ENCEPHALIZATION OF THE KOALA, *PHASCOLARCTOS CINEREUS*

CARMEN DE MIGUEL AND MACIEJ HENNEBERG

Brain size relative to body size is considered to be an indicator of variously defined 'braininess' (=encephalization). Indices of encephalization are based on the ratio of the animal's actual brain size to its expected brain size calculated from an allometric equation derived from a brain size / body weight relationship in a series of taxa. Freshly collected data on brain and body weights of 27 adult koalas *(Phascolarctos cinereus)* from South Australia are analysed here. Sex- averaged brain weight in this sample is 19.2 g and body weight is 8.0 kg. General equations for mammals produce encephalization values for the koala well below the mammalian average: EQ=38.9% according to Jerison's equation (1973), EQ= 49.7% applying Eisenberg's equation (1981) and EQ= 35.3% using Martin's equation (1990). When a 'basal' insectivore line is used, the koala appears to be progressive: IP =155.9% according to Stephan's equation (1972) and ICC= 131.7% using Martin's equation (1990). Use of 'basal' marsupial lines also indicates progressive encephalization of the koala: PI=116.5% according to Pirlot's equation (1981), E=108.4% following Nelson and Stephan's equation (1982) and E=107.9% using Haight and Nelson's equation (1987). These new results are clearly higher than the indices for the koala reported earlier by other authors (Nelson and Stephan 1982; Haight and Nelson 1987). It follows that choice of samples and equations influences conclusions regarding encephalization of a species.

Key words: Brain, allometry, marsupials, body weight, freezing.

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THE encephalization of an animal is commonly regarded as an index of its intellectual abilities although there is neither a universally accepted definition of "intelligence" nor reliable evidence that brain size is related to intellectual performance. It is rather easy, however, to measure encephalization since it is an index of brain size relative to body size. Encephalization indices and brain size/body size relationships have been extensively used in human evolution studies (eg. Tobias 1971; Jerison 1973; Holloway 1979; Passingham 1975; Blumenberg 1983; Martin 1983; Beals, Smith and Dodd 1984; Henneberg 1987, 1988a, 1988b, 1990).

The relation between brain size and body size of mammals is not linear but follows a simple allometric equation $E= a\ W^{b}$, where E is the brain size and W represents the body size, a and b being constants, known as intercept and slope respectively. Logarithmic transformation produces a linear equation $log\ E = b\ log\ W + log\ a$ which is easier to use in statistical analyses. Using variously selected samples, various authors have produced a series of values of the allometric slope and intercept.

Practically all slopes for samples representing a cross-section of mammals fall between 2/3 (0.67) and 3/4 (0.75). The encephalization index (E) is basically calculated as a ratio of actual brain size of an animal to a brain size predicted for the animal of its body size from a basic allometric equation: $E= E_r / E_e$, where E_r is the actual brain size and E_e is the expected brain size $(E_e = a\ W^{b})$. The choice of an equation and of values of its parameters must influence the measure of encephalization index of an animal. Obviously, the accuracy of measurement of brain and body size also influences the index.

Recent studies of encephalization (Martin 1990) suggested that the brain size / body size relationship of an "average" marsupial falls well into the range of eutherian values. Studies of the encephalization of the koala by Nelson and Stephan (1982) and by Haight and Nelson (1987) show poor encephalization of these animals as contrasted with the related wombats, *(Vombatus ursinus* and *Lasiorhinus latifrons)* which are well encephalized. Samples on which these studies were based, however, were small (Nelson and Stephan: 6 koalas and 9 wombats from 2

species; Haight and Nelson: 7 koalas for body mass and 11 for brain mass, 6 wombats for brain and body mass). One of the possible explanations for the poor encephalization of the koala is that the brain is only about 60% of the endocranial volume (Haight and Nelson 1987) in contrast to other marsupials and eutherians where it is usually close to 80% (Tobias 1971, Jerison 1973).

