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Brain Weight-Body Weight Scaling in Breeds of Dogs and Cats

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Abstract. Autopsy data from 2,100 pet dogs are used to demonstrate that mean brain weight (y) in 26 breeds of dogs is related to mean body weight (x) by the function $y = 0.39\,x^{0.27}$. Power functions with the exponent 0.27 appear to define intra-species brain-body weight scaling in several other species. These functions may serve as base lines for measuring increases or decreases in encephalization during species evolution. Curiously, averaged data from 1,250 domestic cats of 2 breeds can be plotted on a line with slope of 0.67, which is known to define inter- rather than intra-species brain-body weight scaling among mammals.

Introduction

The relationship between brain weight and body weight in various animal species has been studied in part because of the supposed correlation between brain size and intelligence [10]. *Jerison* [3] has shown that when brain weight and body weight of many individuals of different species from the same taxonomic class are plotted on log-log paper, a straight line with slope of approximately 2/3 can be fitted to the scattered points. The major difference between classes is that the line representing one, such as mammals, is shifted above that representing another, such as reptiles. Some species within a class may also plot above or below the line representing the class. *Jerison* [4] characterizes such shifts by the expression 'encephalization quotient' (EQ), calculated as the ratio of observed to expected brain weight. The expected brain weight for 'average mammals' is given by the empirical equation: brain weight = 0.12 (body weight) $^{0.67}$ (fig. 1). *Jerison* suggests that EQ is related to intelligence, notwithstanding earlier warnings against too facile equations of brain size with intelligence [11].

Pilbeam and Gould [7] have pointed out that the slope of a line fitted to brain-body weight log-log plots of individuals of the same species is not 0.67 but is between 0.2 and 0.4. *Weidenreich* [12], for example, found a slope of 0.23 when he fitted a line to brain-body weight data for 188 dogs (collected by *Lapicque* [5]) arranged into 10 groups according to body size. Because their slopes are less steep, intra-species lines intersect *Jerison's* inter-species line for average mammals in such a way that animals with larger body weights plot below and to the right of the line (EQ less than 1) and those with smaller body weights plot above and to the left of the line (EQ greater than 1) (fig. 1). If EQ has any relevance to intelligence, it would be concluded that smaller animals of a species are more intelligent than larger ones. This is almost certainly untrue. Thus the mammalian line should not be taken as a base line from which to measure encephalization. However, it remains possible that a within-species line for each species comparable to *Jerison's* between-species line can be established, and that this might be used as a basis for estimating relative intra-species encephalization.

While the relationship between brain and body weight within a species is complicated by individual variation due to such factors as sex, breed, age and health status, this variation might be controlled by the simple procedure of averaging. One might group individuals of the same species into body weight classes; body weights and corresponding brain weights could then be averaged. This was the method employed by *Weidenreich* [12] in the dog study mentioned above. This method does offset individual variation but it could be faulted for its use of arbitrarily chosen unequal weight classes. The effect of *Weidenreich*'s grouping procedure (into average weight classes of 5, 7, 10, 15, 22 kg etc.) is to cause average brain-body weights to plot on nearly a straight line on log-log paper (with, remarkably, a correlation coefficient of 1.0). Had he selected different classes, more scatter, and a different slope would have been found.

A better way of grouping individuals to reduce variation is by breed designation. Since that is independent of both brain and body weight, arbitrary grouping is avoided. Also conclusions can be drawn about genetic influences on relative brain mass. It should be quite simple, for instance, to determine whether a particular breed has an EQ greater or less than 1.

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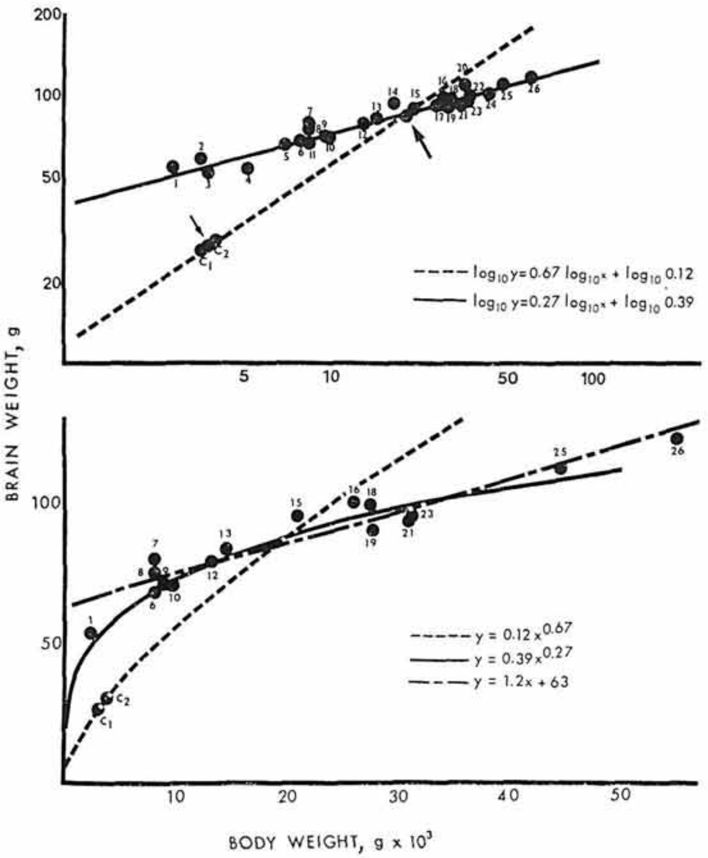

