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RELATION OF LIFESPAN TO BRAIN WEIGHT, BODY WEIGHT, AND METABOLIC RATE AMONG INBRED MOUSE STRAINS*

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SACHER (1959) has previously shown that between mammalian species there is a high degree of correlation between longevity and body weight and between longevity and brain weight. He extended his analysis to show that it is probably not body weight or brain weight *per se* that is of importance in determining longevity, but rather that the metabolic rate which is negatively correlated with body weight and the index of cephalization (the deviation of the brain weight of a species from the regression of brain weight on body weight) are the important variables. He pointed out that the view is widely held that ageing results from irreversible molecular change and postulated that a low metabolic rate and a high index of cephalization would reduce the rate of incidence of two classes of metabolic errors leading to irreversible changes. The first of these is the error rate in the steady state of metabolic activity, i.e. the probability of naturally occurring errors even when the metabolic system is operating under optimum conditions. These errors should be proportional to the metabolic rate and a low metabolic rate (associated with large body size) should lead to increased longevity. A second class of errors are postulated to occur when there is a deviation in metabolic processes from the normal steady state. Such fluctuations will occur spontaneously but their magnitude will be controlled by the efficiency of the integrative control mechanisms which restore these processes to the normal or average state. Presumably the central nervous system in mammals is an important control system. If function is proportional to size then it should follow that species with a high index of cephalization should have superior control systems, deviation in metabolic processes should be minimized, and errors of the second type should also be minimized. This decreased error rate would then lead to increased longevity.

More recently, Sacher (1963) has also demonstrated that between species but within orders (rodents, insectivores, and primates) the brain weight, body weight, and longevity relationships are consistent with his earlier report.

While any general theory of ageing should account for characteristic species differences in longevity, it should also account for individual differences in longevity within a single species. For this reason we decided to use inbred strains of mice to examine the relationships reported by Sacher. Data on longevity, metabolic rate, body weight, and brain weight were obtained on samples of mice of both sexes from eighteen strains. Thus we examined in detail eighteen different genetic constitutions to ascertain whether characteristic differences in brain size and metabolic rate were correlated with longevity. This study is the subject of the present report.

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MATERIALS AND METHODS

All the mice were born and raised in this laboratory. At weaning they were housed four or five to a plastic cage and maintained on Old Guilford Laboratory Chow and water *ad libitum*. The cages were changed at weekly intervals when fresh bedding (wood shavings) and water were provided. The only exception to group caging occurred in the case of AKR/J, BALB/cJ, RF/J, SWR/J, and SJL/J males. Males of these strains fight vigorously and we caged them singly. Brain weight, body weight, and metabolic rate determinations were made on samples of mice when they reached the age of 118–122 days.

The oxygen consumption of individual mice was measured in a commercially available spirometer designed to measure small volume changes in a closed system. The mice were restrained in a wire mesh tube which was placed on a wire screen in a 1-l. bottle. The area under the screen contained "Ascarite" (sodium hydrate absorbed on asbestos particles) to absorb the expired carbon dioxide and "Drierite" (anhydrous calcium sulfate) to absorb moisture. The bottle was then connected to the spirometer to produce a closed system. As carbon dioxide and moisture were absorbed, the pressure in the system was reduced. The reduction in pressure was detected by a pressure transducer which activated a motor-driven piston in a calibrated cylinder. Air was forced into the system to re-establish the original pressure. As additional carbon dioxide and moisture were absorbed, the sequence was repeated. Since the device detected pressure variations of a fraction of a millimeter of water, it was possible to estimate oxygen consumption under conditions of essentially constant pressure. A recording pen connected to the piston by a rigid support recorded the linear movement of the piston. A motor-driven cam deflected the pen downward at one minute intervals so that linear travel of the piston per unit time could be accurately estimated. Since the cylinder containing the piston had a constant and known cross section, the recorded pen travel could be converted to cc. of air injected into the system and the oxygen consumption measured.