The aim of the present study is to test the hypothesis of poor encephalization of the koala using larger samples of fresh brains of animals of known body weight. This also allows further assessment of the relationship between brain size and endocranial volume of the koala.

MATERIALS AND METHODS

The sample consisted of 18 males and 9 females. All individuals had completely erupted fourth molars and hence were adults of a minimum age of two years (Eberhard 1972). The animals studied died of natural or accidental causes in the Adelaide Hills or on Kangaroo Island. They were collected under University of Adelaide Animal Ethics Permit 5/3/96 and National Parks Permit K23749-02. They were weighed to the nearest 200 g on electronic scales upon delivery to the Department of Anatomical Sciences, University of Adelaide.

Procedure for brain extraction was specifically developed for this study so as to provide maximum accuracy of the measurement of the fresh brain volume and brain weight and of the endocranial volume. The heads were frozen at - 80° C in a deep freezer (Forma Scientific 8538) and then cut through a midsaggital plane with a band saw 'Hobart model 5801' using a 4 teeth per inch carbon tip blade (Fig 1). After thawing, halves of the brains were removed from the skull, reunited and measured. The weight of each brain was taken to the nearest 0.01 g with electronic scales (Mettler 5801) and the volume was measured to the nearest ml by liquid displacement (0.1 M phosphate buffered saline, pH=7.6).

In order to control for possible effects of freezing on the brain weight and volume, an experiment was conducted on fresh commercially available lamb brains. Three entire fresh brains, one half brain (an antimere) and two fragments of the volume aproximating this of a koala brain (ie. 15 - 20 ml) were weighed on the same scales as mentioned above.

In addition the volume of the two fragments was measured in the same way as koala brains. The brains and fragments were frozen at -80° C overnight and measured again before and after thawing. Changes in their weight are shown in Table 1.
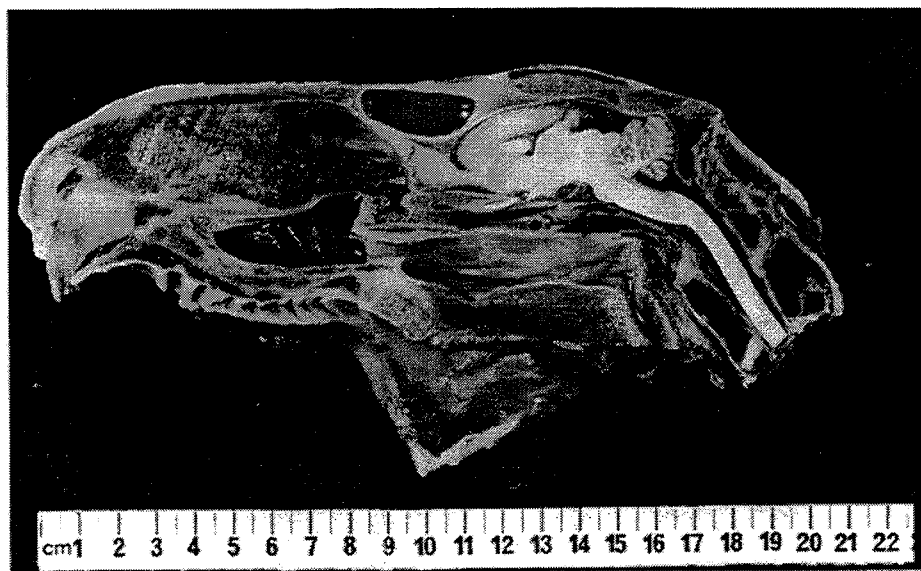

Fig 1. Mid saggital section of a *Phascolarctos cinereus* head showing the half brain '*in situ*'.

