CARNIVORE BRAIN SIZE, BEHAVIORAL ECOLOGY, AND PHYLOGENY

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ABSTRACT.—This paper examines relationships between brain size (relative to body size) and differences in ecology and behavior within the order Carnivora. After removing the effects of body size (either body weight or head and body length) significant differences in brain size exist among families. Variation in relative brain size across the order and comparative brain size within families might relate to differences in diet (carnivores and omnivores have larger brain sizes than insectivores) and breeding group type. These findings are discussed and compared with those found in small mammals (rodents, insectivores, lagomorphs), primates and bats.

Recent studies have revealed correlations between relative brain size—measured as gross brain size after body size effects are removed—and behavior (Clutton-Brock and Harvey, 1980; Hafner and Hafner, 1984; Rensch, 1959), ecology (Clutton-Brock and Harvey, 1980; Eisenberg and Wilson, 1978, 1981; Mace et al., 1981), life histories (Sacher and Staffeldt, 1974), and taxonomy (Bauchot and Stephan, 1966, 1969; Jerison, 1973). In this paper, these factors are examined for correlations with relative brain size in the order Carnivora, a group that has not previously received quantitative analysis as a whole.

From qualitative comparisons of encephalization in primates and insectivores, Bauchot and Stephan (1966, 1969) concluded that habitat complexity, dietary specialization and activity patterns are associated with increased relative brain size. Pirlot and Stephan (1970) and more recently Eisenberg and Wilson (1978) showed that relative brain size in Chiroptera is correlated with foraging strategies that involve the location of energy rich food resources. Clutton-Brock and Harvey (1980) and Mace et al. (1981) found a parallel relationship between brain size and diet in primates and small mammals: folivores have smaller brain sizes for their body weight than frugivores, insectivores, and granivores. Lastly, Eisenberg and Wilson (1981) and Meier (1983) found that in didelphid marsupials and North American sciurids, respectively, arboreality tends to be associated with relatively large brain size. All of these studies therefore illustrate that variation in relative brain size among eutherian mammals can be partly explained in terms of behavioral and ecological factors.

In light of recent discussion (see Harvey and Bennett, 1983), one further explanation of differences in brain size must be mentioned. Following re-evaluation of the standard brain-body weight relationship across a wide range of mammals, it has been observed that the interspecific scaling is closer to a three-quarters exponent (Bauchot, 1978; Eisenberg, 1981; Hofman, 1982, 1983; Martin, 1981; Martin and Harvey, 1985) than a two-thirds exponent, as previously calculated (Jerison, 1973). This revised relationship suggests that variation in brain size may relate to energetics: basal metabolic rate, measured as energy needs per unit body weight in a given time period, increases to the three-quarters power of body weight. Although energetic needs may be an important factor influencing brain size, it cannot be taken into account in this analysis because few values of basal metabolic rate are available across carnivores (Eisenberg, 1981; Gittleman, 1984).

METHODS

Brain and body weights.—Data on adult body weights and body lengths (length of head and body without tail) were taken from the published literature (Table 1; references are given in Gittleman, 1984). Mean

TABLE 1.—*Species and data used for analysis. Taxonomy follows Ewer (1973) except for* Ailurus *and* Ailuropoda *(see Corbet and Hill, 1980; Eisenberg, 1981; Roberts and Gittleman, 1984). Following family and species names, columns indicate: (1) Activity pattern: D = diurnal; N = nocturnal; A = arrhythmic; C = crepuscular; O = crepuscular and nocturnal. (2) Vegetation: N = open grassland and forest; O = open grassland; R = forest; S = open grassland and woodland; D = dense brush and scrub; T = desert; W = woodland; Q = aquatic. (3) Zonation: T = terrestrial; S = terrestrial and occasionally arboreal; B = arboreal and terrestrial; A = arboreal; Q = aquatic. (4) Diet: M = carnivorous (flesh eater); O = omnivorous; I = insectivorous; F = piscivorous; V = frugivore and folivore. (5) Breeding system: P = polygynous; M = monogamous. (6) Breeding type: S = single-male; M = multi-male. (7) Body weight (kg). (8) Brain weight (g). (9) Body length (mm). (10) Parental care: 1 = female only (mother); 2 = biparental; 3 = communal females; 4 = communal male(s) and females. (11) Gestation length (days); (12) Eyes open (days); (13) Population group size.*