Determinations were made on ten male and ten female mice from each of the eighteen strains. In order to minimize the effect of diurnal variations in the mice, all measurements were made between one and five P.M. Room temperature varied between 22 and 25°C. The mice were not fasted before testing since the primary interest of the study was the estimation of the normal level of oxygen consumption. After the mice were placed in the test system, 10 min were allowed for the system to reach equilibrium. Recordings of the rate of injection of air into the system were then made for 20 min. Metabolic rate was expressed as cc of oxygen consumed per hour per gram of body weight. These values are related by a constant to the more usual measurement of calories per gram per unit time.

Wet brain weight was measured on samples of mice from each sex and strain at 120 days of age. Additional weights were obtained in some of the strains at 250 days. Since the weights in the older mice did not differ significantly from those in the younger animals, it was concluded that adult brain weights remain reasonably constant at least over a significant portion of adult life and that the 120-day weights adequately characterized those strains.

Methods and the data for the longevity portion of the study have been published previously (Storer, 1966).

Body weights were obtained at 120 days in the mice used in the longevity study.

Body weights were also obtained on the mice whose metabolic rates were measured as well as on the mice killed for brain weights. In preliminary computations the body weight values from all three sources were used in obtaining various regression relationships. Since the conclusions were the same regardless of which set of body weight data were used, we have elected to reduce the number of variables and have used only the weight data from the metabolism study in this report.

Data on weights were transformed to logarithms before computing means and variances since they tended to show a log normal distribution. The logarithm of the arithmetic means of the other variables were used in calculating regression relationships since allometric relationships are classically of this type and transformed variables were used by Sacher. The standard statistical methods used were as described by Snedecor (1956).

RESULTS

The strain means and standard errors for all the variables are shown in Appendix Tables 1–4. Analysis of variance with F-testing showed highly significant ($P < 0{\cdot}001$) strain differences in mean lifespan, body weight, brain weight, and metabolic rate. The mean values obtained for each strain were considered to characterize each strain adequately and these means were used to examine correlation and regression relationships between the variables.

Correlations were examined first for both males and females and the coefficients are shown in Table 1. The metabolic rate was the only variable to show consistent significant correlations with the other variables. As anticipated it was highly negatively correlated with body weight in both males and females. There was also a significant positive correlation with lifespan. This finding contrasts sharply with Sacher's study between species in that his correlation was of opposite sign, i.e. a low metabolic rate was associated with a long lifespan. Note also that the correlations between lifespan and body weight and lifespan and brain weight, though not significant, are nevertheless consistently negative in contrast to Sacher's finding of positive correlations.

TABLE 1. COEFFICIENTS OF CORRELATION BETWEEN LOG MEAN LIFESPAN, MEAN LOG BODY WEIGHT, MEAN LOG BRAIN WEIGHT, AND LOG MEAN METABOLIC RATE IN MALE AND FEMALE MICE FROM EIGHTEEN INBRED STRAINS

	Body weight		Brain weight		Metabolic rate	
	Males	Females	Males	Females	Males	Females
Lifespan	−0·266	−0·334	−0·090	−0·328	+0·511*	+0·535*
Body weight	—	—	+0·226	+0·314	−0·742†	−0·756†
Brain weight	—	—	—	—	−0·356	−0·539*

* $P<0{\cdot}05$.
† $P<0{\cdot}01$.

The analysis was extended to examine the regression relationships between the variables. The appendix lists the statistical parameters in sufficient detail that further extension to multiple regression, partial correlation, etc., can be easily accomplished. The only regression coefficients that differed significantly from zero were, of course, for those variables showing significant correlations (Table 1).

It was concluded that for the strains of mice studied there was no evidence of a significant association between longevity and either body weight or brain weight. Further, since the regression coefficient for brain weight on body weight did not differ significantly from zero there was no justification for calculating the index of cephalization. In effect the brain weight data *per se* are equivalent to the index of cephalization.