		Fresh	Frozen	Thawed
Brain 1	g	113.22	113.38	113.30
	%	100.00	100.14	100.07
Brain 2	g	99.5€	99.64	99.59
	%	100.00	100.08	100.03
Brain 3	g	95.33	95.40	95.33
	%	100.00	100.07	100.00
Half-brain	g	54.82	54.94	54.82
	%	100.00	100.22	100.00
Sample 1	g	19.9⁵	20.05	19.94
	%	100.00	100.50	99.95
Sample 2	g	15.71	15.79	15.69
	%	100.00	100.51	99.87

Table 1. Changes in weight of fresh lamb brains and their fragments resulting from freezing to -80°C and subsequent thawing.

Both in the frozen and in the thawed state brain weights changed by no more than one half of one percent. This change is negligible. The volume of the two fragments was not altered at all by freezing and subsequent thawing. Therefore koala brain weights and volumes as reported here represent weights and volumes of fresh brains.

After removal of koala brains, skull halves were macerated, cleaned and glued together, thus allowing measurement of the endocranial volume by filling the cranial cavity with mustard seeds.

Data on brain weights, cranial capacities and body weights were used in regression analyses performed by standard methods of the Excel 5.0 program. T-tests were used at a probability level 0.05 to test differences between means.

RESULTS

Data for brain weight and body weight of koalas are presented in Table 2. Significant differences were found between males and females for both variables, an unweighted average was calculated for the sample to allow for the different number of males and females. Had a weighted mean been calculated for the entire sample, the preponderance of males would bias it towards higher values.

Measurement of endocranial volume was obtained for 17 males and 8 females because two specimens were kept for a different study and therefore data for their endocranial volume could not be recorded. An average endocranial volume of 26.65 ml was obtained for males and of 23.81 ml for females. These values correspond to an average brain weight of 19.82 g for the same males and 18.48 g for the females. Since the brain density is very close to 1.0 g/ml, values of brain weight and brain volume are considered interchangeable in this study, same as in the calculations of Haight and Nelson (1987). On this calculation, the brain weight represents 74.2 % of the endocranial volume for the male sample and 77.6 % for the female sample. The unweighted average for males and females is 75.8 %, a value that does not differ substantially from the values for other mammals (Tobias 1971, Jerison 1973).

The plot of the koala brain size against body weight, conforms to the allometric relationship (Fig 2).

SEX/VARIABLE	Body weight (g)	Brain weight (g)
Mean males (N=18)	9216.7	19.8
s.d. males	2315.5	1.6
CV males (%)	25.1	8.3
Mean females (N=9)	7986.1	19.2
s.d. females	902.9	1.0
CV females (%)	11.3	5.3
Mean males & females (N=27)	8396.3	19.4
s.d. males & females	2270.3	1.6
CV males & females (%)	27.0	8.2
Unweighed average	7986.1	19.2

Table 2: Phascolarctos cinereus sample. Average, standard deviation and coefficient of variation for body weight and brain weight.

The regression line of brain weight /body weight relationship for basal marsupials established by Haight and Nelson in 1987 passes through the scatter of our koala values. Nevertheless, our male, female and joint averages, lie above the basal marsupial line This relationship is even clearer when cranial capacity rather than the brain weight is related to body weight (Fig 3).

