

RELATIVE BRAIN SIZE AND FEEDING STRATEGIES IN THE CHIROPTERA

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Pirlot and Stephan (1970) demonstrated that the relative brain size varied greatly when nine families of Chiroptera were compared. Some 51 species were studied and an average index of encephalization for each family was calculated. They pointed out that the Pteropidae, Desmodontinae, and Noctilionidae had the highest indices of encephalization for their sample. Stephan and Pirlot (1970) expanded the above observations by comparing the relative volumes of 11 brain structures for 18 species drawn from eight families. These volumes were then compared with equivalent volumes derived for a series of "basal" insectivores (*Suncus*, *Sorex*, *Tenrec*, *Hemicentetes*). Although specific brain structures evolve at different rates within each family with some structures declining in relative size and others increasing, a generalized correlation of brain size with feeding habits could be made. The relative size of the neocortex showed a strong positive correlation with the degree of encephalization. This correlation in turn could be related to dietary specializations. They proposed that the Noctilionidae, Desmodontinae, and Pteropidae showed the highest development of the neocortex, but were broadly overlapped by certain species of the Phyllostomatidae.

The order Chiroptera includes two distinct lineages which have been separated since the Eocene: the Pteropidae or Megachiroptera and the Microchiroptera. The ancestral Pteropidae may have attained the capacity for flight after diverging from a flightless common ancestor which in turn gave rise to the ancestral microchiropteran. The species of the microchiropteran family Phyllostomatidae are rather unified morphologically, but

their origins are somewhat obscure (Smith, 1976). No doubt they separated from ancestral microchiropterans before the Oligocene and radiated in the Neotropics without competition from the Megachiroptera. In their exploitation of feeding niches in the Neotropics through adaptive radiation, the phyllostomatid bats exhibit the principle of complementarity (Darlington, 1957) in that they parallel the niche subdivision seen in the radiation of the Megachiroptera in the Palaeotropics.

We measured the cranial capacities of 225 species of bats from 14 families including all families and genera previously studied by Stephan and Pirlot (1970). We wished to confirm their conclusions about encephalization and refine their first order correlation with dietary specializations. We did not use actual brain weights but estimated brain volume from a measurement of cranial capacity, using lead shot and volumetric correction constants.

METHODS

Specimens were selected from the research collections at the National Museum of Natural History which had both an intact skull and a field recorded body weight. To eliminate weight changes induced by pregnancy, we used only adult males in the computations. We selected at least four specimens of each species and determined the cranial capacity of each specimen twice, according to the following procedure. The skull was weighed to the nearest 0.01 g. If the freshly collected specimen weighed less than 150 g, No. 3 dust shot was introduced into the cranial cavity through the foramen magnum and the skull reweighed. The procedure was repeated after emptying out the original shot. Larger specimens were treated in the

TABLE 1. Comparisons of absolute and estimated brain weight for 11 species of bats.

Taxon	Known brain weight ¹ (g)	Estimated brain weight (g) ²	
		Range	\bar{X}
<i>Rhinolophus hipposideros</i>	0.150	0.11–0.20	0.15
<i>Glossophaga soricina</i>	0.358	0.38–0.41	0.40
<i>Phyllostomus discolor</i>	0.836	1.03–1.11	1.08
<i>Carollia perspicillata</i>	0.442	0.55–0.60	0.58
<i>Sturnira lilium</i>	0.487	0.53–0.59	0.56
<i>Artibeus jamaicensis</i>	0.87	0.91–1.15	1.04
<i>Artibeus lituratus</i>	0.98	1.12–1.35	1.26
<i>Desmodus rotundus</i>	0.78	0.89–1.00	0.94
<i>Noctilio leporinus</i>	1.189	1.23–1.35	1.29
<i>Cynopterus brachyotis</i>	0.803	0.95–1.19	1.05
<i>Cynopterus horsfieldi</i>	1.144	1.06–1.31	1.20

¹ Pirlot and Stephan (1970).

² See text for method of estimation

same manner with the exception that No. 10 dust shot was used. We then calculated species averages based on at least eight measurements for each species. The weight (*Wt.*) of the shot was converted to volume (*V*) in cubic centimeters (cm³) by using an empirically derived constant (*K*) and the formula $Wt. \div K = V$. For No. 10 shot, $K = 6.0$; for No. 3 shot, $K = 6.4$. The accuracy of the method was tested by comparing the calculated volume of the cranial capacity with known brain weights, as published by Pirlot and Stephan (1970) (see Table 1). Since the brain nearly fills the cranial cavity and the specific gravity of the brain nearly equals the specific gravity of water, cranial volumes in cm³ should approximate the brain weight in grams.