There was a significant positive association between longevity and metabolic rate. Regression of log lifespan on log body weight reduced the variance in lifespan by 22 and 24 per cent, respectively, for males and females. Because of the very high negative correlation between body weight and metabolic rate we decided to eliminate the effect of body weight on metabolic rate and re-examine the relationship to lifespan. This was accomplished as follows. The regression of metabolic rate (v) on body weight (x) is given by:

Males	$v = 1{\cdot}4765 - 0{\cdot}5471x$
Females	$v = 1{\cdot}4210 - 0{\cdot}5162x$

We then defined a new variable (m) which we have tentatively called the "index of metabolism" to make it analogous to the index of cephalization. This new variable is the deviation of a strain metabolic rate value from the overall regression of metabolic rate on body weight and is the logarithm of the fraction of metabolic rate that is independent of body size. The deviation is given by the following equations:

Males	$m = V_0 - 1{\cdot}4765 + 0{\cdot}5471x$
Females	$m = V_0 - 1{\cdot}4210 + 0{\cdot}5162x$

where V_0 is the observed strain metabolic rate.
By this definition the index of metabolism (m) is orthogonal to body weight (x).

The index of metabolism was calculated for each strain and the regression coefficients for log lifespan (y) on this index were found to be:

Males	$b_{ym} = 1{\cdot}7800 \pm 0{\cdot}6670$	$P < 0{\cdot}02$
Females	$b_{ym} = 1{\cdot}1637 \pm 0{\cdot}6664$	$P = 0{\cdot}10$

Inasmuch as only one of the regression coefficients differ significantly from zero, we cannot conclude that a relationship between the index of metabolism and longevity has been established. The evidence is suggestive, however, and indicates an area of research meriting further study.

DISCUSSION

Between species of mammals there is a high degree of correlation between log lifespan and log body weight, log lifespan and log brain weight, log body weight and log brain weight, and log lifespan and index of cephalization (Sacher, 1959, 1963). When we examined these relationships between genotypes within a species (as represented by eighteen inbred mouse strains) we were unable to demonstrate a significant correlation between any of these variables. When we consider possible reasons for this negative result we must first consider whether samples from inbred mouse strains are adequately analogous to genotypes from a natural population. This can probably be seriously questioned. Many of the strains originated through selection for particular attributes such as the incidence of certain tumors which may normally arise infrequently in natural outbred populations. This tendency to specific disease incidence in some of the strains creates considerable doubt that all the strains die from age related or senescent disease

processes. We have previously reported on the diseases present at death in these strains and know that especially in females, a number of strains have a very high early incidence of tumors or polydipsia and polyuria. We have elected not to reject data from these strains from the computations since there is no sound basis for doing so and because by rejecting some strains and keeping others we could arive at any predetermined correlations we might desire. There is uncertainty, then, that samples from inbred strains are adequately analogous to natural populations.

On the other hand, the very process of selection and inbreeding may have resulted in a greater variability between strains with respect to the characteristics investigated than would normally be encountered in the wild. If true, this should make it easier to identify correlated characteristics. This dilemma will probably not be solved until direct comparisons of inbreds and wild stocks are made.

If we can assume that our sampling technique adequately characterized the species, there are other reasons why the negative results might have emerged. The brain weights, while showing significant strain differences, represented a relatively narrow weight range. Brain development may be optimum for the species and the relatively small variations from genotype to genotype may not reflect any significant differences in the functional adequacy of the system to maintain metabolic homeostasis. Similarly, the relatively small strain differences in metabolic rate would not necessarily lead to significant effects on the metabolic error rate postulated by Sacher (1959).

The meaning of the possible correlation between a component of metabolic rate which is independent of body size and the mean lifespan is not clear. It is tempting to speculate that a high value for this component may ensure rapid repair or recovery from spontaneously occurring or environmentally inflicted injury. We really have no evidence for this and the relationship should be adequately established before further speculation is justified. Further study of this relationship seems desirable since it might, if confirmed, lead to insight into a factor responsible in part for individual differences in survival time within a species.

On the basis of the data presented we must conclude that we found no evidence that two of the factors (metabolic rate and index of cephalization) postulated by Sacher (1959) to account for species differences in longevity are of significance in explaining characteristic differences in longevity within a species, at least to the extent that a species can be represented by an array of inbred mouse strains. The metabolic rate was significantly correlated with longevity but of opposite sign to that found between species. Brain weight was not significantly correlated with longevity. It appears, therefore, that the explanation for individual differences in survival time must be sought elsewhere.