Table 3 presents a number of encephalization indices using various standard formulae and brain weight or cranial capacity for the sample of 27 koalas; *Homo sapiens* values from Henneberg (1990) are added for comparison. The koala is clearly less encephalized than might be an eutherian of its size. Compared to basal marsupials and basal insectivores, the koala is more encephalized. Calculated with data on cranial capacity as a measure of brain size, values for the koala are somewhat higher due to the fact that the brain weight represents 76% of the endocranial volume, but the general pattern remains the same.
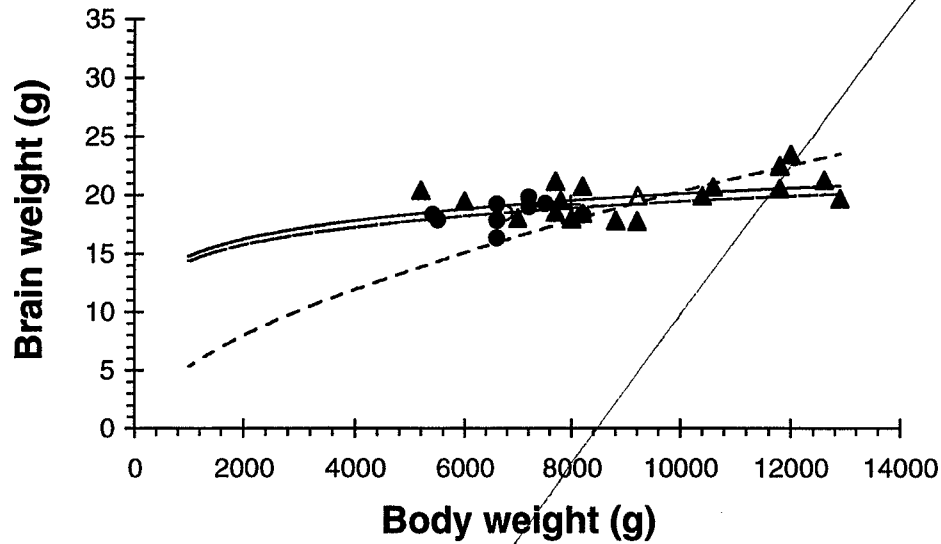
Fig. 2. Scatterplot of brain weight against body weight in *Phascolarctos cinereus*. Crosses are males and solid triangle is an average for males. Solid line is the power allometric trendline for males (r = 0.425). Open circles are females and solid circle is an average for females. Broken line is the power allometric trendline for females (r = 0.318). The solid rhomboid is an unweighted average for males and females. The dotted line is the power line from the allometric equation for basal marsupials (Haight and Nelson 1987).
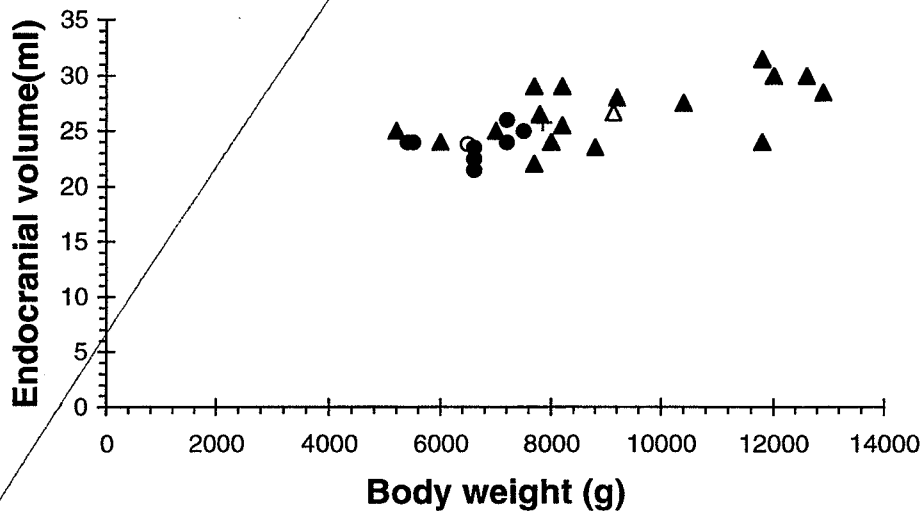

Fig. 3. Scatterplot of endocranial volume against body weight in *Phascolarctos cinereus*. Crosses are males and solid triangle is an average for males. Solid line is the power allometric trendline for males (r = 0.549). Open circles are females and solid circle is an average for females. Broken line is the power allometric trendline for females (r = 0.228). The solid rhomboid is an unweighted average for males and females. The dotted line is the power line from the allometric equation for basal marsupials (Haight and Nelson 1987).

