Relative brain size in the mammalian carnivores of the Cape Province of South Africa

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Relative brain sizes (encephalization quotients; EQ) of the 30 Cape mammalian carnivores were calculated by regressing cranial volume against body mass. Within this taxon relative brain size appears to show no association with sociality, locomotion, activity regimen or habitat, but is positively correlated with body mass. It is suggested that EQ may be associated with feeding efficiency which is in turn positively correlated with body mass.

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Relatiewe breingroottes (enkefalisasiekwosiente; EK) vir die 30 Kaapse soogdierkarnivore is bepaal deur regressie van skedelvolume teen liggaamsmassa. Binne hierdie groep blyk dit dat relatiewe breingrootte geen korrelasie met sosialiteit, bewegingsmetode, aktiwiteitspatroon of habitat toon nie, maar dat daar 'n positiewe korrelasie met liggaamsmassa is. Daar word voorgestel dat daar 'n korrelasie tussen EK en voerdoeltreffendheid mag bestaan. Laasgenoemde toon 'n positiewe korrelasie met liggaamsmassa.

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Encephalization quotient (EQ) or relative brain size of a number of mammalian taxa has been examined in relation to aspects of behaviour, ecology and physiology. It has been shown that EQ can be correlated with climbing ability (Eisenberg & Wilson 1981; Mace, Harvey & Clutton-Brock 1981; Roth & Thorington 1982); foraging strategies (Eisenberg & Wilson 1978) and diet, where folivores have a lower EQ than insectivores, frugivores and granivores (Stephan & Nelson 1981; Mace *et al.* 1981). Hofman (1983) has shown that, in mammals, EQ is correlated with metabolic rate and longevity.

In this study EQ (Jerison 1973) has been calculated for the 30 species of mammalian carnivores from the Cape Province of South Africa. These species fall into five families: Canidae, Mustelidae, Viverridae, Felidae and Hyaenidae. In this paper, the behavioural and ecological aspects that may be associated with variations in EQ are examined and discussed.

Materials and Methods

Cranial volumes of the 30 species (Table 1) were measured by introducing lead shot via the foramen magnum into the cranial cavity. Shot size numbers 4, 6 and 8 were used, dependent on the size of the skull; no significant difference was found in the volumetric measurements obtained using these different sizes. The mass of lead shot was weighed and converted to a volume using an empirically derived calibration curve. This process was repeated three times for each specimen and a mean cranial volume was calculated for each species (Table 1). A target number of 10 specimens per species was attempted, drawn from the mammalian skull collections of the Albany and Kaffrarian Museums.

Ideally mass data and cranial volumes should be taken from the same specimens however, much of the museum material used to calculate cranial volume was unaccompanied by any records of either sex, age or body mass. Mass data, for all the species, were therefore taken from Roberts (1951); Smithers (1971); Kingdon (1977); Stuart (1981) and Rautenbach (1982) and these data were compared with, and found to be similar to actual specimens where such data were known. Male and female data for species showing sexual dimorphism were averaged, and only skulls from adult specimens were used.

Cranial volume was regressed against body mass and a least mean squares regression program, using a first degree polynomial, was used to calculate the line of best fit. The allometric equation,

$$\text{cranial volume (ml)} = 31{,}58 + 1{,}46 \text{ body mass (g)} \qquad (1)$$

describes the regression ($r = 0{,}849$; $P < 0{,}001$).

Table 1 Complete data for the Cape mammalian carnivores including mean body mass, cranial volume (CV) and its standard deviation (SD) and sample size (n), and the encephalization quotient (EQ) for each species