Species	1	2	3	4	5	6	7	8	9	10	11	12	13
Canidae													
Canis lupus	A	N	T	M	M	M	33.11	131.63	1,107.65	4	62.80	14.01	7.0
Canis latrans	C	N	T	M	M	S	10.49	88.23	804.32	4	61.55	11.94	2.1
Canis aureus	O	O	T	O	M	M	8.76	72.24	845.56	—	63.43	—	3.3
Canis adustus	N	S	T	O	—	S	11.25	51.94	765.09	—	—	—	2.0
Canis mesomelas	C	W	T	O	M	S	7.69	56.83	706.27	4	59.74	—	2.0
Lycaon pictus	D	O	T	M	M	M	21.98	129.02	972.63	4	70.81	11.94	8.0
Cuon alpinus	D	R	T	M	—	—	17.64	94.63	906.87	4	62.18	14.01	6.3
Alopex lagopus	A	O	T	M	—	M	3.19	35.52	550.04	2	53.52	15.03	—
Vulpes bengalensis	O	S	T	O	—	S	2.27	25.79	523.22	4	51.94	—	2.0
Vulpes ruppelli	O	T	T	M	—	—	3.60	24.29	415.72	—	—	—	—
Vulpes pallida	—	—	—	—	—	—	3.60	25.03	441.42	—	—	—	—
Vulpes chama	N	O	T	O	M	—	3.10	33.45	533.79	2	—	—	—
Vulpes velox	N	O	T	O	M	S	2.20	32.14	497.70	—	—	—	1.5
Vulpes vulpes	N	R	T	M	M	S	4.14	43.38	632.70	4	54.60	14.01	3.0
Fennecus zerda	O	T	T	O	M	—	1.51	17.29	368.71	2	54.05	16.95	—
Nyctereutes procyonoides	N	R	T	O	M	—	7.46	28.50	523.22	—	—	—	—
Otocyon megalotis	O	S	T	I	M	S	3.94	26.84	528.48	2	62.80	—	2.0
Urocyon cinereoargenteus	O	D	T	O	M	—	3.63	40.85	578.25	—	62.80	—	—
Urocyon littoralis	—	—	—	—	—	—	2.05	27.66	482.99	—	—	—	—
Dusicyon culpaeus	A	S	T	M	M	—	7.32	51.42	620.17	2	57.40	—	—
Dusicyon gymnocercus	N	O	T	M	—	—	4.39	40.04	—	—	57.97	—	—
Atelocynus microtus	—	—	—	—	—	—	9.03	62.18	862.64	—	—	—	—
Chrysocyon brachyurus	N	N	T	—	—	—	23.10	120.30	1,248.88	2	63.43	9.03	—
Speothos venaticus	N	R	T	—	—	—	5.99	40.45	665.14	2	64.72	—	—
Ursidae													
Ursus arctos	A	N	T	V	P	S	298.87	336.97	1,719.86	1	223.63	31.82	1.0
Ursus americanus	D	S	S	V	P	S	109.95	259.82	1,685.81	1	90.92	38.86	1.0
Thalarctos maritimus	D	—	—	—	—	S	365.04	459.44	1,844.57	1	249.64	34.12	1.0

TABLE 1.—*Continued.*

Species	1	2	3	4	5	6	7	8	9	10	11	12	13
Selenarctos thibetanus	A	R	S	V	—	S	100.48	314.19	1,510.20	1	225.88	7.03	1.0
Helarctos malayanus	N	R	B	V	—	—	79.84	354.25	1,248.88	—	—	—	—
Melursus ursinus	A	N	B	V	—	—	101.49	304.90	1,510.20	1	—	—	—
Procyonidae													
Bassariscus astutus	N	W	B	O	—	—	0.84	16.44	387.61	2	51.94	33.12	—
Jentinkia sumichrasti	—	—	—	—	—	—	0.90	19.30	424.11	—	—	—	—
Potos flavus	N	R	A	O	—	—	2.05	25.53	411.58	1	106.70	16.95	1.0
Nasua nasua	—	—	—	—	—	—	5.00	29.96	584.06	3	73.70	5.00	—
Procyon lotor	O	S	T	O	—	—	6.17	40.04	566.80	1	64.72	20.91	1.0
Ailuridae													
Ailurus fulgens	N	R	S	V	—	—	3.74	40.85	572.49	—	—	—	—
Ailuropoda melanoleuca	C	R	S	V	—	—	117.92	235.10	1,352.89	—	142.59	179.47	—
Mustelidae													
Mustela erminea	A	R	T	M	—	—	0.09	4.01	202.35	—	70.11	35.10	—
Mustela nivalis	A	S	T	M	—	—	0.10	1.99	159.17	—	42.10	29.08	—
Mustela rixosa	—	—	—	—	—	—	0.05	1.00	149.90	—	36.97	29.08	—
Mustela frenata	A	S	B	M	—	—	0.23	4.01	254.68	2	42.95	35.87	—
Mustela altaica	O	N	T	M	—	—	0.19	4.48	247.15	—	40.04	—	—
Mustela sibirica	O	N	S	M	—	—	0.57	6.75	304.90	—	—	27.94	—
Mustela lutreola	O	R	—	M	—	—	0.59	8.50	383.75	—	38.47	29.96	—
Mustela vison	N	R	—	M	—	—	0.91	8.50	365.04	—	29.08	35.16	1.0
Mustela putorius	N	R	S	M	—	—	1.03	8.25	357.80	1	40.85	29.08	—
Mustela nigripes	—	—	—	—	—	—	0.58	8.50	387.61	—	—	—	—
Vormela peregusna	C	N	T	I	—	—	0.59	4.76	330.30	1	61.56	—	—
Martes martes	N	R	B	M	—	—	—	20.09	512.86	2	29.96	37.00	1.5
Martes foina	—	—	—	—	—	—	1.80	20.91	415.72	—	—	—	—
Martes americana	N	R	B	M	—	—	0.86	15.80	407.48	1	27.11	36.97	1.0
Martes pennanti	A	—	—	—	—	—	3.46	31.82	555.57	—	76.71	—	—
Martes zibellina	N	R	T	O	—	—	1.17	18.54	450.34	1	27.94	35.16	—
Martes flavigula	D	R	B	M	M	S	2.51	34.12	—	—	—	—	—
Gulo gulo	A	N	T	S	P	—	11.13	78.26	713.37	1	36.60	27.94	1.0
Tayra barbara	—	—	—	—	—	—	4.39	35.87	639.06	—	64.07	—	—
Grison vittatus	D	N	T	M	—	—	2.44	24.29	512.86	—	—	—	—
Grison cuja	—	—	—	—	—	—	1.0	15.03	424.11	—	—	—	—
Ictonyx striatus	N	S	T	O	—	S	0.75	9.78	347.23	1	35.87	35.16	—