Fig. 1. Log-log plots of mean brain and mean body weights for 26 dogs (numbers) and two breeds of cat (C_1 and C_2). A line has been fitted to the canine data by linear regression. The line with steeper slope was found by *Jerison* [3] to fit plots of brain and body weights of animals of different species. The mean brain and body weights of all 1,037 dogs in the sample (long arrow) and of all 696 cats (short arrow) are included.

Fig. 2. Linear plots of mean brain and body weights of breeds for which larger samples were collected. A linear function has been fitted by linear regression. Included are the two power functions from figure 1.

The study reported here was designed to make use of extensive post-mortem data in finding how average brain weight is related to average body weight in two groups of breeds of animals, dogs *(Canis familiaris)* and cats *(Felis catus)*. As far as the author is aware the large samples desirable in such studies have not been available hitherto for dogs and cats or indeed for any other mammalian species.

Materials and Methods

Between the years 1962 and 1976 complete post-mortem examinations were performed on some 3,350 dogs and cats by staff pathologists at the Angell Memorial Animal Hospital, a veterinary hospital serving the Boston area. These animals had died from a large variety of diseases. Not all dead animals were necropsied; only those of clincial interest were selected for pathologic study. Smaller bodies and all organs were weighed on the same laboratory balance. The larger animals were generally weighed on a bathroom scale as they were held in the arms of the pathologist whose personal weight was then subtracted from the total. The brains were removed by severing them from the spinal cord at the level of the low medulla. They were weighed immediately, without the dura and without any deliberate drainage of cerebrospinal fluid.

The breed, age, sex, brain weight, body weight, coat color and cause of death were available for most animals. Data from all adult animals 1 year old or more were accepted into the analysis regardless of the pathologic diagnosis. Domestic long-haired and domestic short-haired cats of all coat colors were considered to be of the same breed. The only other cat breed represented in large numbers was the Siamese. Some 26 pure breeds and 4 mixed breeds of dogs were represented, usually in reasonable numbers. Weights of males, females, and neutered males and females of each breed were all averaged together. The male to female ratio was identical in the two cat breeds and quite similar in all dog breeds. In the few cases where one weight for an individual was missing, the other was nevertheless included in the analysis. In 11 cases, brain weights for cats, which had been recorded at 60 or more grams, were rejected; as these greatly exceed the maximum known weight for any cat brain, an error of recording was suspected. The mean brain weight and mean body weight for each dog breed were plotted on log-log paper (fig. 1). The power curve which best fitted the array of points was determined by regression analysis with the aid of a programmable calculator, which also supplied the correlation coefficient of the two measurements. The line which best fitted linearly plotted data of the 16 dog breeds for which samples were largest (fig. 2) was calculated as was the correlation coefficient. Regression analysis was also used to analyze data for the two breeds of cats. Using the same statistical methods, power functions and correlation coefficients were calculated for three other random samples: (a) individual brain and body weights for 5 adult dogs of each of the 26 breeds studied; (b) individual weights for 100 adult German shepherd dogs; (c) individual weights for 100 adult male domestic cats.

Results

The sample sizes, mean body weight and mean brain weight, plus or minus 1 SD for each of the breeds in the analysis are listed in table I. Included are data for sheep and horses drawn from the literature [1, 2, 12]. Figure 1 is a log-log plot with slope of 0.27 of mean brain and mean body weight for each of the 26 breeds of dogs. The correlation coefficient of the points along the line is 0.95. Also plotted is *Jerison*'s curve which defines scaling between mammalian species [4]. The line passes through the points which represent the mean brain-body weights of all dogs (large arrow) and all cats (small arrow) in the study. The curve also passes almost directly through the two cat breed points. Figure 2 is a linear plot of the points for dog breeds for which large samples were available. A straight line with slope of 1.2 is fitted to the 16 points by linear regression. The correlation coefficient of points with respect to this line is 0.94. The same curves plotted in figure 1 are plotted here as well.