Family	Species	Mean body mass (kg)	CV (ml)	SD	n	EQ
Canidae	1 Otocyon megalotis	3,2	27	1,8	9	0,75
	2 Lycaon pictus	26,5	131	7,0	7	1,86
	3 Vulpes chama	2,65	32	1,9	5	0,90
	4 Canis mesomelas	7,8	56	4,9	10	1,30
Mustelidae	1 Aonyx capensis	14,0	108	14,9	10	2,08
	2 Lutra maculicollis	4,5	49	6,5	9	1,28
	3 Mellivora capensis	10,3	88	4,9	4	1,89
	4 Poecilogale albinucha	0,36	5	1,1	10	0,16
	5 Ictonyx striatus	0,68	10	1,4	10	0,31
Viverridae	1 Genetta genetta	1,85	17	1,4	7	0,50
	2 Genetta tigrina	1,72	17	0,8	8	0,50
	3 Suricata suricatta	0,68	10	1,9	9	0,31
	4 Cynictis penicillata	0,93	10	1,1	10	0,30
	5 Herpestes ichneumon	2,94	24	1,7	4	0,67
	6 Herpestes sanguineus	0,44	7	0,5	3	0,22
	7 Herpestes pulverulentus	0,77	11	0,8	10	0,34
	8 Ichneumia albicauda	3,38	23	2,3	7	0,63
	9 Atilax paludinosus	2,76	29	2,2	9	0,81
	10 Mungus mungo	0,79	10	1,0	7	0,31
	11 Helogale parvula	0,27	5	0,6	7	0,16
Hyaenidae	1 Proteles cristatus	9,4	39	2,2	10	0,86
	2 Hyaena brunnea	42,0	120	6,5	9	1,29
	3 Crocuta crocuta	68,0	155	10,2	4	1,19
Felidae	1 Acinonyx jubatus	50,0	117	0,00	1	1,12
	2 Panthera pardus	26,1	144	6,9	8	2,07
	3 Panthera leo	161,5	217	8,7	3	0,81
	4 Felis lybica	4,3	34	3,7	9	0,90
	5 Felis nigripes	2,0	25	5,4	6	0,73
	6 Felis serval	10,4	54	2,9	3	1,16
	7 Felis caracal	11,4	62	4,6	10	1,28

Table 2 Ecological data for the Cape mammalian carnivores. Habitat is either aquatic (A) or terrestrial (T), activity regimen is nocturnal (N) or diurnal (D), (N* indicates species where nocturnal activity is thought to be a result of human interference), sociality is social (S) or non-social (N) and locomotion is either with climbing ability (A) or without (T)

Species	Habitat	Activity regimen	Sociality	Locomotion
Otocyon megalotis	T	N*	S	T
Lycaon pictus	T	D	S	T
Vulpes chama	T	N	N	T
Canis mesomelas	T	N*	N	T
Aonyx capensis	A	N	N	T
Lutra maculicollis	A	N	N	T
Mellivora capensis	T	N*	N	T
Poecilogale albinucha	T	N	N	T
Ictonyx striatus	T	N	N	T
Genetta genetta	T	N	N	T + A
Genetta tigrina	T	N	N	T + A
Suricata suricatta	T	D	S	T
Cynictis penicillata	T	D	S	T
Herpestes ichneumon	T	D	N – S	T
Herpestes sanguineus	T	D	N	T
Herpestes pulverulentus	T	D	N	T + A
Ichneumia albicauda	T	N	N	T
Atilax paludinosus	A	N	N	T
Mungus mungo	T	D	S	T
Helogale parvula	T	D	S	T
Proteles cristatus	T	N	N	T
Hyaena brunnea	T	N	N	T
Crocuta crocuta	T	N	N – S	T
Acinonyx jubatus	T	D	N	T
Panthera pardus	T	N	N	T + A
Panthera leo	T	N	S	T
Felis lybica	T	N	N	T + A
Felis nigripes	T	N	N	T + A
Felis serval	T	N	N	T + A
Felis caracal	T	N	N	T + A

This regression was then used to calculate the EQ for each species, EQ being defined as the ratio of the observed cranial volume (approximating brain size) to the expected cranial volume, predicted by regression equation (1), for a given mass (Jerison 1973). This ratio is expressed as a fraction, 1,0 indicating an observed EQ equal to the expected; a value greater than 1,0 indicating a brain larger than predicted, and a value less than 1,0 representing a brain volume lower than the expected (Eisenberg 1981). The function of this ratio is to eliminate factors related to body size, allowing the comparison of relative brain sizes in species with greatly differing body mass.

Tests for possible associations between EQ and habitat (aquatic or terrestrial), activity regimen (nocturnal or diurnal), sociality (social or non-social) and locomotion (climbers or non-climbers) were made by classifying the 30 species into one of each pair (Table 2), calculating the mean EQ for each group and comparing these means for statistically significant differences. The equality of variance assumption holds for these data. Data on habitat, activity regimen, sociality and locomotion were taken from Rautenbach & Nel (1978), Stuart (1981), Rautenbach (1982) and personal observations.

Results

The $\log_{10}$ mean cranial volume of each species has been plotted against $\log_{10}$ mean body mass (Figure 1A) and a linear relationship demonstrated ($r = 0,98$; $P < 0,001$). EQs have been presented as a bar diagram for clarity (Figure 1B).

The EQs of the 30 species show great fluctuation within each family (Figure 1B). The Mustelidae exhibit the greatest intra-family fluctuation, from Aonyx capensis, with the highest EQ of all the species to Poecilogale albinucha, with the lowest EQ of the same group. The Hyaenidae are the most uniform family (also with the least number of species), with little variation between Hyaena brunnea and Crocuta crocuta. Proteles cristatus does vary somewhat but belongs in separate subfamily, the Protelinae.