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Summary—Mean values for lifespan, brain weight, body weight, and metabolic rate were determined for male and female mice in 18 different inbred strains. No significant correlation between means for log lifespan and log brain weight, log lifespan and log body weight, or log brain weight and log body weight could be demonstrated. The mean metabolic rate was significantly positively correlated with longevity in both sexes. A component of metabolic rate which is independent of body size may also be positively correlated with longevity. The findings contrast sharply with the between-species correlations of these variables. Possible reasons for this disparity are discussed.

Résumé—On a déterminé chez des souris mâles et femelles de dix-huit souches consanguines différentes la moyenne de la durée de vie, du poids du cerveau, du poids du corps et du taux du métabolisme. Il n'a pas été possible de démontrer une corrélation significative permettant de relever des diagrammes sur la durée de vie et le poids du cerveau, sur la durée de vie et le poids du corps, ou sur le poids du cerveau et le poids du corps. On a trouvé une corrélation positive significative entre la moyenne du taux métabolique et la longévité chez les deux sexes. Il pourrait y avoir aussi une corrélation positive entre un élément du taux métabolique, indépendant du volume du corps, et la longévité. Il y a un contraste marqué entre ces résultats et les corrélations des mêmes variables chez les espèces intermédiaires. On discute des raisons possibles pour une telle disparité.

Zusammenfassung—Die Mittelwerte für Lebensdauer, Hirngewicht, Körpergewicht und Stoffwechselrate wurden bei männlichen und weiblichen Mäusen von 18 verschiedenen Inzuchtstämmen ermittelt. Zwischen den Mittelwerten (alle Werte im logarithmischen Maßstab) von Lebensdauer und Hirngewicht, Lebensdauer und Körpergewicht bzw. Hirngewicht und Körpergewicht konnte keine Korrelation hergestellt werden. Für die mittlere Stoffwechselrate bestand mit der Lebenserwartung bei beiden Geschlechtern eine deutliche positive Korrelation. Eine von der Körpergröße unabhängige Komponente der Stoffwechselrate könnte ebenfalls mit der Lebenserwartung in positiver Korrelation stehen. Die Ergebnisse widersprechen den Interspezies-Korrelationen dieser Variablen erheblich. Es werden mögliche Gründe für diese Diskrepanz diskutiert.

Резюме—Были установлены средние величины продолжительности жизни, веса мозгов, веса тела и быстроты обмена веществ для мышей мужского и женского пола у 18 различных инбредных пород. Не было выявлено никакого важного соотношения между средними величинами журнальной продолжительностью жизни и журнальным весом мозгов, между журнальной продолжительностью жизни и журнальным весом тела, или между журнальным весом мозгов и журнальным весом тела. Средняя величина быстроты обмена веществ положительно соотносилась в значительной степени с продолжительностью жизни обоих полов. Составная часть быстроты обмена веществ, которая не зависит от размера тела, может тоже положительно соотноситься с продолжительностью жизни. Эти открытия резко противоречат с соотношениями промежуточных видов этих переменных величин. Обсуждаются возможные причины этого несоответствия.

APPENDIX

1. Strain means and standard errors for the four variables (lifespan, log body weight, metabolic rate, and log brain weight) are given in Appendix Tables 1–4. Weight data were transformed to logarithms before calculating means and standard errors. The antilog of the mean log weight is shown for easy strain comparisons.

2. The values for strain means (Tables 1–4) were considered to characterize each of the individual strains. These values were used in calculations of correlation and regression. The means and standard errors of the variables with their variances are given below.

Males

Log lifespan (days)	$\bar{y} = 2{\cdot}7352 \pm 0{\cdot}02504$	$S^2y = 0{\cdot}01066$
Log body wt. (g)	$\bar{x} = 1{\cdot}5135 \pm 0{\cdot}01581$	$S^2x = 0{\cdot}00425$
Log brain wt. (mg)	$\bar{z} = 2{\cdot}6446 \pm 0{\cdot}00730$	$S^2z = 0{\cdot}00096$
Log metabolic rate (cc of O_2/g per hr)	$\bar{v} = 0{\cdot}6485 \pm 0{\cdot}0133$	$S^2v = 0{\cdot}00231$
Index of metabolism	$\bar{m} = 0 \pm 0{\cdot}00759$	$S^2m = 0{\cdot}00104$

