

Ecological correlates of relative brain size in some South African rodents

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Relative brain size (size of the brain once body size effects have been removed) has been calculated for 16 species of rodent from South Africa and is shown to vary with six species having a positive RBS (that is a brain larger than expected) and 10 a negative RBS. Arboreal species such as *Paraxerus cepapi* and *Graphiurus murinus* and omnivores (*G. murinus*) have relatively larger brains than do the fossorial root eaters such as *Cryptomys hottentotus* and terrestrial folivores (*Otomys irroratus*). It is suggested that the relatively large brains can be linked to the complex behavioural patterns necessary for locomotion in three dimensions and for utilization of a food resource such as insects that is randomly distributed in time and space. The three sciuriform rodents (*Xerus inauris*, *Paraxerus cepapi* and *Pedetes capensis*) have very different life styles but all have a positive RBS and it is suggested that a relatively large brain may be a characteristic of the suborder.

Relatiewe breingrootte (grootte van die brein nadat die effek van liggaamsgrootte uitgeskakel is) is vir 16 spesies van knaagdiere van Suid-Afrika bereken. Ses spesies het 'n positiewe RBG (dit is 'n brein wat groter is as die verwagte waarde) getoon, en 10 spesies 'n negatiewe RBG. Arboriale spesies soos *Paraxerus cepapi* en *Graphiurus murinus* en omnivore (*G. murinus*) het relatief groter breine as die fossoriale wortelvreterers soos *Cryptomys hottentotus* en landlewende blaarvreterers (*Otomys irroratus*). Daar word voorgestel dat 'n relatiewe groot brein gekoppel kan word aan die komplekse gedragspatrone wat nodig is vir beweging in drie dimensies en vir benutting van 'n voedselbron soos insekte wat oneweredig in tyd en ruimte versprei is. Die drie sciuriforme knaagdiere (*Xerus inauris*, *Paraxerus cepapi* en *Pedetes capensis*) se lewenswyses verskil aansienlik maar hulle het almal 'n positiewe RBG en daar word voorgestel dat 'n relatiewe groot brein 'n eienskap van dié suborder kan wees.

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Relative brain size, that is the size of the brain once the influence of body size has been removed, is highly variable within the mammals and numerous papers have attempted to explain such variation in terms of the behaviour, ecology, life-history strategies and phylogeny of the species (Bauchot & Stephan 1966; Jerison 1973; Sacher & Stafeldt 1974; Eisenberg & Wilson 1978; Clutton-Brock & Harvey 1980; Eisenberg & Wilson 1981; Sheppey & Bernard 1985; Gittleman 1986; Bernard, Paton & Sheppey 1988; O'Shea & Reep 1990; Pagel & Harvey 1990).

Hoffman (1982, 1983) and Harvey & Bennett (1983) have proposed that relative brain size may be determined by basal metabolic rate rather than any other aspect of biology or ecology. However McNab & Eisenberg (1989) have shown that once body size effects are removed from both brain mass and basal metabolic rate, there is no correlation between the two, and conclude that relative brain size is controlled by the habits of the mammal.

In this study we describe the relative brain size of 16 species of African rodents and discuss the habits that might influence relative brain size.

Materials and Methods

The cranial volumes (Table 1) of 16 species of Southern African rodents were determined from skulls in the mammal collections of the Albany Museum, Grahamstown; Kaffrarian Museum, King William's Town; and the Transvaal Museum, Pretoria. Cranial volumes were measured by filling the cranial cavity with lead shot which was then weighed and its volume read from a derived calibration curve. Five skulls of each sex of all species except *Hystrix africaeaus-*

tralis (4 ♂♂, 5 ♀♀) were used and each specimen was measured five times. Only undamaged skulls from adult specimens were used (age was determined from dentition and suture lines). Whenever possible, body mass was taken from the museum specimens, but in most cases, masses for the species (Table 1) had to be taken from the literature (De

Table 1 Cranial volume (1) in ml, body mass (2) in g, both value ± 1 SD, and relative brain size (3) for the 16 species of rodent