The exponents of power functions fitted to data from the three samples described above are listed in table II. Also listed are the correlation coefficients of brain weight and body weight for these samples.

Discussion

The present method of data acquisition, using material from individual animals with a great variety of diseases, has the disadvantage of introducing uncontrolled variability in both brain and body weights. It has been assumed here that this variability is random and that averaging can produce a fair estimation of the population mean brain and mean body weight for each breed, particularly for those for which the sample is large. That these assumptions are valid, at least for the overall dog and cat samples, is shown in figure 1. The mean brain weight-mean body weight for 1,037 dogs and 696 cats plot almost exactly on *Jerison*'s line for average mammals. This finding seems to confirm both the unbiased nature of the samples and the validity of *Jerison*'s analysis.

The relatively close fit of points to the canine breed line also suggests that averaging eliminated variation sufficiently to disclose the existence of an underlying mode of inter-breed brain-body weight scaling. Interestingly, even data for the four mixed breeds listed in table I can be shown to plot close to the canine line. Some of the scatter in figure 1 can reason-

Table 1. Brain weight and body weight

	Brain weight, g		Body weight, kg		Code for figures 1 and 2
	n	$\overline{X} \pm \sigma$	n	$\overline{X} \pm \sigma$	
All cats	696	29.0 ± 5.1	696	3.6 ± 1.2	short arrow
Domestic cats	571	29.6 ± 5.5	575	3.7 ± 1.3	C_2
Siamese cats	125	26.1 ± 3.1	123	3.2 ± 0.9	C_1
All dogs	1,037	85.2 ± 11.0	1,090	19.9 ± 5.7	long arrow
Chihuahua	19	53.4 ± 8.1	24	2.6 ± 1.2	1
Toy poodle	13	59.1 ± 12.1	13	3.2 ± 1.8	2
Toy fox terrier	6	52.3 ± 3.6	6	3.4 ± 0.9	3
Pekinese	8	53.4 ± 5.2	9	4.9 ± 1.3	4
Miniature schnauzer	11	65.1 ± 6.3	11	6.7 ± 3.1	5
Miniature poodle	67	67.8 ± 8.6	70	7.7 ± 2.5	6
Boston terrier	31	80.3 ± 11.4	30	8.2 ± 2.9	7
Pug	17	77.1 ± 9.5	17	8.2 ± 2.3	8
Wirehaired fox terrier	30	71.4 ± 9.8	31	9.2 ± 2.5	9
Dachshund	54	70.9 ± 8.3	61	9.5 ± 2.6	10
Standard schnauzer	11	64.5 ± 5.7	12	7.9 ± 2.0	11
Cocker spaniel	76	78.8 ± 10.2	81	13.4 ± 3.7	12
Beagle	51	84.3 ± 11.5	53	14.6 ± 5.5	13
Bulldog	5	97.8 ± 17.1	5	16.9 ± 4.3	14
Standard poodle	57	90.7 ± 12.2	62	21.0 ± 5.2	15
Boxer	83	100.7 ± 12.2	87	26.4 ± 7.0	16
Irish setter	9	94.2 ± 11.9	8	26.5 ± 5.5	17
Doberman pinscher	27	100.4 ± 10.5	28	27.5 ± 6.3	18
Collie	34	90.2 ± 8.1	37	27.6 ± 6.8	19
Weimaraner	10	109.5 ± 6.5	11	31.0 ± 6.2	20
Golden retriever	30	95.0 ± 17.9	31	31.1 ± 6.1	21
Labrador retriever	16	104.6 ± 12.6	19	32.9 ± 6.9	22
German shepherd	110	94.7 ± 11.6	113	31.1 ± 8.0	23
Old English sheepdog	8	104.4 ± 1.8	8	38.6 ± 9.3	24
Great Dane	18	114.9 ± 14.4	17	44.4 ± 9.9	25
Saint Bernard	23	123.2 ± 9.8	27	55.0 ± 15.4	26
Terrier cross bred	54	74.0 ± 10.5	56	13.2 ± 6.3	–
Spitz cross bred	30	77.3 ± 10.4	30	13.6 ± 5.4	–
German shepherd cross bred	70	85.6 ± 14.1	73	23.3 ± 9.0	–
Collie cross bred	59	85.5 ± 12.5	60	19.3 ± 6.4	–
North German moorland sheep [2]	26	112.0 ± 6.5	26	36.8 ± 4.5	–
Blackhead sheep [2]	27	120.3 ± 8.1	27	58.4 ± 8.5	–
Bikaneri and Hissar-Dale sheep [1]	176	86.8 ± 0.7	176	18.4 ± 0.3	–
Heavy Belgian horse [12]		720		1,040	–
Light Camargue horse [12]		525		320	–
Shetland pony [12]		425		128	–

Table II. Results of regression analysis of 5 samples of brain weights and body sizes

Sample	Exponent of power function fitted to log-log plots of data	Correlation coefficient
100 adult German shepherd dogs	0.1	0.22
100 adult male domestic cats	0.01	0.14
130 dogs of 26 breeds	0.25	0.66

ably be attributed simply to the small sizes of some samples. Wider sampling might, then, be expected to reduce the scatter.