In the Canidae, Mustelidae, Hyaenidae and Felidae the average family EQ is higher than the average carnivore EQ (1,0), while the family EQ for the Viverridae is lower than average.

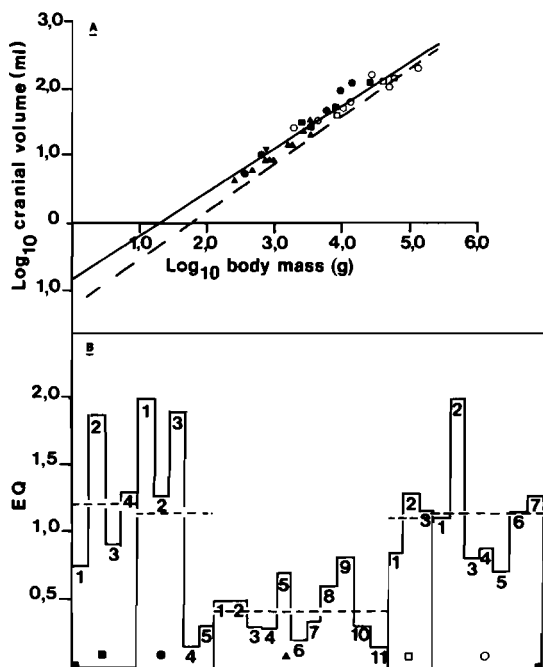Four species (13%), Lycaon pictus, Aonyx capensis, Melli-

Figure 1 (A) Regression of $\log_{10}$ mean cranial volume against $\log_{10}$ mean body mass for the 30 species of Cape carnivores (solid line). $\log_{10} Y = -0,812 + 0,640 \log_{10} X$ ($r = 0,98$; $P < 0,001$). The dashed line represents the regression of Eisenberg (1981) for 547 mammalian species. □ Hyaenidae; ● Canidae; ○ Felidae; ● Mustelidae; ▲ Viverridae. (B) EQ of the 30 species grouped according to family. The horizontal dashed lines indicate mean family EQs.

Figure 2 EQ plotted against $\log_{10}$ body mass for the 30 species. $\log_{10} Y = -1,23 + 0,59 \log_{10} X$ ($r = 0,75$; $P < 0,001$). Symbols are as in Figure 1.

vora capensis and *Panthera pardus,*, from three different families, the Canidae, Mustelidae and Felidae, have EQs above 1,5 (Figure 1). Fifty-three per cent of the species, with representatives from all five families, have EQs lying between 1,5 and 0,5. Thirty-three per cent of the species have EQs lower than 0,5, 80% of these being from the Viverridae and the remainder from the Mustelidae. *Panthera leo* has a surprisingly low EQ, falling below the hypothetical average.

EQ is not associated with habitat. Although mean EQ of the three aquatic species (1,39 ± 0,64) ($\bar{x}$ ± SD) is higher than that of the remaining species (0,83 ± 0,54) this difference is not significant ($P > 0,1$). Similarly EQ is not associated with sociality. Species that occurred singly or in pairs were compared with those that occurred in larger groups and although the mean EQ of solitary species (0,95 ± 0,56) is higher than that of social species (0,71 ± 0,59) this difference is not significant ($P > 0,1$). In relation to activity regimen, care was taken to separate species that are truly nocturnal from those that are nocturnal as a result of human interference. For example, Stuart (1981) reports that *Canis mesomelas* and *Mellivora capensis* are generally regarded as nocturnal but are diurnal in areas where they are undisturbed. Nocturnal species have a higher mean EQ (0,97 ± 0,52) than diurnal species (0,59 ± 0,56) but this difference is not significant (0,1 > P > 0,05). The mean EQ of species reported as having good climbing ability (1,08 ± 0,65) is greater than that of terrestrial species (0,84 ± 0,53), however, this difference is not significant ($P > 0,1$).

EQ has been regressed against $\log_{10}$ body mass for the Cape mammalian carnivores (Figure 2) and a positive correlation demonstrated ($r = 0,75$; $P < 0,001$).

Discussion

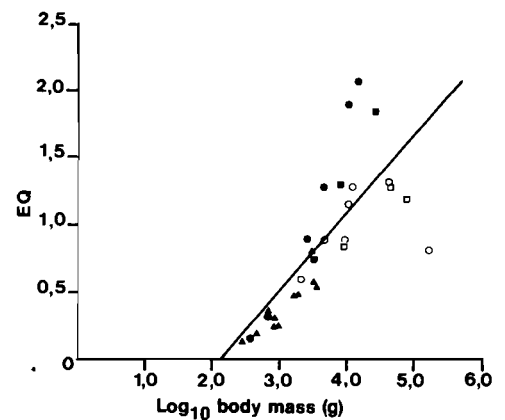From analyses of the results it is concluded that no association

exists within the Cape carnivores between EQ and those aspects of either sociality, activity regimen, locomotion or habitat that were examined.