TABLE 1.—*Continued.*

Species	1	2	3	4	5	6	7	8	9	10	11	12	13
Poecilogale albinucha	N	D	T	M	—	S	0.29	4.76	307.97	1	32.14	32.14	1.0
Poecilictis libyca	—	—	—	—	—	—	0.23	4.48	212.72	—	—	—	—
Mellivora capensis	O	N	T	I	—	—	8.08	72.97	671.83	—	167.34	33.12	1.0
Meles meles	O	S	T	I	M	M	12.94	50.40	639.06	4	42.10	35.16	7.0
Arctonyx collaris	—	—	—	—	—	—	10.49	49.40	692.29	—	—	—	—
Mydaus javanensis	—	—	—	—	—	—	2.51	19.49	441.42	—	—	—	—
Taxidea taxus	A	O	T	M	—	S	4.06	48.91	550.04	1	42.10	—	1.0
Melogale personata	—	—	—	—	—	—	4.06	48.91	399.41	—	—	—	—
Mephitis mephitis	O	N	T	O	—	S	2.36	10.28	383.75	1	62.80	21.98	—
Spilogale putorius	N	O	T	O	—	—	0.54	5.00	275.89	1	29.96	32.14	—
Connepatus leuconotus	—	—	—	—	—	—	3.39	14.44	450.34	—	—	—	—
Lutra lutra	N	Q	Q	F	—	—	8.67	42.10	578.25	2	66.69	35.87	—
Lutra canadensis	—	Q	Q	F	—	—	7.32	52.98	692.29	—	112.17	33.12	—
Lutra annectens	—	—	—	—	—	—	14.73	59.15	578.25	—	—	—	—
Lutra ennudris	N	Q	Q	—	—	—	6.69	57.40	671.83	—	—	—	—
Lutra felina	—	—	—	—	—	—	4.10	38.86	678.58	—	—	—	—
Lutra maculicollis	A	Q	Q	F	—	S	4.01	40.04	595.86	—	—	—	—
Lutrogale perspicillata	—	—	—	—	—	S	8.67	64.72	888.91	2	60.34	—	2.0
Amblonyx cinerea	—	—	—	—	—	—	4.06	38.09	518.01	—	—	—	—
Aonyx capensis	O	Q	Q	O	—	—	19.11	94.63	788.40	—	60.34	27.11	—
Pteronera brasiliensis	—	—	—	—	—	—	27.39	85.63	1,141.39	—	—	—	—
Enhydra lutris	D	Q	Q	F	—	—	27.94	125.21	1,394.09	1	121.51	0.0	—
Viverridae													
Viverra zibetha	N	D	T	—	—	—	9.03	36.97	788.40	1	76.71	9.97	—
Viverra megaspila	—	—	T	—	—	—	8.50	36.60	845.56	—	—	—	—
Viverra tangalunga	—	—	T	—	—	—	4.71	24.05	645.48	—	—	—	—
Civettictis civetta	N	D	T	O	—	—	12.06	36.97	845.57	—	—	—	1.0
Viverricula indica	N	N	B	O	—	S	2.66	16.78	533.79	—	—	—	—
Genetta genetta	N	W	S	O	—	—	1.90	14.01	478.19	1	71.52	8.00	—
Genetta tigrina	N	R	B	O	—	S	2.05	15.18	502.70	1	70.11	11.94	—
Genetta servalina	N	R	B	O	—	—	1.25	15.03	487.85	—	—	—	—
Genetta angolense	N	R	—	—	—	—	2.10	15.49	473.43	—	—	—	—
Prionodon linsang	N	R	A	—	—	—	0.67	8.50	350.72	—	—	—	—
Prionodon pardicolor	—	R	A	—	—	—	0.45	9.03	354.25	—	—	—	—
Nandinia binotata	N	R	B	V	—	S	3.19	17.29	473.43	1	64.07	—	—
Arctogalidia trivirgata	N	R	A	O	—	—	2.46	21.98	528.48	—	45.16	11.02	—

TABLE 1.—*Continued.*

Species	1	2	3	4	5	6	7	8	9	10	11	12	13
Paradoxurus zeylonensis	N	R	A	—	—	—	2.72	17.81	497.70	—	—	—	—
Paguma larvata	N	R	A	—	—	—	4.31	30.88	533.79	—	—	9.03	1.0
Arctictis binturong	N	R	—	V	—	—	11.47	40.85	788.40	—	—	—	—
Hemigalus derbyanus	N	R	B	I	—	—	0.83	18.92	459.44	—	—	—	—
Cynogale bennetti	N	—	—	O	—	—	4.01	29.96	626.41	—	—	—	—
Fossa fossa	N	R	T	O	—	S	1.79	19.69	492.75	—	84.77	3.00	2.0
Eupleres goudoti	O	R	T	O	—	—	2.10	16.95	473.43	—	—	—	—
Galidia elegans	D	R	B	O	M	—	0.81	10.70	361.41	1	83.10	5.00	3.0
Salanoia unicolor	D	R	—	I	—	—	0.78	11.02	365.03	—	—	—	—
Herpestes ichneumon	A	D	T	O	—	—	3.03	23.34	572.49	—	62.80	—	—
Herpestes naso	N	R	—	—	—	—	3.00	25.53	533.79	—	—	—	—
Herpestes pulverulentus	D	N	S	O	—	—	0.84	11.02	340.36	—	—	—	—
Herpestes sanguineus	D	N	S	O	—	—	0.49	8.76	284.29	—	—	—	1.3
Herpestes auropunctatus	D	N	T	I	—	—	0.74	7.24	307.97	—	44.70	16.95	—
Herpestes edwardsi	D	D	T	O	—	—	1.26	10.49	399.41	—	60.34	—	—
Herpestes smithi	N	R	—	O	—	—	1.75	13.74	407.48	—	—	—	—
Herpestes fuscus	A	—	—	—	—	—	1.12	12.55	354.25	—	—	—	—
Herpestes vitticollis	A	R	—	—	—	—	2.29	25.79	478.19	—	—	—	—
Herpestes urva	N	D	—	O	—	—	2.36	20.91	507.76	—	60.34	—	—
Mungos mungo	D	S	T	I	—	M	1.26	10.49	327.01	4	60.34	9.97	—
Crossarchus obscurus	D	R	S	O	—	—	1.31	9.78	368.71	—	73.70	—	—
Helogale parvula	D	W	T	I	M	—	0.27	4.76	204.38	4	49.40	—	—
Bdeogale crassicaudata	—	W	—	I	—	—	1.25	16.95	445.86	—	—	—	—
Rhyncogale melleri	N	W	T	M	—	—	2.72	16.95	459.44	—	—	—	—
Ichneumia albicauda	N	S	T	O	—	—	3.86	24.29	566.80	—	—	—	1.0
Atilax paludinosus	N	R	T	O	—	—	3.67	28.50	512.86	—	—	—	—
Cynictis penicillata	D	O	T	I	—	—	0.59	10.49	307.97	—	—	—	—
Paracynictus selousi	N	S	T	I	—	—	1.70	15.80	428.38	—	—	—	—
Suricata suricatta	D	O	T	I	M	—	0.73	10.28	273.14	4	73.70	12.94	—
Cryptoprocta ferox	O	O	A	O	—	—	9.49	32.14	749.95	—	—	—	—
Hyaenidae													
Hyaena hyaena	N	O	T	O	—	S	26.84	97.51	1,043.15	2	90.12	7.03	1.0
Hyaena brunnea	N	S	T	O	—	M	43.38	106.70	1,152.86	4	—	8.00	9.0
Crocuta crocuta	N	O	T	M	P	M	66.02	144.03	1,480.30	1	109.95	1.00	55.0
Proteles cristatus	N	O	T	I	—	—	8.33	35.16	699.24	2	99.48	—	—

