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Population Biology

Brain size and ecology in small mammals and primates

(behavioral ecology)

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ABSTRACT **Comparisons of brain–body size relationships within small mammal and primate families reveal intergeneric differences related to diet and foraging strategy. These same associations between relative brain size and ecology are also evident among interfamily comparisons.**

Brain weight, measured by using cranial capacities, increases with body weight across vertebrates as a whole (1). However, the form of the relationship differs between taxa and also between taxonomic levels (2, 3). Presumably, these differences are, to some extent, a product of differing levels of behavioral and sensory capabilities being favored by natural selection among species occupying different ecological niches (4–6). Few studies have both considered the likely selective forces and attempted to identify them. In this paper we discuss intergeneric comparisons of brain–body size relationships within small mammal (rodents, insectivores, and lagomorphs) and primate families. Detailed descriptions of our methodology, ecological classifications, and sources of data, as well as the data themselves, are presented elsewhere (7–9, §, ¶).

METHODS

Body weight and body length (head and body without tail) measures for sexed adults of each species were extracted from the literature. Brain weights were calculated from braincase volumes of undamaged sexed skulls [measured by using 2-mm glass beads and, for the smallest skulls, x-ray techniques (10); several skulls were measured by using both techniques to ensure comparability¶]. Values for the two sexes were averaged for subsequent analysis. Species were then allocated to various ecological categories (Table 1). Because species are unevenly distributed across genera and congeneric species, partly for phylogenetic reasons, tend to be both morphologically and ecologically similar, species were not treated as statistically independent points for analysis. Instead, single "generic" values of brain weight, body weight, and body length were calculated as average measures from congeneric species with the same ecology (defined by Table 1). This meant that some genera provided more than one datum point for ecological comparisons.

Comparative brain size (CBS) for each "genus" was estimated as the deviation (on the brain weight axis) from its family regression line of $\log_e$(brain weight) regressed on $\log_e$(body weight). Relative brain sizes for each *family* were calculated as the mean of that family's "generic" deviations from the "common" regression line (11), placed to pass through the mean "generic" point for each order. The slope of the common regression line is an estimate of the slope of family regression lines, rather than that of each order as a whole. It was used because family regression lines differed from each other in elevation but not in slope (7, 8). In view of the statistical error inherent in measuring body size, the analyses were repeated, using both major axis and reduced major axis (12) methods to calculate weightings on minor axes rather than deviations from regression lines. The statistical conclusions are the same (7, 8), and we present only the results from the regression analyses here.

Table 1. Ecological classifications

Characteristic	Small mammals	Primates
Diet type and foraging strategy	(Insectivore, granivore, frugivore), generalist, folivore	(Insectivore, frugivore), folivore
Stratification	Arboreal, terrestrial	Arboreal, terrestrial
Activity	Nocturnal, diurnal	Nocturnal, diurnal
Breeding system	—	Monogamous, polygynous
Habitat	(Forest, woodland), (grassland, desert)	—

Classes in parentheses were combined for analysis—in no case was there statistical heterogeneity between members of combined classes.

RESULTS

Measures of CBS in the different ecological categories are compared in Table 2. Only families containing genera which differed in their relevant ecological classifications were used for analysis. Among the small mammals, CBSs differ between all ecological categories. However, ecological classifications are not independent of one another, and when two-way analyses of variance were used to isolate the effects of each classification (Table 3) only dietetic differences remained significant.

In both small mammals and primates, folivores have small CBSs. This trend is also true within each of the seven families employed in the dietetic analyses (Sciuridae, Cricetidae, Muridae, Lemuridae, Cebidae, Cercopithecidae, and Pongidae). There are two obvious explanations for this pattern. First, folivores have particularly large digestive systems (13), which may not require increased brain size. If these large guts result in a change of shape rather than length, then the fact that the differences persist when brain size is regressed on body length tends to argue against this hypothesis (see Table 2). Second (or

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Abbreviation: CBS, comparative brain size.

§ Clutton-Brock, T. H. & Harvey, P. H. (1980) Deposit (British Museum of Natural History, London).

¶ Mace, G. M. (1979) Deposit (British Museum of Natural History, London).

