly influenced by a single taxonomic group that occupies an ecological niche different from the remaining subfamilies. Removing that group makes the sample more homogeneous for diet, increases the goodness of fit between brain weight and body weight (narrower confidence intervals around slopes) and, for two of the three suborders, the slopes are reduced to a value similar to those within subfamilies.

The increase in slope across suborders in the Primates does not seem to have an obvious ecological explanation. The slope of

0.83 (95% C.I., 0.65, 1.12) is due primarily to the Prosimians which have small body weights, small relative brain weights, and retain some primitive characters compared to other primates. The slope linking the remaining two suborders is 0.73 (two points).

The Carnivores also support the argument that increases in slope with taxonomic level are associated with ecological differences among taxa. There are no reported ecological correlates of encephalization in Carnivores (22), and slopes do not increase with taxonomic level in this order.

The slopes adjusted for ecological associations in the Chiroptera, Primates, and Rodentia are reported in Table 1. Increases in slope with taxonomic level have largely disappeared, with the exception of the Primates. A three (orders) by three (taxonomic level) ANOVA with the adjusted slopes now only approaches statistical significance [$F(1,118) = 2.54$, $P < 0.15$]. This effect disappears when the Primates are excluded [$F(1,83) = 0.28$, $P > 0.50$]. Within the Primates, the mean of the within-genus slopes (Table 1) differs from the value 0.69 (average of the adjusted higher taxa for Primates: $t = 2.89$, $P < 0.025$). Thus, with the exception of the Primates, nearly all the increase in slope at higher taxonomic levels can be accounted for by evolution of brain weight in a few taxa away from shallower allometric trends describing the remaining taxa.

Most slopes, regardless of taxonomic level, are below the slope of 0.74 derived for the entire class. This need not be interpreted as evidence for a generalized increase in slope with taxonomic level for three reasons. First, different orders of mammals appear to have characteristically different brain weight–body weight slopes. Since slopes do not generally increase with taxonomic level within orders, there is no sense in which the across-order slope should be thought of as a value toward which the orders are moving. Second, there are four instances where the across-order slope is exceeded by the average slope within a lower taxon (Table 1). Third, the average generic and family slopes for Chiroptera fall within the 95% C.I. around the 0.74 slope.

Measures of encephalization are frequently used to compare the brain weights (corrected for body weight) of different species. Body weight is controlled for by using a single allometric slope for all mammals. However, given the differences in slope in different orders, measures of encephalization for mammals should be made specifically with reference to a particular baseline group.

In conclusion, some of the patterns of brain and body weight scaling in mammals

may arise from different patterns of selection on brain and body weight in closely related versus distantly related taxa (3), or as a consequence of large differentiation in body weight (4). Primates, especially the Platyrrhini, and the Hystricomorph rodents are potential examples. But it may not be necessary to invoke these mechanisms to explain the general patterns of brain weight–body weight slopes in the mammals. Artiodactyls, for example, range from less than 10 kg (for example, Duikers, genus *Cephalophus*) to 1200 or more kilograms (for example, giraffe and hippopotamus). But the Artiodactyls show no increase in slope with taxonomic level. The results presented here suggest that most differences in encephalization among higher taxonomic groups are adaptations to the demands of particular ecological conditions.

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9. Three regression models are commonly used in allometric studies: least-squares (model 1) regression, major axis or principal axis regression (model 2), and reduced major axis regression. Least-squares regression assumes that there is no error variance in the x variate (error being defined in this instance as independent variation in a variable that is unrelated to its bivariate distribution with another variable and which results in the true value of the variable being unknown). Major axis regression estimates are obtained by assuming that the error variances in brain and body weight are equal. Reduced major axis regression assumes that the ratio of the true variances (measured without error) of the y and x variates is equal to the ratio of their respective error variances. M. D. Pagel and P. H. Harvey [*Am. Nat.* 132, 344 (1988)] showed that none of these assumptions is realistic for brain and body weight measurements in mammals. Within-population variances in brain and body weight were examined in 23 data sets on 17 species. Since allometric studies employ means for species and higher level taxa, the within population variances give an estimate of how much variation to expect in species typical means: the expected variance of the mean is the within-population variance divided by the sample size. On average, the ratio of the variance in brain weight within a species to the variance in body weight within a species is 0.19; the variance of mean body weight is roughly five times as great as the variance of mean brain weight. For comparison, the ratio of the within-population variances in 11 primate species reported by R. L. Holloway [*Am. J. Phys. Anthropol.* 53, 109 (1980)] is 0.18, and Lande (3) derived an estimate for this ratio of between 0.16 and 0.25. Ratios in this range violate the assumptions of each of the regression models and in such a way that they can each be expected to underestimate the true allometric slope (see M. D. Pagel and P. H. Harvey, above).
10. When the x and y variates are measured with error, a maximum likelihood estimate of the allometric slope