DISCUSSION

Although marsupials lie very close to the regression line for the plot of average log values for brain and body weight for placental mammals, they are, on average, less encephalized than the placental mammals (Martin 1990). The results obtained in this study for the koala are consistent with what was expected for marsupials.

Some previous reports state that marsupials do not differ distinctly from eutherians in relative brain size (Eisenberg and Wilson 1981; Meyer 1981; Pirlot 1981). There is also variability in encephalization of various eutherians (Martin 1990). It is not surprising then, that the koala was found in this study to be more encephalized than basal insectivores.

Haight and Nelson (1987) calculated an encephalization index of 84.3 based on a sample of 11 koala brains. In this study, for a sample of 27 koalas a higher encephalization index of 107.9 was obtained. Haight and Nelson (1987) used brains fixed for several days in formaldehyde and saline solution without correcting for a reduction in brain volume that can be caused by such fixation, which, according to the authors, can be up to 10 % in several months. Moreover, the different sample sizes for koalas used in their calculation of body weight (N=7), brain mass (N=11) and endocranial volume (N=16) averages, indicate that different specimens were used to calculate averages for each variable. These differences in the methods may explain the low values these authors found for the encephalization and for the brain mass / endocranial volume relationship in the koala.

Haight and Nelson (1987) reported for the common wombat (Vombatus ursinus) a very high encephalization index of 212.8. Their sample size was 6 and the average weight reported in their study - 15,979 g - is much lower than the average body weight of 26,000 g reported by Strahan (1983) for this species: V. ursinus specimens in the records of the South Australian Museum have average weight of 40,350 g.

The high variability in body weight and small samples will obviously affect the results of encephalization calculated for a species. Our pilot study of two southern hairy-nosed wombats (Lasiorhinus latifrons) yielded a level of encephalization of 122.5, similar to that found in this study for the koala. Obvious differences exist between the lifestyle and behaviour of the koala and vombatids. The arboreal lifestyle of the koala seems to be similar to that of some primates, yet even encephalization indices in strepsirhines (lemurs and lorises), measured as indices of cranial capacity, (ICC) range from 230 to 630 (Martin 1990). These values are higher than the ICC= 175.9 calculated for the koala in this study.

References	Base for Comparison	Index	P. cinereus	H. sapiens
Eisenberg (1981)		Encephalization Quotient (EQ) $Ee = 0.05\ W^{0.74}$	49.7 (66.5)	838.5
Jerison (1973)	MAMMALS	Encephalization Quotient (EQ) $Ee = 0.12\ W^{0.67}$	38.9 (51.9)	750.1
Martin (1981)		Encephalization $\log Ee = 0.76\ \log W + 1.77$	35.3 (47.2)	572.3
Haight & Nelson (1987)		Encephalization $Ee = 0.0962\ W^{0.581}$	107.9 (143.7)	2471.8
Nelson & Stephan (1982)	BASAL MARSUPIALS	Encephalization $Ee = 0.0867\ W^{0.592}$	108.4 (144.5)	2432.3
Pirlot (1981)		Progression Index (PI) $\log Ee = 2.1446 + 0.5315\ \log W$	116.0 (154.4)	2925.7
Martin (1990)	BASAL INSECTIVORES	Index of Cranial Capacity (ICC) $\log Ce = 0.68\ \log W + 1.51$	131.7 (175.9)	2493.9
Stephan (1972)		Index of Progression $\log Ep = 0.63\ \log W + 1.632$	155.9 (207.9)	3250.2

Table 3: Encephalization indices for Phascolarctos cinereus and Homo sapiens. Values from brain weight in bold and values from endocranial volume in brackets. Data for Homo sapiens from Henneberg (1990), average brain size 1350cm³, average body weight 55,000g, N = approximately 10,000

Given the inconsistency of encephalization indices and animal lifestyles and behaviour, one can wonder what we can learn from encephalization quotients.

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