Pirlot and Stephan analyzed only single brains for each species and our volumes represent a series of at least eight measurements of four different specimens, thus it is difficult to compare the two samples. The data for actual brain weights of *Rhinolophus hipposideros* and *Cynopterus horsfieldi* fall within our volumetric ranges for these species. The actual brain weights for *Glossophaga soricina*, *Artibeus jamaicensis*, and *Noctilio leporinus* fall within 0.04 g of our low range. This implies that our volumetric values could be from 4 to 6% higher than the actual brain weights. Since our technique takes

no account of the space occupied by the meninges, this discrepancy seems plausible. The striking fact is that the correspondence is rather good. We decided to proceed with the comparison of the cranial volumes to body weight ratios, bearing in mind that a slight overestimate of actual brain size might be involved.

RESULTS

We examined 225 species from 88 genera and 14 families (see Fig. 1). The average cranial capacity of each species has been regressed on the average body weight by using a double log₁₀ plot. Given the general equation $Y = bX^\alpha$ this can be expressed in log form: $\log Y = \log b + \alpha \log X$ where Y = average cranial capacity; X = average body weight; α = slope of the log regression and b = the Y intercept. In surveying the data the following statements can be made: over a series of body weights, the cranial volumes for almost all families show similar slopes. The Pteropidae, Mormoopidae, Molossidae, and Rhinolophidae have the highest correlation coefficients. The Vespertilionidae show the most variation within a family (see Table 2). The Rhinopomatidae, Molossidae, Emballonuridae, Mormoopidae and Vespertilionidae have the lowest b values (log₁₀ Y intercept) and show on the average only a slight increase in average cranial capacity over that of the "basic in-

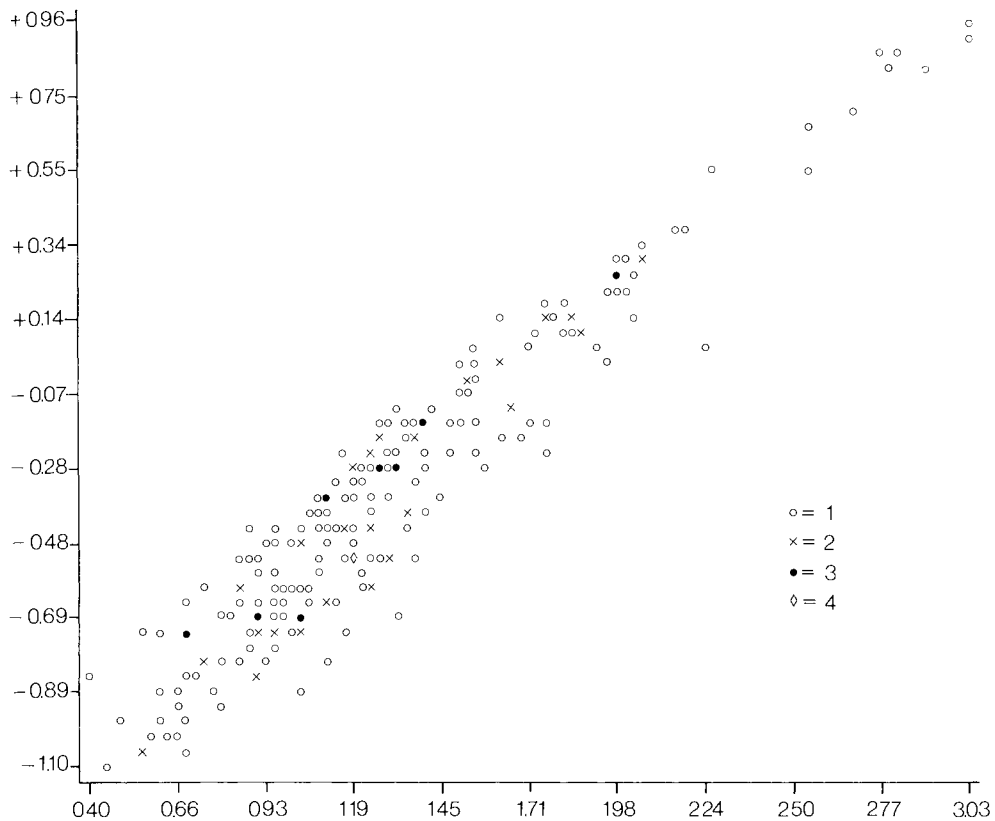


FIG. 1. Distribution of \log_{10} average cranial volumes (ordinate) regressed against \log_{10} average body weights (abscissa) for 225 species of Chiroptera. Where points overlap appropriate symbols have been used to indicate the numbers of species involved. 1, 2, 3, and 4 = numbers of species.