TABLE 1.—*Continued.*

Species	1	2	3	4	5	6	7	8	9	10	11	12	13
Felidae													
Felis silvestris	A	F	T	M	—	S	4.66	37.34	533.79	1	66.69	9.97	1.0
Felis libyca	N	S	T	O	—	S	4.31	36.23	561.16	1	54.60	11.94	1.0
Felis chaus	A	S	T	M	—	—	7.03	39.25	706.27	—	66.69	11.94	—
Felis nigripes	O	O	T	O	—	—	2.20	20.09	383.75	—	—	—	—
Leptailurus serval	A	N	T	M	—	S	10.80	5.26	772.78	1	73.70	9.03	1.0
Prionailurus bengalensis	A	R	B	M	—	S	5.47	29.37	720.54	2	66.69	9.97	—
Prionailurus rubiginosa	N	N	S	—	—	—	1.42	18.92	399.41	—	—	—	—
Prionailurus viverrinus	A	R	B	M	—	—	8.41	46.53	692.29	—	90.02	—	—
Ictailurus planiceps	N	—	T	O	—	—	2.10	21.98	497.70	—	—	—	—
Otocolobus manul	A	T	T	M	—	—	3.00	34.47	555.57	—	—	—	—
Profelis temmincki	—	N	T	—	—	—	4.22	68.03	796.32	—	—	—	—
Profelis aurata	O	R	B	M	—	—	11.94	57.97	757.48	—	—	—	—
Caracal caracal	N	S	S	O	—	S	11.47	55.15	742.48	—	73.70	9.97	1.0
Puma concolor	—	W	T	M	—	—	50.40	125.21	1,176.15	1	90.17	8.00	1.0
Leopardus pardalis	A	R	B	—	—	—	13.46	63.43	915.99	—	73.70	9.97	—
Herpailurus yagouaroundi	A	N	T	O	—	—	7.46	40.04	671.83	—	—	—	—
Lynx lynx	A	R	T	M	—	S	11.03	70.11	757.48	1	66.69	11.94	1.0
Lynx rufus	A	R	T	M	—	S	6.11	57.97	651.97	1	60.34	8.00	1.0
Panthera leo	N	S	T	M	P	M	154.47	223.63	2,591.52	4	109.95	3.00	8.7
Panthera tigris	N	R	T	M	—	S	159.17	278.66	2,230.54	—	—	9.03	1.0
Panthera pardus	O	W	S	M	—	S	50.91	125.21	1,152.86	1	99.48	9.03	1.0
Panthera onca	N	R	T	—	—	—	85.63	151.41	1,352.89	—	—	5.00	—
Panthera uncia	A	M	T	—	—	S	32.46	101.49	1,053.63	—	—	7.03	—
Neofelis nebulosa	N	R	B	—	—	—	19.49	68.71	837.15	—	—	—	—
Acinonyx jubatus	D	S	T	M	—	S	58.56	111.05	1,619.71	1	90.02	9.03	—

weights and lengths were calculated for each sex of each species, and species values were based on the mean for the two sexes. Juvenile or pregnant animals were not included, and average figures were calculated for species that undergo large seasonal fluctuations in body size (e.g., *Ursus arctos*).

Brain weights were measured from braincase volumes of skulls stored at The British Museum (Natural History), Museum of Comparative Zoology, and The Smithsonian Institution. Bauchot and Stephan (1966, 1969), Jerison (1973), and Martin (1980) have shown that braincase volumes can be used as estimators of brain weight. The cranial capacity of at least ten, and in larger species 18 (e.g., species in *Ursus* and *Panthera*), individuals of each sex were measured using 2 mm glass beads. Damaged skulls were not used, and skulls were thoroughly cleaned out before measuring. Brain weight values were established for 169 species in 98 genera, but data were analyzed only for 153 species (in 94 genera) where behavioral and ecological information was available.