Females

Log lifespan (days)	$\bar{y} = 2{\cdot}7353 \pm 0{\cdot}02783$	$S^2y = 0{\cdot}01395$
Log body wt. (g)	$\bar{x} = 1{\cdot}4494 \pm 0{\cdot}02141$	$S^2x = 0{\cdot}00825$
Log brain wt. (mg)	$\bar{z} = 2{\cdot}6608 \pm 0{\cdot}00744$	$S^2z = 0{\cdot}00100$
Log metabolic rate (cc of O_2/g per hr)	$\bar{v} = 0{\cdot}6728 \pm 0{\cdot}01462$	$S^2v = 0{\cdot}00385$
Index of metabolism	$\bar{m} = 0 \pm 0{\cdot}00957$	$S^2m = 0{\cdot}00165$

3. Additional statistical parameters are shown below. Extension to multiple regression or partial correlation can easily be made. In this notation the sum of squares for variables x and y are shown as Sxx and Syy. The sum of products for variables x and y or y and z are shown as Sxy or Syz.

Males

Sums of squares	*Sums of products*
$Syy = 0{\cdot}181261$	$Syx = -0{\cdot}030398$
$Sxx = 0{\cdot}072247$	$Syz = -0{\cdot}004879$
$Szz = 0{\cdot}016324$	$Syv = +0{\cdot}043133$
$Svv = 0{\cdot}039249$	$Sym = +0{\cdot}031367$
$Smm = 0{\cdot}017622$	$Sxz = +0{\cdot}007771$
	$Sxv = -0{\cdot}039527$
	$Szv = -0{\cdot}009021$

Females

Sums of squares	*Sums of products*
$Syy = 0{\cdot}237066$	$Syx = -0{\cdot}060966$
$Sxx = 0{\cdot}140334$	$Syz = -0{\cdot}020809$
$Szz = 0{\cdot}016960$	$Syv = +0{\cdot}066662$
$Svv = 0{\cdot}065420$	$Sym = +0{\cdot}032611$
$Smm = 0{\cdot}028023$	$Sxz = +0{\cdot}015319$
	$Sxv = -0{\cdot}072443$
	$Szv = -0{\cdot}017940$

4. Coefficients for regression of one variable on another are listed below with their standard errors. The coefficient for regression of variable y or x or y on z is denoted as b_{yx} or b_{yz}. The residual variance remaining in variable y after removing the variance due to its regression on x is denoted as $S^2y \cdot x$.

Males

Log lifespan on log body weight $b_{yx} = -0{\cdot}4208 \pm 0{\cdot}3818$	$S^2y.x = 0{\cdot}01053$
Log lifespan on log brain weight $b_{yz} = 0{\cdot}2989 \pm 0{\cdot}8297$	$S^2y.z = 0{\cdot}01124$
Log lifespan on log metabolic rate $b_{yv} = 1{\cdot}0990 \pm 0{\cdot}4617$	$S^2y.v = 0{\cdot}00837$

Males

Log brain weight on log body weight
$b_{zx} = 0{\cdot}1076 \pm 0{\cdot}1158$ $S^2z.x = 0{\cdot}00097$
Log metabolic rate on log body weight
$b_{vx} = -0{\cdot}5471 \pm 0{\cdot}1235$ $S^2v.x = 0{\cdot}00110$
Log metabolic rate on log brain weight
$b_{vz} = 0{\cdot}5526 \pm 0{\cdot}3622$ $S^2v.z = 0{\cdot}00214$
Log lifespan on index of metabolism
$b_{ym} = 1{\cdot}7800 \pm 0{\cdot}6670$ $S^2y.m = 0{\cdot}00784$