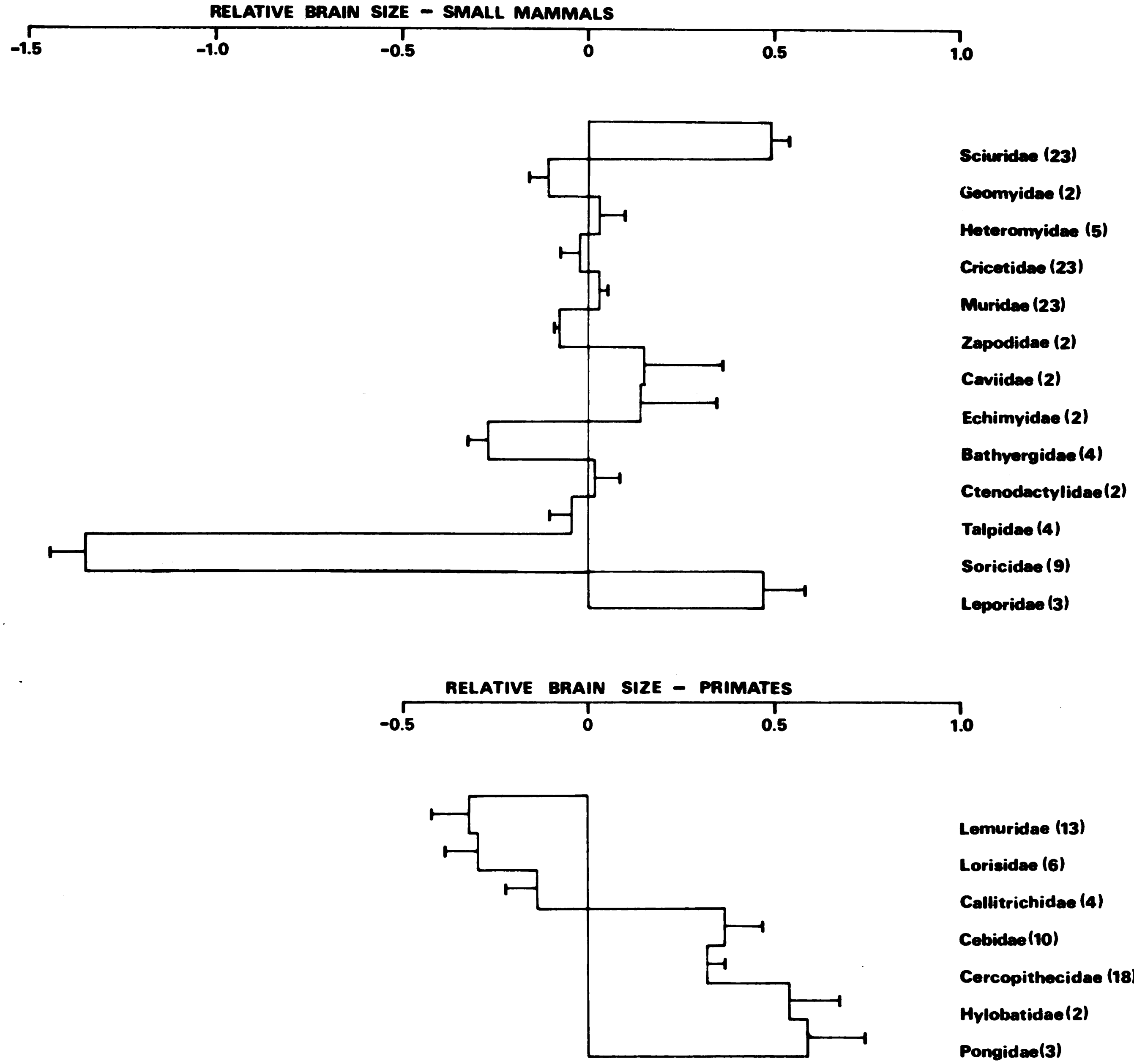

FIG. 1. Relative brain sizes of small mammal and primate families, measured as mean deviation of component genera from the common regression line for each order (see text), using body weight as the independent variable. Bars denote one standard error. Number of genera in the sample for each family is given in parentheses.

additionally), folivores depend on a food source that is both less sparsely and more evenly distributed in time and space than that of other dietetic groups. For a given body size in both small mammals¶ and primates (14), folivores have smaller home ranges than other dietetic groups. Consequently, they may not require such extensive memory storage for efficient exploitation of their food supply. Eisenberg and Wilson (6) argue, in similar vein, that convergently evolved large brains in bats are associated with complex foraging strategies.

Among the primates, monogamous genera have small CBSs. However, this result depends on only three genera from two families (*Indri*, *Callicebus*, and *Aotus*), although the genera are all frugivorous and, in the light of the dietetic association with CBS, they would be expected to have relatively large CBSs.

Differences between families in relative brain size are marked (Fig. 1). In both small mammals and primates, relative brain sizes of the different families are positively correlated with mean generic body weight of family members (Fig. 2).

The dietetic association with CBS within families is also evident in a comparison of relative brain size among families whose genera all fall into the same dietetic category. When body weight differences are removed (Fig. 2), the purely folivorous families—the Caviidae and Leporidae—have small relative brain sizes (lie below the line of best fit). Four of the insectivorous, frugivorous, and granivorous families (the Zapodidae, Heteromyidae, Talpidae, and Callitrichidae) have large relative brain sizes, one lies approximately on the line of best fit (Lorisidae) and one lies below it (Soricidae).