Ecological variables.—Species were assigned to one type in each of the following ecological categories. (1) Vegetation: forest; woodland; dense brush or scrub; open grassland; and aquatic. Occasionally species could not be accurately described by one category and types were combined (e.g., *Ictonyx striatus*: open grassland and woodland; *Rhyncogale melleri*: open grassland and forest). (2) Activity pattern: nocturnal; diurnal; crepuscular; arrhythmic. Some species could only be accurately described by the combined type of nocturnal and crepuscular. (3) Diet: type of food constituting at least 60% of the diet. Those species that do not feed on any single food type comprising 60% of the diet were classified as omnivores. Species that are primarily scavengers (e.g., *Gulo gulo*) were not included in dietary analyses. Categories were: carnivores (flesh eaters); insectivores (this includes other invertebrate prey such as earthworms because of similar availability and distribution); frugivores/folivores; piscivores; and omnivores. (4) Zonation: terrestrial; terrestrial and occasionally arboreal (primarily ground living but adept at tree climbing); arboreal and terrestrial (both ground and tree living); and aquatic.

Behavioral and life history variables.—Species were classified, or values were calculated, for each of the following categories: (1) Breeding system: monogamy, polygyny. (2) Breeding group type: single-male, multi-male. (3) Population group size: the average number of individuals which regularly associate together and share a common home-range. (4) Parental care: number and sex of individuals caring for the young prior to independence from natal area. Types were: mother only, biparental, mother and communal females, communal females and male(s). (5) Home-range size: the total area (km^2) used by the group (or individual in solitary species) during normal activities. In some cases, estimates of home-range were not made on a daily basis (e.g., *Lycaon pictus, Gulo gulo*) and values were not standardized temporally. Data on home-range size were taken from Gittleman and Harvey (1982) and Gittleman (1984). (6) Gestation length: average time from conception to birth, minus the period of delayed implantation in some mustelids and ursids. (7) Eyes open: mean age at which eyes first open (days).

Analysis.—Prior to examining relationships of behavior, ecology or phylogeny with brain size, the effects of body size must be removed. Various problems arise in attempting to establish such an index of relative brain size, and these have been discussed at length (Gould, 1966, 1975). In brief, the main problem is how to calculate a line of best fit while measuring variation at different taxonomic levels. Previous studies (e.g., Jerison, 1973) have used an encephalization quotient by dividing the observed brain weight by the predicted brain weight based on the equation: Log (brain weight) = Log (0.12) + 0.67 Log (body weight).

The difficulty with such an equation is that a constant slope calculated for one group of related species (e.g., Carnivora) does not adequately describe slopes at different taxonomic levels (e.g., Canidae, Ursidae). Characteristically, slopes increase at ascending taxonomic levels (Martin and Harvey, 1985). A further problem arises from the uneven distribution among species within genera. For example, some genera (e.g., *Mustela*) have 10 or more species whereas many other genera (e.g., *Meles, Enhydra*) have only single species. Within a large genus, species tend to cluster together morphologically and ecologically (Cherry et al., 1982; Clutton-Brock and Harvey, 1977, 1984; Eisenberg, 1981). Such groups cannot necessarily be considered as independent points for analysis and therefore could bias relationships (see Harvey and Mace, 1982).

In order to alleviate some of the aforementioned difficulties, I have used the methodology adopted by Clutton-Brock and Harvey (1980) for analyzing primate brain size. First, after data were normalized by logarithmic transformation, all analyses were performed using "congeneric" values. These values were calculated from the medians of congeneric species that shared ecological, breeding system, or parental care category. Means of body weights, body lengths, home-range sizes, gestation lengths, and days that eyes first open were used for these species (certain species of *Canis, Vulpes, Dusicyon, Ursus, Mustela, Martes, Lutra, Viverra, Genetta, Herpestes, Hyaena, Felis, Prionailurus, Profelis, Lynx, Panthera*).

Second, to account for taxonomic effects, measurement of Relative Brain Size (RBS) for any given family was defined as the mean deviation of generic values from the common family slope. At the generic level,