Females

Log lifespan on log body weight
$b_{yx} = -0{\cdot}4344 \pm 0{\cdot}3062$ $S^2y.x = 0{\cdot}01316$
Log lifespan on log brain weight
$b_{yz} = -1{\cdot}2269 \pm 0{\cdot}8829$ $S^2y.z = 0{\cdot}01322$
Log lifespan on log metabolic rate
$b_{yv} = 1{\cdot}0190 \pm 0{\cdot}4020$ $S^2y.v = 0{\cdot}01057$
Log brain weight on log body weight
$b_{zx} = 0{\cdot}1092 \pm 0{\cdot}0825$ $S^2z.x = 0{\cdot}00096$
Log metabolic rate on log body weight
$b_{vx} = -0{\cdot}5162 \pm 0{\cdot}1117$ $S^2v.x = 0{\cdot}00175$
Log metabolic rate on log brain weight
$b_{vz} = -1{\cdot}0578 \pm 0{\cdot}4137$ $S^2v.z = 0{\cdot}00290$
Log lifespan on index of metabolism
$b_{ym} = 1{\cdot}1637 \pm 0{\cdot}6664$ $S^2y.m = 0{\cdot}01244$

APPENDIX TABLE 1. MEAN LIFESPAN OF MICE FROM EIGHTEEN INBRED STRAINS*

Strain	Males n	Males Mean ± S.E. (days	Females n	Females Mean ± S.E. (days)
A/J	70	490 ± 18·4	78	590 ± 18·8
AKR/J	39	326 ± 15·9	72	276 ± 8·9
BALB/cJ	28	539 ± 33·0	76	575 ± 14·9
BDP/J	80	421 ± 12·4	75	468 ± 16·7
CBA/J	73	527 ± 17·0	75	527 ± 15·4
C57BL/6J	74	676 ± 20·3	75	692 ± 15·7
C57BR/cdJ	76	703 ± 17·4	73	694 ± 19·9
C3HeB/FeJ	82	652 ± 16·6	78	657 ± 14·5
DBA/1J	29	728 ± 28·0	70	750 ± 19·9
DBA/2J	75	707 ± 22·4	80	714 ± 21·4
MA/J	76	459 ± 19·4	74	585 ± 13·7
P/J	78	384 ± 13·7	81	510 ± 15·1
RF/J	33	651 ± 24·5	81	452 ± 13·1
SJL/J	30	472 ± 25·1	76	395 ± 11·3
SM/J	75	572 ± 17·0	77	591 ± 14·5
ST/bJ	72	433 ± 22·9	80	511 ± 15·1
SWR/J	34	616 ± 29·2	66	496 ± 20·8
129/J	79	679 ± 18·9	78	648 ± 24·4

* Storer (1966).

APPENDIX TABLE 2. BODY WEIGHT AND METABOLIC RATE IN 120-DAY OLD MALE MICE FROM EIGHTEEN INBRED STRAINS

Strain	n	Mean log body wt. ± S.E.	Antilog of mean body wt. (g)	Mean metabolic rate ± S.E. (cc O_2/g/hr)
A/J	10	1·5470 ± 0·02150	35·2	4·08 ± 0·241
AKR/J	10	1·6483 ± 0·01512	44·5	3·53 ± 0·081
BALB/cJ	10	1·4974 ± 0·00725	31·4	4·36 ± 0·156
BDP/J	10	1·4727 ± 0·01378	29·8	4·32 ± 0·291
CBA/J	10	1·6140 ± 0·01403	41·1	4·22 ± 0·145
C57BL/6J	10	1·4639 ± 0·00829	29·1	4·55 ± 0·148
C57BR/cdJ	10	1·5161 ± 0·01214	32·8	4·60 ± 0·184
C3HeB/FeJ	10	1·5727 ± 0·02362	37·4	4·22 ± 0·179
DBA/1J	10	1·5353 ± 0·01833	34·3	4·53 ± 0·317
DBA/2J	10	1·4466 ± 0·02326	28·0	5·71 ± 0·266
MA/J	10	1·4808 ± 0·02734	30·3	4·81 ± 0·268
P/J	10	1·4619 ± 0·01308	29·0	4·16 ± 0·158
RF/J	10	1·5680 ± 0·01394	37·0	4·40 ± 0·148
SJL/J	10	1·4301 ± 0·01478	26·9	5·52 ± 0·138
SM/J	10	1·4543 ± 0·01269	28·5	4·45 ± 0·236
ST/bJ	10	1·6037 ± 0·01896	40·2	3·92 ± 0·183
SWR/J	10	1·4584 ± 0·00914	28·7	4·68 ± 0·242
129/J	10	1·4726 ± 0·01428	29·7	4·54 ± 0·159