sectivores" (Bauchot and Stephan, 1966). The Megachiroptera (Pteropidae), Phyllostomatidae, Megadermatidae, Noctilionidae and Nycteridae display the highest cranial capacities for their weight classes. The Rhinolophoidea are interme-

diate. (When the families Hipposideridae and Rhinolophidae are referred to as a unit, we employ the superfamilial category Rhinolophoidea.)

Given that the Pteropidae show many adaptations differing from the other families of the Chiroptera, it is interesting to note that many phyllostomatid bats attain a cranial capacity equal to that shown by the pteropids in the same weight class.

The data suggest that aerial insectivores that capture prey by flying and rely almost completely on echolocation have the lowest brain size to body weight ratios. On the other hand, insectivorous bats that discretely sample microhabitats (e.g., Hipposideridae) or utilize a complex foraging strategy involving vision and sonar to exploit micro-niches in the vegetation

TABLE 2. Summary of regression and correlation analysis, using $\log Y = \log b + \alpha \log X$.

Taxon	Slope (α)	Intercept $\log_{10}(b)$	SE
Chiroptera	.802	-1.368	—
Pteropidae	.661	-1.0186	.04
Emballonuridae	.697	-1.323	.07
Rhinolophidae	.597	-1.195	.04
Hipposideridae	.565	-1.136	.08
Mormoopidae	.737	-1.332	.02
Phyllostomatidae	.683	-1.120	.04
Vespertilionidae	.589	-1.300	.09
Molossidae	.686	-1.359	.05

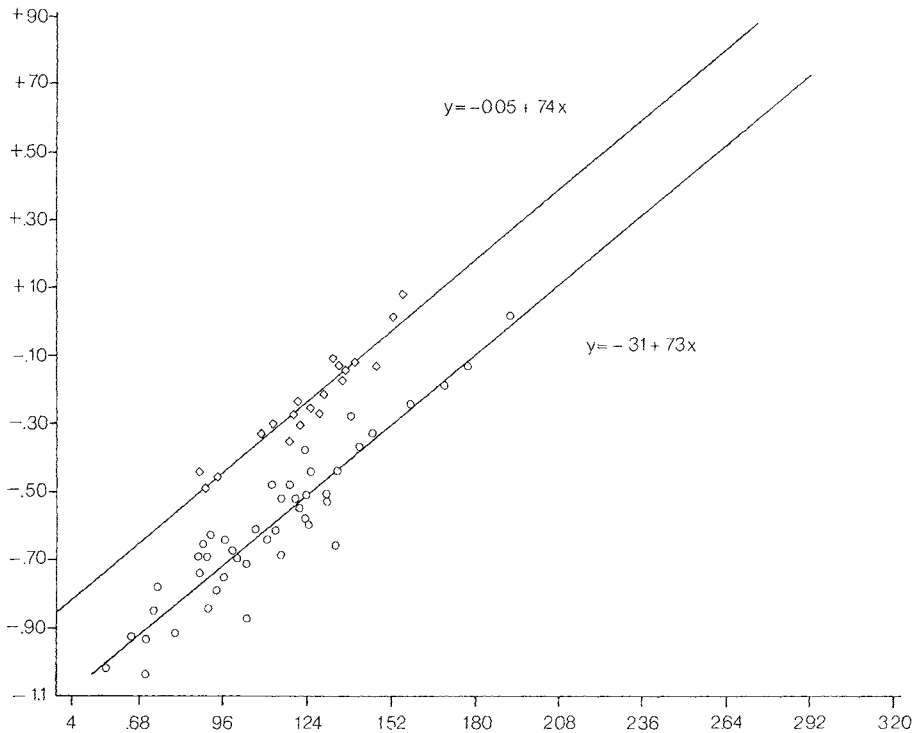


FIG. 2. Regression analysis comparing the slopes and intercepts (in logs) for frugivores (higher slope) and aerial insectivores (lower slope), according to Wilson (1973). Scales as in Fig. 1.

have "intermediate" brain size to body weight ratios (e.g., some Vespertilionidae and some Phyllostomatidae). The strong correlation ($r = 0.95$) for the data in Figure 1 encouraged us to examine subsets of the data in order to suggest functional reasons for the variation demonstrated.