The small mammals contain several exclusively fossorial families. Because this habit must represent one of the simplest sensory niches, we might expect relative brain sizes of these

Table 2. CBSs within the ecological categories

Category	Small mammals	Primates
Diet		
F.I.G.†	0.06 ± 0.03 (26)	0.05 ± 0.04 (30)
Generalist	−0.02 ± 0.04 (19)	—
Folivore	−0.22 ± 0.04 (9)	−0.17 ± 0.06 (13)
	$F_{2,51}$ = 10.81***	$F_{1,41}$ = 10.34***
Stratification		
Arboreal	0.07 ± 0.03 (25)	−0.04 ± 0.06 (21)
Terrestrial	−0.05 ± 0.03 (32)	0.06 ± 0.03 (13)
	$F_{1,55}$ = 6.88*	$F_{1,32}$ = 1.60 n.s
Activity		
Nocturnal	0.02 ± 0.02 (33)	−0.03 ± 0.13 (7)
Diturnal	−0.10 ± 0.04 (17)	0.01 ± 0.08 (16)
	$F_{1,48}$ = 9.35**	$F_{1,21}$ = 0.06 n.s.
Breeding system		
Monogamous	—	−0.39 ± 0.09 (3)
Polygynous	—	0.10 ± 0.08 (11)
		$F_{1,12}$ = 4.70*
Habitat		
Forest, woodland	0.06 ± 0.02 (39)	—
Grassland, desert	−0.12 ± 0.04 (18)	—
	$F_{1,55}$ = 14.94***	
Diet (CBS body length)		
F.I.G.†	0.06 ± 0.04 (23)	0.05 ± 0.05 (31)
Generalist	0.01 ± 0.05 (14)	—
Folivore	−0.20 ± 0.03 (7)	−0.10 ± 0.06 (15)
	$F_{2,41}$ = 5.52**	$F_{1,44}$ = 7.27*

For each ecological group, the mean and standard deviation of generic deviations from the family regression line of brain on body weight (or body length for diet) are shown, together with sample sizes in parentheses. Differences between groups are tested by one-way analysis of variance (n.s., not significant; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$).

†F.I.G. = frugivore, insectivore, granivore combined category. There are no granivorous primates in the sample.

families to be smaller than those of other, closely related families. The Bathyergidae (mole rats) and Geomyidae (gophers) have small relative brain sizes compared with other families in their suborders (Echimyidae, Caviidae, and Ctenodactylidae;

Table 3. Differences in CBSs of small mammal genera classified within two ecological categories

Analysis	Results
Diet and habitat	
Diet, habitat effects removed	$F_{2,41}$ = 4.13*
Habitat, diet effects removed	$F_{1,41}$ = 3.58 n.s.
Diet and stratification†	
Diet, stratification effects removed	$F_{2,29}$ = 5.54**
	$F_{1,15}$ = 0.04 n.s.
Stratification, diet effects removed	$F_{1,20}$ = 1.52 n.s.
	$F_{1,16}$ = 0.29 n.s.
Diet and activity	
Diet, activity effects removed	$F_{2,34}$ = 5.03*
Activity, diet effects removed	$F_{1,34}$ = 0.47 n.s.

Results of two-way analyses of variance are given (n.s., not significant; *, $P < 0.05$; **, $P < 0.01$).

†Because of the absence of arboreal folivores, one-way tests were performed separately within diet and zonation groups.

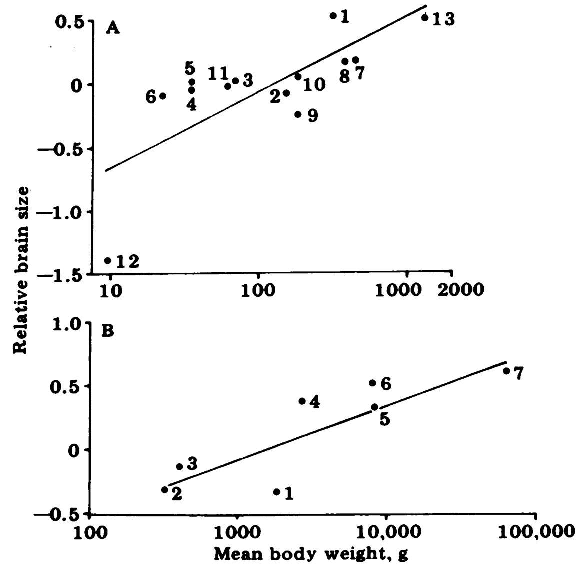

FIG. 2. Relative brain sizes of each family for small mammal (*A*) and primate (*B*) data plotted against mean body weight. Numbers refer to families ordered as in Fig. 1. Major axis analysis was used to produce lines of best fit. Correlation coefficients are significant in each case (Spearman's r = 0.67 and 0.79 respectively; $P < 0.05$).

Sciuridae and Heteromyidae, respectively); however, the insectivorous moles (Talpidae) have large relative brain sizes compared with the more primitive shrews (Soricidae) (Fig. 1).

Similar comparative studies on other vertebrate groups should allow a more precise evaluation of the factors that select for large or small brain size.

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