APPENDIX TABLE 3. BODY WEIGHT AND METABOLIC RATE IN 120-DAY OLD FEMALE MICE FROM EIGHTEEN INBRED STRAINS

Strain	n	Mean log body wt. ± S.E.	Antilog of mean body wt. (g)	Mean metabolic rate ± S.E. (cc O_2/g/hr)
A/J	10	1·5442 ± 0·02138	35·0	4·39 ± 0·252
AKR/J	10	1·6214 ± 0·02151	41·8	3·40 ± 0·098
BALB/cJ	10	1·4026 ± 0·01661	25·3	4·84 ± 0·144
BDP/J	10	1·3863 ± 0·01190	24·3	4·42 ± 0·115
CBA/J	10	1·5780 ± 0·01686	37·8	3·91 ± 0·191
C57BL/6J	10	1·3690 ± 0·01138	23·4	4·89 ± 0·194
C57BR/cdJ	10	1·3857 ± 0·00782	24·3	6·04 ± 0·440
C3HeB/FeJ	10	1·5687 ± 0·02033	37·0	4·14 ± 0·262
DBA/1J	10	1·4494 ± 0·02190	28·1	4·60 ± 0·300
DBA/2J	10	1·4379 ± 0·02797	27·4	5·50 ± 0·278
MA/J	10	1·4804 ± 0·01473	30·2	4·69 ± 0·236
P/J	10	1·3549 ± 0·01839	22·6	4·23 ± 0·174
RF/J	10	1·5558 ± 0·01668	36·0	4·34 ± 0·194
SJL/J	10	1·3486 ± 0·02356	22·3	5·48 ± 0·154
SM/J	10	1·4166 ± 0·01962	26·1	5·01 ± 0·214
ST/bJ	10	1·4906 ± 0·02581	30·9	4·68 ± 0·335
SWR/J	10	1·3462 ± 0·01033	22·2	5·49 ± 0·265
129/J	10	1·3526 ± 0·01593	22·5	5·50 ± 0·157

APPENDIX TABLE 4. BRAIN WEIGHT IN 120-DAY OLD MICE FROM EIGHTEEN INBRED STRAINS

Strain	Females			Males		
	n	Mean log brain wt. ± S.E.	Antilog (mg)	n	Mean log brain wt. ± S.E.	Antilog (mg)
A/J	10	2·6417 ± 0·00395	438	10	2·6353 ± 0·00388	432
AKR/J	10	2·6847 ± 0·00942	484	4	2·6499 ± 0·00523	447
BALB/cJ	10	2·7239 ± 0·00338	529	10	2·7191 ± 0·00238	524
BDP/J	10	2·6662 ± 0·00506	464	10	2·6132 ± 0·00446	410
CBA/J	10	2·6915 ± 0·00322	491	18	2·6779 ± 0·00307	476
C57BL/6J	10	2·6517 ± 0·00419	448	17	2·6523 ± 0·00268	449
C57BR/cdJ	10	2·6192 ± 0·00614	416	10	2·6332 ± 0·00288	430
C3HeB/FeJ	10	2·6943 ± 0·01512	495	10	2·6753 ± 0·00621	473
DBA/1J	10	2·6077 ± 0·00277	405	10	2·6087 ± 0·00276	406
DBA/2J	10	2·6259 ± 0·00366	423	10	2·6030 ± 0·01114	401
MA/J	10	2·6696 ± 0·00540	467	10	2·6577 ± 0·00521	455
P/J	10	2·6853 ± 0·00849	485	10	2·6729 ± 0·00471	471
RF/J	10	2·6906 ± 0·00235	490	10	2·6555 ± 0·00570	452
SJL/J	10	2·6191 ± 0·00607	416	12	2·6070 ± 0·00365	405
SM/J	10	2·6632 ± 0·00643	460	10	2·6133 ± 0·00962	410
ST/bJ	10	2·6412 ± 0·00458	438	13	2·6208 ± 0·00743	418
SWR/J	10	2·6738 ± 0·00664	472	20	2·6636 ± 0·00547	461
129/J	10	2·6455 ± 0·00479	442	12	2·6438 ± 0·00267	440