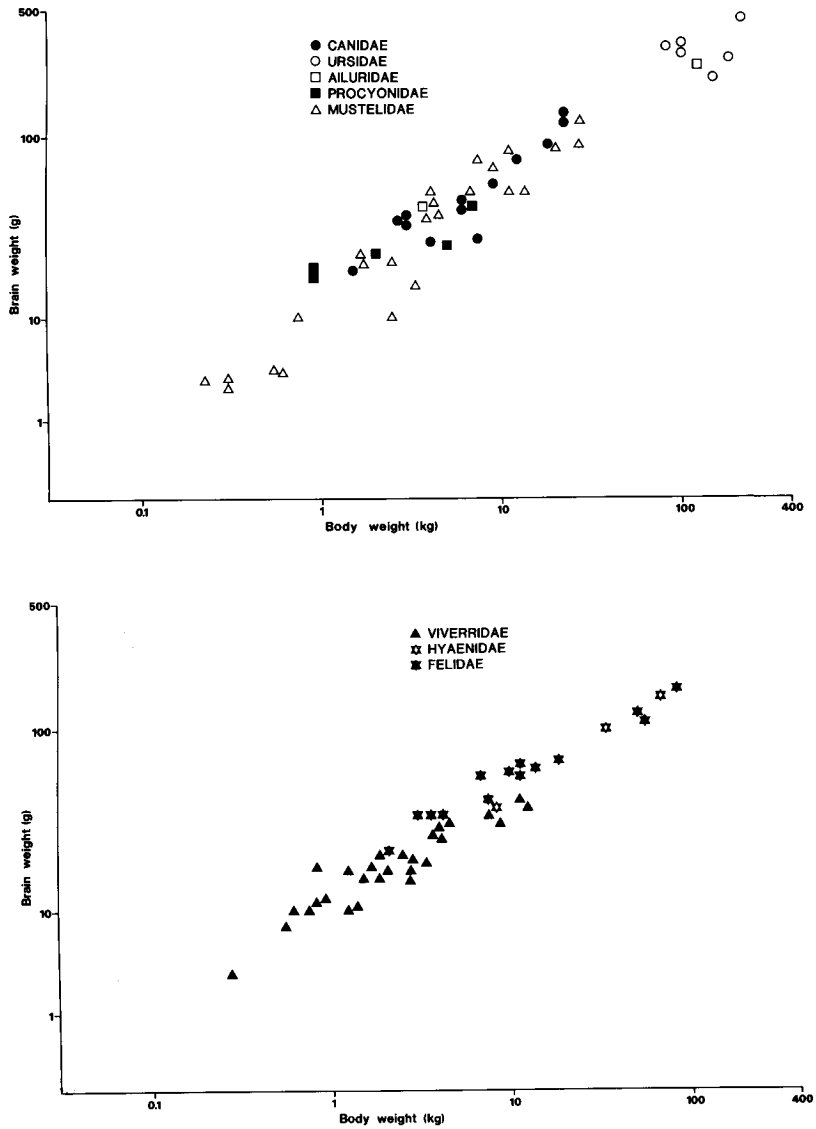

FIG. 1.—Brain weight plotted against body weight for congeneric species (see text) belonging to different families within Canoidea (top) and Feloidea (bottom).

relative brain size was established by calculating separate slopes and intercepts for each family and tabulating deviations for particular genera from these family values. This measure is referred to as Comparative Brain Size (CBS).

Lines of best fit were derived from major axis analysis and heterogeneity among slopes was assessed using a maximum likelihood ratio test (see Harvey and Mace, 1982). RBS for each family was based on the mean deviation of respective genera from the common major axis line across the order. To compare CBS's among ecological and behavioral categories, mean deviations for congeneric values were examined from family major axis lines. When differences among categories were found, pairwise comparisons were made between types using a t-test in which sample variances were not assumed equal.

TABLE 2.—*Slopes and elevations for $\log_e$ (body weight) and $\log_e$ (body length) regressed on $\log_e$ (brain weight), respectively. In all cases, data used in the analysis were based on mean estimates for adult males and females from each congeneric group (see text). The standard errors are of generic deviations from the common major axis line. % variance accounted for is correlation coefficient squared.*

Family	No. of genera	Slope	Elevation	Standard error	% variance
(a) Body weight analyses					
Canidae	13	0.713	0.197	0.24	85
Ursidae	6	0.225	0.346	0.39	52
Procyonidae	5	0.369	0.001	0.21	93
Mustelidae	24	0.771	−0.041	0.36	93
Viverridae	28	0.510	−0.174	0.20	71
Hyaenidae	3	0.695	−0.073	0.15	96
Felidae	14	0.506	0.048	0.21	92
(b) Body length analyses					
Canidae	13	1.878	0.143	0.16	95
Ursidae	6	1.020	0.397	0.34	59
Procyonidae	5	2.000	0.126	0.19	75
Mustelidae	24	2.578	−0.047	0.44	84
Viverridae	28	1.599	−0.232	0.20	90
Hyaenidae	3	1.969	−0.213	0.13	97
Felidae	14	0.599	−0.054	0.24	90

RESULTS

Allometric relationships.—The total major axis slope (across genera within the order) of brain weight on body weight was 0.57 (see Fig. 1). This is shallower than the slope of 0.69 quoted by Bauchot (1978) for 107 carnivore species but is identical to the regression slope calculated by Eisenberg (1981).

Families differed both in slope (body weight: $\chi^2_6 = 27.93$, $P < 0.005$; body length: $\chi^2_6 = 22.03$, $P < 0.005$) and, based on a best approximated slope through the order, in elevation (body weight: $F_{6,78} = 7.48$, $P < 0.001$; body length: $F_{6,78} = 5.47$, $P < 0.001$). Two families produce overall heterogeneity of slope: Ursidae are shallower and Mustelidae are steeper in slope than the remaining families (Table 2). Family differences in slope and elevation were similar when using either body weight or body length on the abscissa. Inter-family comparisons reveal that Ursidae have the greatest relative brain sizes; Procyonidae, Mustelidae and Felidae lie in the mean range; and Viverridae and Hyaenidae have the smallest relative brain sizes (Table 2; Fig. 2).

Brain size, ecology and behavior.—In the following, results of statistical tests using body weight are listed first and those with body length second.

Ecology: Differences in CBS's were not detected between activity categories ($F_{4,85} = 1.00$, n.s.; $F_{4,85} = 0.57$, n.s.), vegetation categories ($F_{6,85} = 0.89$, n.s.; $F_{6,85} = 0.75$, n.s.), or zonation categories ($F_{4,81} = 0.49$, n.s.; $F_{4,84} = 0.62$, n.s.). CBS is slightly greater (with body weight only) in carnivorous and omnivorous species and lower in insectivores ($F_{4,71} = 2.05$, $P < 0.10$). Within the Mustelidae and Viverridae, differences in CBS are in the same direction but are not statistically significant ($F_{3,10} = 2.71$, $P < 0.10$; $F_{3,21} = 2.37$, $P < 0.10$). No other ecological effects were found within families.

Even though home-range size is closely related to body size (Gittleman and Harvey, 1982), home-range size is not related to CBS ($r = 0.34$, $n = 31$), although there is a slight trend between home-range and CBS in Procyonidae ($r = 0.66$, $n = 3$) and Canidae ($r = 0.46$, $n = 5$).