The authors realize the significance of the positive correlation between EQ and body mass because the ratio (EQ) is designed to obliterate the effects of body size when considering relative brain size, and previous authors (Eisenberg 1981; Eisenberg & Wilson 1981) have shown EQ not to be correlated with body mass. The reason for this positive correlation is that EQ values in this study were obtained using an expected cranial volume generated from a regression of brain volume against body mass for the Cape carnivores only. Eisenberg's values for EQ were obtained using expected cranial volumes generated from a regression of brain volume against body mass for 547 mammals with representatives from all ordinal taxa. When the two regressions are plotted together (Figure 1A) Eisenberg's line falls below that for the Cape carnivores and has a steeper slope (0,74 compared to 0,64). The result of this is that for the lighter species our EQ value is always less than that of Eisenberg while for the heavier species, the EQ values are similar. It is for this reason that, in the present study, EQ is positively correlated with body mass.

When dealing with a single group of mammals it makes better sense to generate expected cranial volumes from a regression using members of that particular group rather than to mask possible group-specific phenomena by using a general mammal regression.

It should be noted that although the slope reported in the present study is lower than the general mammal slope of Eisenberg (1981), Eisenberg reports a slope of 0,57 based on data from about 30 carnivores.

It is unlikely that the positive correlation between EQ and body mass represents a cause and effect relationship, it is more likely that some other factor, related to body mass is positively correlated with EQ. Feeding efficiency (energy return from feeding per unit time) may be related to body mass in that the larger the carnivore, the greater the pool of potential food sources that it can exploit and therefore the greater its potential feeding efficiency. Several examples support the relationship between feeding efficiency and EQ. *A. capensis* and *Lutra maculicollis* share a similar diet although a predominance of crustacea is evident in the diet of the former, the latter preferring fish (Rowe-Rowe 1977a; Van der Zee 1981). However, the prey capture techniques utilized by these species vary considerably and these affect the feeding efficiency of the animal. *A. capensis* has fore-paws lacking webbing between the digits,

resulting in a high degree of dexterity (Rautenbach 1982) (e.g. the anvil-using behaviour of this species, Donnely & Grobler 1976). *A. capensis* uses the forelegs extensively in the search for, capture and holding of prey while eating, but the forelegs of *L. maculicollis* are not used for any of these functions (Rowe-Rowe 1977b). *A. capensis* utilizes a greater pool of prey animals than does *L. maculicollis* (Smithers 1983) and it is suggested that this is due to the dexterity of the former species and that it results in a high feeding efficiency. It is therefore suggested that within a given habitat, the relative advantage of the greater food resource available to *A. capensis* over *L. maculicollis* is related to their feeding efficiencies, and that this factor is mimicked by EQ trends.

L. pictus and *P. leo* are both social species (Rautenbach 1982) with greatly differing feeding efficiencies and corresponding differences in EQ. *L. Pictus* has a high hunting success rate, 85% of hunting attempts culminating in a kill, while *P. leo* has a hunting success rate of only 32% (Ester & Goddard 1967; Kruuk 1975). Hunting success rate will be directly correlated with feeding efficiency and in the case of *L. pictus* high feeding efficiency corresponds to a high EQ, while *P. leo* has a low feeding efficiency and a corresponding low EQ.

In comparing two canids, *L. pictus* and *Otocyon megalotis*, the former has both a high feeding efficiency (owing to the high attempt/success rate and the little time spent hunting each day) and high EQ. *O. megalotis* is an opportunistic omnivore, showing preference for insectivory (Nel 1978). Because of the opportunistic nature of its feeding, time spent foraging each day is extensive and as time taken for feeding is negatively correlated with feeding efficiency, *O. megalotis* will have a low feeding efficiency which corresponds to its low EQ (Table 1).

In conclusion, we suggest that EQ is related to feeding efficiency which is in turn related to the size of the animal. We hypothesize that factors such as increased body mass, cooperative hunting, dexterity and simple tool use will increase the pool of potential prey species available to the predator. This would require decision-making by the predator to select the most energetically suitable prey (prey that offer the greatest net energy gain) and would be associated with more demanding information processing and therefore increased EQ. Although we report no positive association between EQ and sociality, locomotion, habitat or activity regimen, such factors may be associated with feeding efficiency and in this way have some effect on relative brain size.

Acknowledgements

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