Taxon	1	2	3
Sciuromorpha	5,33	1324,5	+0,14
<i>Xerus inauris</i>	3,7 \pm 0,1	624,5 \pm 34,6	+0,2
<i>Paraxerus cepapi</i>	1,6 \pm 0,1	192,5 \pm 3,5	+0,2
<i>Pedetes capensis</i>	10,7 \pm 0,4	3156,5 \pm 34,6	+0,17
Hystricomorpha	6,48	4560,8	-0,16
<i>Hystrix africaeaus-</i>	21,7 \pm 0,6	17650,0 \pm 1060,6	-0,04
<i>Thryonomys swinderianus</i>	7,5 \pm 1,6	4060,0 \pm 678,8	-0,05
<i>Bathyergus suillus</i>	1,7 \pm 0,2	625,0 \pm 176,7	-0,14
<i>Cryptomys hottentotus</i>	0,5 \pm 0,04	126,5 \pm 10,6	-0,18
<i>Georychus capensis</i>	1,0 \pm ,03	343,0 \pm 24,0	-0,19
Myomorpha	0,56	87,98	-0,02
<i>Otomys irroratus</i>	0,8 \pm 0,1	143,0 \pm 4,2	-0,05
<i>O. unisulcatus</i>	0,6 \pm 0,09	124,5 \pm 20,5	-0,10
<i>Parotomys brantsii</i>	0,6 \pm 0,1	96,4 \pm 16,5	-0,014
<i>Aethomys namaquensis</i>	0,5 \pm 0,07	46,1 \pm 2,8	+0,13
<i>Rhodomys pumilio</i>	0,3 \pm 0,09	42,3 \pm 1,2	-0,07
<i>Mastomys natalensis</i>	0,29 \pm 0,04	58,0 \pm 5,7	-0,16
<i>Rattus rattus</i>	1,0 \pm 0,13	167,0 \pm 11,3	+0,04
<i>Graphiurus murinus</i>	0,4 \pm 0,17	27,8 \pm 0,2	+0,18

Graaff 1981; Rautenbach 1982; Smithers 1983).

Because of the allometric relationship between brain mass and body mass, it is necessary to remove body size effects before comparing the brain size from species of differing body mass. This is done by comparing the observed brain size with an expected value which is generated from the regression of brain mass on body mass. The slope of the regression of brain mass on body mass increases with increasing taxonomic level (Mace, Harvey & Clutton-Brock 1981; Pagel & Harvey 1988) and in the past the trend has been to calculate a measure of brain size for one taxon (e.g. Genus) based on a regression line for the next higher taxon (e.g. Family; Clutton-Brock & Harvey 1980; Mace *et al.* 1981; Gittleman 1986; Bernard *et al.* 1988). Recently, however it has been suggested that the increase in slope with increasing taxonomic level is a statistical artifact (Pagel & Harvey 1988) and that deviations from slopes calculated at low taxonomic levels are often biased. In this study we have followed the suggestion of Pagel & Harvey (1988) and have measured relative brain size for both the species and suborders as the deviation from the regression line for the Order Rodentia. For example, RBS for a given suborder = \log_{10} (observed mean brain mass for the suborder) - [elevation for the Order + slope for the Order $\times \log_{10}$ (mean body mass for the suborder)].