Two objections can be made to the analytic method used here. First it is generally improper statistical practice to fit regression lines to pairs of measurements both of which are independent and subject to error. This is particularly true if the two parameters are not well correlated. For example individual brain weight and body weight were poorly correlated in the three samples of table II, and the scaling exponents have little or no meaning. On the other hand, if two independent parameters such as mean brain weight and mean body weight for breeds of dogs are well correlated, regression analysis can be applied with little chance of error [7]. (The regression line of figure 1 could as well be fitted by eye as by calculation.)

A second objection to the present method is that the canine brain weights and body weights may not be related allometrically. The relationship between the two may be linear. Given the scatter in the data presented, both the linear and the power functions fit the data about equally well. Perhaps larger samples, particularly of the toy breeds, would help to resolve the issue by fixing data points in the left-hand curved portion of the power function as depicted in figure 2.

Figure 1 shows that the mean body and mean brain weights for two cat breeds plot almost exactly on *Jerison*'s mammalian line. A trend line cannot be fitted with complete certainty to two points so close together. However, the standard errors of the four means involved are small enough that no highly unlikely shift of points to within 2 SE of any of the means would place them on a line with slope less than 0.50. In contrast, the relationship between most adjacent points in the canine breed line of figure 1 is relatively less well fixed because of the small size of the samples involved. A further argument that the two cat points are situated on the graph by factors other than chance is precisely that they fall on *Jerison*'s line, which was derived by completely independent sampling and analytic procedures.

That brain-body weights scale in this way in domestic cats seems to contradict the results of *Schauenberg* [8]. He found that brain weight (cranial capacity) in the species is related to the longest skull length (presumably a function of body size) along a log-log plot with slope of approximately 0.20. However, *Schauenberg*'s data for domestic cats actually describe within-breed not between-breed scaling. The scatter intrinsic to such individual animal data has not been controlled by averaging; as previously discussed regression analysis applied to such data is an uncertain procedure. Therefore it may not be meaningful to draw conclusions about intra-species scaling from *Schauenberg*'s findings. This does not, it should be added, in any way detract from the validity of his methods or conclusions which involve questions unrelated to those discussed here.

Inter-breed brain-body weight scaling has not been studied in other mammalian species by averaging methods. There is evidence, though, that breeds of some other species scale in the canine fashion. The data cited by *Weidenreich* [12] for three breeds of horses plot on log-log paper along a line with slope of 0.27. A similar plot of averaged data for two breeds of domestic sheep at least 1 year old [2] and of the averaged data for two other breeds combined together [1] has the same slope. Thus the slope of the canine function, 0.27, might have general application to intra-species scaling much as *Jerison*'s slope of 0.67 has general application to inter-species scaling.

F. catus appears to be an exception to this rule since the data for the two breeds studied scale along a line with a slope of 0.67. The reasons for this aberrancy are not known; conceivably the intensive breeding of Siamese cats has produced a morphological approximation of a different species with respect to domestic long-haired/short-haired cats.

It would be interesting to know whether brain and body weights of the races of man scale in the canine or in the feline fashion. The necessary data to answer the question are unavailable, since body weight is not routinely recorded in most human autopsies. In fact, presumably because body weight fluctuates so markedly in disease, there has been a general tendency to disregard it and to favor body stature as the measure with which to compare brain weight in studies of human beings [6, 9]. Brain weight and stature have indeed been shown to be correlated [6] but it is not known how the two parameters are related allometrically, nor have such data been analyzed by the averaging method used in this study of dogs and cats.

A question which cannot be answered by this study is whether any dog breed has a greater or lesser average brain weight than expected for the average breed body weight. An answer would require first that a suitable base line be established. The log-log plot with slope of 0.27 may be taken as such a line, both because individual breed points plot with reasonably little scatter along the line and because the slope appears to have a general application to several species. However, one would also have to establish the statistical significance of deviations from the line, and for that large samples for all breeds are required. This condition could not be met here.

In the future other investigators may add data to those presented in table I. If a dog breed is eventually shown to have a significantly larger or smaller average brain weight than expected, then suitable behavioral testing can be applied to answer whether the brain size, once individual variation has been removed, correlates with intelligence.

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