Behavior and life histories: Differences in CBS were not found between monogamous and polygynous species ($F_{1,18} = 1.74$, n.s.; $F_{1,18} = 1.25$, n.s.) or between types of parental care ($F_{2,48} = 0.19$, n.s.; $F_{2,48} = 0.29$, n.s.); nor was CBS related to population group size ($r = 0.04$, $n = 32$, $r =$

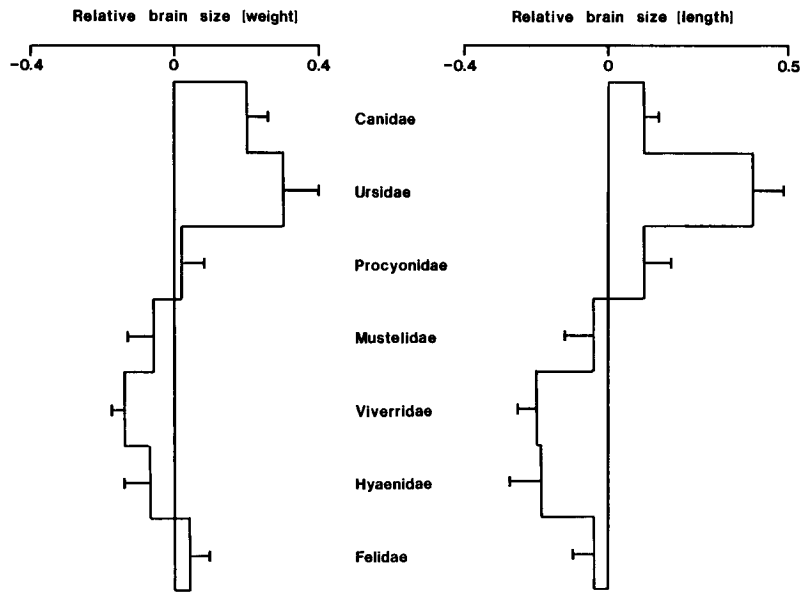

FIG. 2.—Relative brain size, measured as mean deviation of congeneric species from the common slope using each body weight and body length as independent variables. Error bars denote one standard deviation.

0.12, $n = 30$). However, comparisons between breeding group types revealed that single-male species have smaller CBS's than multi-male species ($F_{1,31} = 4.44$, $P < 0.05$; $F_{1,31} = 3.11$, $P < 0.01$).

CBS did not correlate with either gestation length ($r = 0.10$, $n = 58$; $r = 0.13$, $n = 58$) or days that eyes first open ($r = 0.03$, $n = 42$; $r = 0.22$, $n = 42$).

DISCUSSION

The most consistent results from analyses of comparative brain size in Carnivora are the significant differences among families. Similar differences have been found in rodents, insectivores and lagomorphs (Mace et al., 1981), Chiroptera (Eisenberg and Wilson, 1978), marsupials (Eisenberg and Wilson, 1981), and primates (Clutton-Brock and Harvey, 1980). Two explanations are commonly suggested for these taxonomic effects. First, historical events through evolutionary time might have selected for increased brain size; therefore differences in brain size should be apparent from comparison of "ancestral" with "derived" forms (Jerison, 1973). Second, interfamily differences might represent functional trends resulting from behavioral or ecological factors, or both (e.g., Clutton-Brock et al., 1980; Eisenberg and Wilson, 1978, 1981; Harvey et al., 1980; Mace et al., 1981; Meier, 1983). These two explanations will be discussed in turn.

The phylogeny of the modern carnivores is somewhat uncertain because most ancestral carnivores (Miacidae) lived in forests where fossilization was rare. From the fragmentary data that exist, the following picture emerges (see Flynn and Galiano, 1982; Hunt, 1974; Radinsky, 1982; Tedford, 1976). Two independent assemblages, the Canoidea and Feloidea, rapidly radiated in the late Eocene and early Oligocene (around 35 million years ago). The Canoidea consists of the Canidae, Procyonidae, Ailuridae (*Ailurus fulgens*), Ailuropodidae (*Ailuropoda melanoleuca*), Ursidae and Mustelidae; Feloidea consists of Viverridae, Hyaenidae, and Felidae. Modern families have larger brains for their body sizes than fossil carnivores (Hunt, 1974; Jerison, 1973; Radinsky, 1982) and, at the family level, brain sizes of ancient canids, felids, and probably mustelids are smaller than their respective modern representatives (Radinsky, 1982). The causal

factors underlying the radiation of modern carnivore lineages remain unclear (Radinsky, 1981*a*, 1981*b*, 1982) and therefore it is difficult to interpret interfamily differences from a phylogenetic explanation. Nevertheless, it is useful to compare the results in this study with others on cranial morphology to examine how robust such familial differences are.

Radinsky (1975) used brain weight : foramen magnum ratios in his analysis of brain size patterns in viverrids and found that except for *Nandinia*, the Paradoxurines (*Nandinia, Paradoxurus, Arctogalidia, Paguma, Arctictis*) have larger brain sizes than other genera within the family. My results corroborate Radinsky's findings with the exception of *Paradoxurus* which has a small CBS. Furthermore, my results using a larger data set are consistent with inter-family differences found by Wirz (1966) and Radinsky (1975, 1978) in which Viverridae have smaller relative brain sizes than Felidae and Canidae, and Canidae have larger relative brain sizes than Mustelidae and Felidae. Observed differences in slope, where mustelids are steeper and ursids are shallower than the remaining families, also parallel findings in Radinsky (1981*a*, 1981*b*). These differences in slope may lie in some allometric change resulting from the unusual body proportions found in long and thin mustelids and large and heavily built ursids.

Interfamilial differences in brain size could relate to certain taxa being fatter or having larger gastro-intestinal tracts, therefore resulting in smaller RBS's (see Roth and Thorington, 1982). This confounding variable may be accounted for by plotting brain size on head and body length rather than on body weight. Using head and body length as an independent variable, RBS differs significantly between taxonomic families (see Table 2; Fig. 2): Ursidae have large brain sizes and Viverridae have small brain sizes. Only in the Felidae is there a difference in using head and body length, which may relate to homogeneity of head and body length across the family. In sum, interfamilial differences in RBS across Carnivora are consistent when measured allometrically either from body weight or head and body length. Such taxonomic differences must be considered in further work on brain size (for review, see Martin and Harvey, 1985) and cranial morphology (see Radinsky, 1981*a*, 1981*b*, 1982) in order to derive meaningful functional explanations of variation in brain size.