To test for possible associations between RBS and life

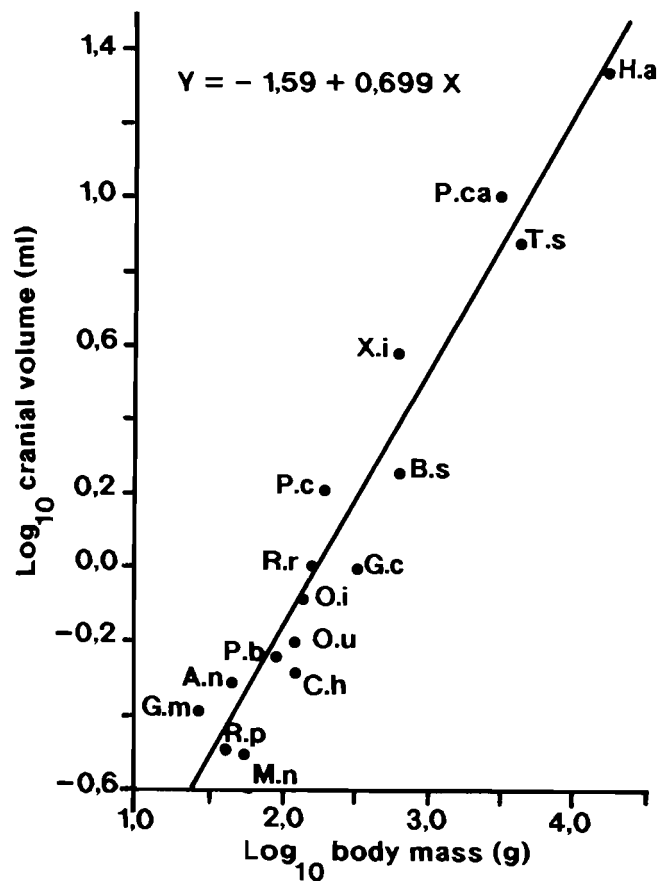


Figure 1 Regression of \log_{10} body mass on \log_{10} cranial volume for the 16 species of rodent. The regression line represents the expected brain size, and species that fall to the left of the regression line will have a brain larger than expected and therefore a positive RBS.

style, species have been assigned to a single group in each of the following categories. (1) Locomotion; arboreal, including the truly arboreal species and those with a climbing ability, fossorial and terrestrial. (2) Diet; folivores (eating mostly green plant material; after Mace *et al.* 1981 and Meier 1983), bulb-eaters, granivores and omnivores. (3) Activity; diurnal, crepuscular or nocturnal. (4) Sociality; colonial, family groups or solitary. (5) precocial or altricial. Information regarding the habits and habitats of the rodents was collected from the literature. Mean values for RBS for each category were calculated and compared using ANOVA and Tukey's multiple range test.

Results

Taxonomic relationships

Relative brain size of the 16 species varies, with six having a positive RBS (that is a brain larger than expected) and 10 a negative RBS (Figures 1, 2; Table 1). The 16 species represent three suborders and the RBS of the Sciuromorpha is positive and significantly larger than that of the Hystricomorpha ($p < 0.001$) and the Myomorpha ($p < 0.05$) (Table 1).

RBS and ecological/behavioural groupings (Table 2)

In order to overcome the potential problem of the positive RBS of the sciuromorphs masking relationships between RBS and life style (for example, of the four fossorial

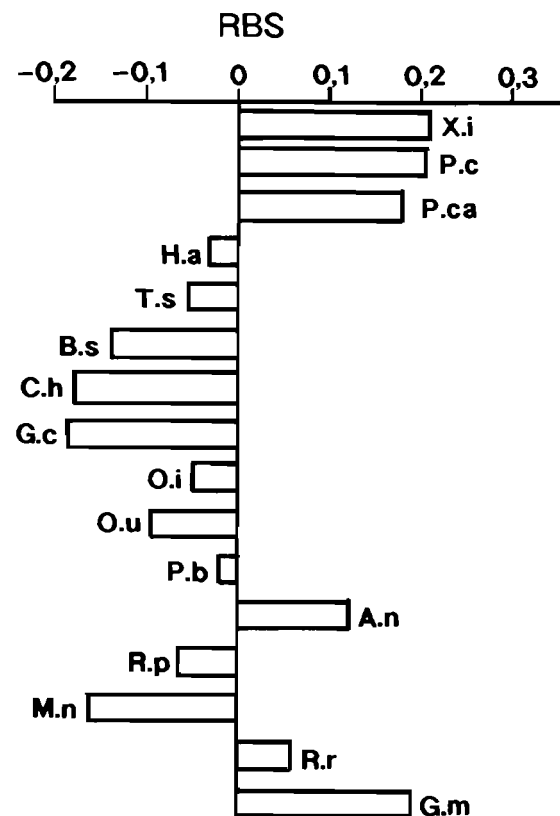


Figure 2 Relative brain size (RBS) for the 16 species of rodent. The zero value represents the expected brain size for rodents, a negative value, a brain smaller than expected, and a positive value, a brain larger than expected.