- can be obtained from the structural relations model [P. Sprent, *J. R. Stat. Soc. (B)* **28**, 278 (1966); *Models in Regression and Related Topics* (Methuen, London, 1969); J. M. V. Rayner, *J. Zool.* **206**, 415 (1985); B. Kuhry and L. F. Marcus, *Syst. Zool.* **26**, 201 (1977)]. This model requires that the ratio (denoted by λ) of the error variance in the y observations to that in the x observations is known. Model 1, model 2, and reduced major axis regression estimates are simply special cases of this model: model 1 estimates are found by assuming that λ^{-1} is zero, model 2 is found by assuming that λ is 1.0, and reduced major axis by assuming that λ equals the ratio of the true variances in x and y . λ has previously been estimated as 0.19 [M. D. Pagel and P. H. Harvey, in (9)]. λ can also be estimated by a different procedure: the variance in mean brain and body weight was calculated in 117 species for which two or more mean values were reported from different sources. This direct estimate of the amount of variation in species, mean brain and body weights reported in the literature produces λ of 0.22. λ used in this study is the mean of the two values (0.205), although either used alone gives similar results.
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because it has two degrees of freedom, and yet the linear effect with only one degree of freedom accounts for about 98% of the variation among the means.

17. The presence of an association cannot be taken as evidence that the particular ecological factor identified is the cause of the difference in encephalization, but it does suggest that a single group with a different ecology than the rest is responsible for the trend. Any other factor that differs between the single group and the remaining taxa could also be responsible for the differences in encephalization.
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Freeze Avoidance in a Mammal: Body Temperatures Below 0°C in an Arctic Hibernator

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Hibernating arctic ground squirrels, *Spermophilus parryii*, were able to adopt and spontaneously arouse from core body temperatures as low as -2.9°C without freezing. Abdominal body temperatures of ground squirrels hibernating in outdoor burrows were recorded with temperature-sensitive radiotransmitter implants. Body temperatures and soil temperatures at hibernaculum depth reached average minima during February of -1.9° and -6°C , respectively. Laboratory-housed ground squirrels hibernating in ambient temperatures of -4.3°C maintained above 0°C thoracic temperatures but decreased colonic temperatures to as low as -1.3°C . Plasma sampled from animals with below 0°C body temperatures had normal solute concentrations and showed no evidence of containing antifreeze molecules.

HIBERNATION IN MAMMALS IS EXPRESSED by a fall in body temperature (T_b) to near the ambient temperature of the hibernaculum. Torpid animals maintain low T_b 's for up to several weeks until a brief (<24 hours) spontaneous arousal to high T_b occurs, after which animals recool. The lowest T_b 's previously reported for natural hibernation in a variety of mammalian hibernators are between 0.5° and 2°C and in ambient conditions of 0° to 3°C (1). In experimental conditions, slowly lowering ambient temperatures below 0°C leads either to an increase in an animal's metabolism and stabilization of T_b or an "alarm arousal" after which the animal, upon returning to torpor, will actively regulate T_b at 2° to 3°C (2). Some ectothermic vertebrates can endure subzero T_b 's either by avoiding or tolerating freezing. For example, many species of polar and north

temperate fish, through use of blood antifreeze proteins or glycoproteins, live at temperatures of -1.9°C (3), and painted turtles and four species of frogs can pass the winter frozen at temperatures of -3° to -7°C (4). Accounts of endotherms surviving subzero T_b 's are either anecdotal (5) or describe the artificial induction of subzero body temperatures, a condition from which the animal could not independently arouse (6). I report telemetric and direct evidence of the regular, prolonged, and spontaneously reversible adoption of core T_b of as low as -2.9°C in the arctic ground squirrel, *Spermophilus parryii*, hibernating in outdoor enclosures.

Arctic ground squirrels were captured during late August 1987 in the northern foothills of the Brooks Range, Alaska, near the Toolik Field Station of the University of Alaska Fairbanks ($68^{\circ}38'\text{N}$, $149^{\circ}38'\text{W}$; ele-

vation 809 m) and transported to Fairbanks. Animals were implanted abdominally with miniature temperature-sensitive radiotransmitters that had been previously calibrated (7). On 19 September 1987, seven males and five females were released in Fairbanks into outdoor wire cages (0.9 by 0.9 by 1.8 m, buried to 1.3 m) where they dug burrows and remained for the next 8 months (8). Each cage was fitted with copper wire loop antennas (two or four each) housed in plastic pipe and connected to coaxial leads. Each lead was connected to a radio receiver with an interface to a computerized data acquisition system (9). Bandpass filters were used to overcome radio interference from a local AM radio station, and data collection began in mid-February 1988. In spring, after each animal emerged from the hibernaculum, transmitters were recovered and recalibrated (10). Soil and air temperatures at the site were recorded with thermocouples and a thermocouple thermometer. To determine the temperature regimes arctic ground squirrels experience during hibernation in the environment at which they were collected, soil temperatures at a depth of 1.0 m at two natural burrow sites near the Toolik Field Station were recorded over winter on automated remote recorders (11).

Minimum T_b 's of six hibernating ground squirrels occurred in February and March and averaged $-1.9^{\circ} \pm 0.3^{\circ}\text{C}$ (range -2.9° to -1.1°C). The T_b of the individual that reached the lowest T_b (-2.9°C) is shown

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