Analyses of behavioral and ecological associations with CBS only revealed suggestive trends which were not as marked as in previous studies on mammalian brain size (see Harvey et al., 1980; Eisenberg and Wilson, 1978, 1981). First it is worth mentioning how results from the present study (using a larger data base) compare with two previous studies on carnivore brain size. Fagen and Wiley (1978) analyzed encephalization (from body weight) in small felids and concluded that *Leopardus* has a larger CBS than *Prionailurus*, while *Felis chaus* and *Herpailurus* were intermediate in size. They explain this result on the basis that increased brain size (in *Leopardus*) is influenced by long gestation length and slow somatic cell development as measured by the age at which the eyes first open. I found similar differences in CBS between *Leopardus* and *Prionailurus*, although no correlation relating these life history variables to CBS was apparent, either within the Felidae or across Carnivora as a whole. Hemmer (1979) compared encephalization values between social and solitary species in Canidae, Hyaenidae, and Felidae. Although the brain and body size data were not given and differences among families were not accounted for, Hemmer claimed that social species (*Canis lupus, C. latrans, C. mesomelas, Lycaon pictus, Cuon alpinus, Crocuta crocuta, Panthera leo*) have larger brain sizes than solitary species (e.g., *Alopex lagopus, Vulpes vulpes, Proteles cristatus, Felis silvestris*). My analysis of a substantially larger data set than Hemmer's showed no such pattern and, therefore, suggests that his results were incorrect.

Previous studies repeatedly have shown a relationship between diet or foraging strategy and brain size. Independently, in four primate families (Lemuridae, Cebidae, Cercopithicidae, Pongidae), CBS is significantly greater in frugivores than folivores (Clutton-Brock and Harvey, 1980). Among Chiroptera, RBS is greater in frugivores of the family Pteropidae and the subfamily Stenodermatinae than in aerial insectivores from Mormoopidae, Emballonuridae, Vespertilionidae, and Molossidae (Eisenberg and Wilson, 1978). Similarly, among other small mammals (rodents, insectivores, lagomorphs), frugivores, insectivores, granivores and generalists have larg-

er CBS's than folivores (Mace et al., 1981). In each of these studies it was suggested that increased brain size results from selection for increased sensory and perceptual capacities for locating relatively clumped food resources which are evenly and widely distributed.

Although dietary effects across Carnivora were significant at only the 10% level, it is meaningful to report these because they parallel findings in other mammalian groups and, as in other studies, were the only ecological associations out of four examined factors to suggest functional relationships. Across the order, carnivores and omnivores have larger RBS's than insectivores. However, because of the significant heterogeneity of slope across the order (mainly due to Ursidae and Mustelidae), these results are less meaningful than comparisons of CBS among dietetic groups.

Within Mustelidae and Viverridae, carnivorous species have greater CBS's than insectivores. In other taxa (e.g., lizards: Platel, 1974, 1975; fishes: Bauchot et al., 1977; dinosaurs: Hopson, 1977), it has been observed that active predators have large brain sizes. Differences in relative brain size in the Mustelidae and Viverridae might be explained by the different hunting and foraging strategies.

Comparative studies have revealed that carnivorous mustelids (species within *Mustela* or *Martes*) and viverrids (species with *Genetta* or *Rhyncogale*) are more adept than insectivorous species (e.g., *Ictonyx, Mungos, Meles*) at running down, grasping and manipulating prey with the forepaws, as well as accurate delivery of a killing bite (see Eisenberg and Leyhausen, 1972; Rowe-Rowe, 1978; Leyhausen, 1979; Waser, 1980). While searching for food, insectivorous species use an irregular walk or trot with frequent stops at potential prey sites, whereas carnivorous species adopt a slow cat-like stalk followed by a sudden pounce (Ewer, 1973; Waser, 1980). Once prey are captured, insectivores are effective at eating invertebrates (e.g., moths, mantids, beetles) by either picking them up directly off the ground with their mouth, or pinning them to the ground with a forepaw and then eating them (Rasa, 1973); flying or jumping insects are captured primarily on the ground. Insectivorous carnivores usually eat their prey very quickly, and if the prey move they are either caught immediately or they escape. Although the forepaws may be used to pull insects to the mouth, generally less manipulation and grasping of prey is employed in insectivorous species than carnivorous ones (Rasa, 1973; Waser, 1980). Comparative evidence on small carnivores in the Serengeti indicates that rate of prey capture is higher in insectivores than carnivores (Waser, 1980), suggesting perhaps less need for complex foraging behavior in insectivores.

Therefore, carnivorous species within Carnivora may have increased brain sizes because of a more complex foraging strategy involving selection for rapid prey detection, pursuit, capture (especially forepaw manipulation) and consumption. In contrast, selection for increased brain size in insectivorous species may be less intense because of more stereotyped foraging patterns involved in successful capture of invertebrate prey. Certainly, this explanation must be considered tentative until more detailed measurements are available of specific foraging patterns among carnivores and insectivores, and the accompanying neurological data are supportive.

Lastly, the analysis suggests that CBS may differ between species with different breeding group types. These differences might be explained by multi-male species displaying greater behavioral complexity (see Bekoff et al., 1984) and thus requiring the capacity to process relatively more complex information than single-male species. However, there are exceptions to this trend. *Meles meles* and *Mungos mungo* are both multi-male species which have small CBS's; and *Vulpes velox* and *Martes flavigula* are single-male species which have large CBS's. Clearly, further behavioral information is needed before this result may be accepted for carnivores.

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