Table 2 Ecological/behavioural data for the 16 rodents. Categories are 1, locomotion (A = arboreal, F = fossorial, T = terrestrial); 2, diet (F = folivore, O = omnivore, B = bulbs, roots & tubers, G = granivore); 3, sociality (S = solitary, C = colonial, F = family groups); 4, activity regimen (N = nocturnal, D = diurnal, C = crepuscular); 5, development at birth (P = precocial, A = altricial)

Taxon	1	2	3	4	5	RBS
Sciuromorpha						
<i>Xerus inauris</i>	F	B	C	D	-	+0,2
<i>Paraxerus cepapi</i>	A	G	F	D	A	+0,2
<i>Pedetes capensis</i>	T	F	S	N	P	+0,17
Hystriocomorpha						
<i>Hystrix africaeaustralis</i>	T	B	F	N	P	-0,04
<i>Thryonomys swinderianus</i>	T	F	S	C	P	-0,05
<i>Bathyergus suillus</i>	F	B	F	-	A	-0,14
<i>Cryptomys hottentotus</i>	F	B	C	N	A	-0,18
<i>Georchus capensis</i>	F	B	S	-	A	-0,19
Myomorpha						
<i>Otomys irroratus</i>	T	F	F	D	P	-0,05
<i>O. unisulcatus</i>	T	F	F	D	?	-0,10
<i>Parotomys brantsii</i>	T	F	F	D	A	-0,014
<i>Aethomys namaquensis</i>	T/A	G	F	N	A	+0,13
<i>Rhabdomys pumilio</i>	T	F	S	C	A	-0,07
<i>Mastomys natalensis</i>	T	G	C	N	A	-0,16
<i>Rattus rattus</i>	T/A	O	C	N	A	+0,04
<i>Graphiurus murinus</i>	T/A	O	S	N	A	+0,18

Table 3 Summary of the analyses of the relationships between RBS and life style. Columns within a single ecological/behavioural grouping which share a common superscript are not significantly different at the 0,05 level

Ecological/behavioural category	RBS \pm 1 SD full data set	RBS \pm 1 SD sciuromorphs omitted
1. Locomotion		
Arboreal	+0,140 \pm 0,07 ^a	+0,12 \pm 0,08 ^a
Terrestrial	-0,041 \pm 0,09 ^b	-0,07 \pm 0,05 ^b
Fossorial	-0,078 \pm 0,19 ^b	-0,17 \pm 0,03 ^c
2. Diet		
Omnivore	+0,11 \pm 0,10 ^a	+0,11 \pm 0,10 ^a
Granivore	+0,05 \pm 0,19 ^a	-0,02 \pm 0,21 ^b
Folivore	-0,019 \pm 0,09 ^a	-0,06 \pm 0,02 ^b
Bulbs	-0,07 \pm 0,16 ^a	-0,14 \pm 0,07 ^c
3. Sociality		
Solitary	+0,01 \pm 0,16 ^a	-0,03 \pm 0,16 ^a
Family group	+0,002 \pm 0,12 ^a	-0,03 \pm 0,09 ^a
Colonial	-0,03 \pm 0,18 ^a	-0,10 \pm 0,12 ^a
4. Activity regimen		
Diurnal	+0,05 \pm 0,13 ^a	-0,05 \pm 0,04 ^a
Nocturnal	+0,02 \pm 0,15 ^a	-0,003 \pm 0,15 ^a
Crepuscular	-0,06 \pm 0,01 ^a	-0,06 \pm 0,01 ^a
5. Development at birth		
Precocial	+0,008 \pm 0,11 ^a	-0,054 \pm 0,006 ^a
Altricial	-0,05 \pm 0,15 ^a	-0,10 \pm 0,09 ^a

species, it is only the sciuromorph *Xerus inauris* that has a positive RBS), analyses have been made using the full data set and with the sciuromorphs omitted.

There is a significant relationship between RBS and locomotion ($p < 0,05$) with the arboreal species having a significantly larger RBS than the terrestrial species ($p < 0,01$). When the sciuromorphs are omitted from the analysis, the RBS of arboreal species is significantly greater than that of terrestrial species which is significantly greater than that of fossorial species (Table 3).

The RBS of root-eaters and folivores is negative and smaller than that of granivores and omnivores (Table 3) but for the full data set the differences are not statistically significant ($p > 0,1$). When the sciuromorphs are omitted from the analysis, the root-eaters have a significantly smaller RBS than the others and the omnivores have the largest RBS.

There is no obvious relationship between RBS and either activity regimen, degree of sociality or the level of development at birth of the rodents, and omitting the sciuromorphs does not alter the analyses (Table 3).

Discussion

A relatively large brain has been linked to a variety of life styles ranging from frugivory in bats and primates (Clutton-Brock & Harvey 1980; Eisenberg & Wilson 1981), through arboreality in the squirrels (Meier 1983) to sociality in the sciurids (Mace *et al.* 1981). McNab & Eisenberg (1989) conclude that relative brain size is dependent on the habits of the species, with arboreal species and those feeding on vertebrates, seeds and fruit having relatively larger brains than the terrestrial folivores. In general, it is suggested that the complex behavioural patterns associated with the acquisition of food that is dispersed in time and space, and with locomotion in three dimensions are reliant upon an increased brain size (Mace *et al.* 1981). Such arguments, however, can not be used to explain the high RBS of the sciuromorphs (present study; Eisenberg 1981; Mace *et al.* 1981; Roth & Thorington 1982) since the three examples in the present study have very different life styles. It is more likely that the generally high RBS of a major taxon such as the Sciuromorpha should be explained in terms of phylogeny. However, the phylogeny of the sciuromorphs is unclear and it is not known whether arboreal forms evolved from terrestrial forms or *vice versa*. If the ancestral sciuromorphs were arboreal then they may have had relatively large brains and, since it is difficult to imagine evolution favouring a reduction in brain size, then a relatively large brain becomes a characteristic of the taxon. If, on the other hand, the ancestors were terrestrial, it is possible that evolutionary pressures favouring a reduction in body size necessary for the fossorial and arboreal life styles could cause a reduction in body size without any change in brain size (Deacon 1990) thus producing species with large brains (Mace *et al.* 1981). Similar arguments have been used to explain the relatively small brains of the Sirenia (O'Shea & Reep 1990) and of the gorilla (Shea 1983), and the relatively large brain of the Talapoin monkey (Bauchot & Stephan 1969).

The results from the present analyses of the relationship between RBS and life style support the established view that

a relatively large brain is associated with complex behavioural patterns and/or the integration of a greater number of stimuli (Harvey & Krebs 1990). Fossorial rodents have the lowest RBS and the fossorial habit probably represents the simplest sensory and perceptual niche (Mace *et al.* 1981). Terrestrial locomotion and particularly locomotion in three dimensions as in the arboreal species will require integration of information from a wider range of senses and consequently these groups have relatively larger brains.

Closely linked to fossoriality is a diet of roots, bulbs and tubers, and the major food of *Cryptomys hottentotus* is the roots of grasses (Bernard, unpublished data). These rodent moles, and the folivorous (or grass eating) rodents have a ubiquitous food resource and both have relatively small brains. Only the omnivores have a positive RBS and it is reasonable to assume that these species will require more complex foraging behaviour to locate and catch their animal prey.

The similarity in relative brain size of altricial and precocial species supports the results of Pagel & Harvey (1990) who showed that although neonatal brain size might be greater in precocial species, this difference is not apparent in adults.

In conclusion, arboreal rodents and species that are omnivorous have a relatively large brain, while fossorial root eaters and terrestrial folivores have relatively small brains. These differences can satisfactorily be explained in terms of the increasing complexity of behavioural patterns necessary for locomotion in three dimensions and utilizing a food that is randomly distributed in time and space. Such arguments can not be used to explain the high RBS of the sciuriform rodents where it appears that a relatively large brain is a general characteristic of the taxon.

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