In order to test the hypothesis that relative brain size is a reflection of feeding strategy, we used only species which Wilson (1973) had unequivocally allocated as either "Frugivores," or "Aerial Insectivores." A regression analysis comparing these two groups (Fig. 2) showed that frugivores of the family Pteropidae and the phyllostomatid subfamily Stenoderminae had consistently larger brain volumes for a given body weight than aerial insectivores drawn from the families Mormoopidae, Emballonuridae, Vespertilionidae, and Molossidae. That there is no overlap

between these two groups is central to our hypothesis: relative cranial capacity is a reflection of feeding strategy.

Once regression lines for aerial insectivores and frugivores are established, it was possible to plot other species of the Chiroptera with different feeding strategies in comparison with those lines (Fig. 3). Carnivores, piscivores, sanguivores, and foliage gleaners fall between the aerial insectivore and frugivore regression lines. For some of these species for which food habits and feeding strategy are poorly known, it may be possible to infer something about their habits from their brain size. For example, *Nycteris arge* and *Microonycteris megalotis* both have relatively larger cranial volumes than their congeners, and in fact fall on the regression line for frugivores. *Nycteris arge* and *N. gambiensis* are exactly the same size, but *N.*

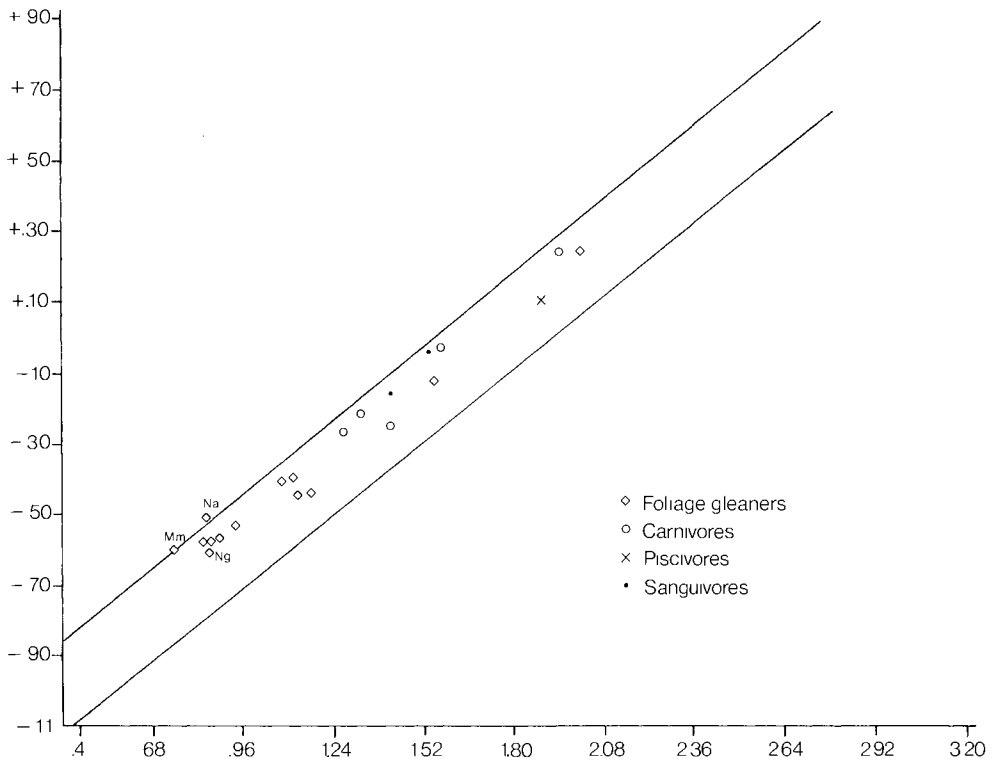


FIG. 3. The average cranial volumes for foliage gleaners, carnivores, piscivores and sanguivores shown with the regression lines for frugivores and aerial insectivores from Fig. 2. Na = *Nycteris arge*; Mm = *Micronycteris megalotis*; Ng = *Nycteris gambiensis*.

arge has a larger volume; that increase may well relate to differences in feeding strategy and habitat selection.

Nectarivorous bats (Fig. 4) fall close to the frugivore line, and might be considered to use the same strategy for locating flowers as do frugivores for locating fruit. The two species of pteropid nectar-feeders, *Megaloglossus* and *Nanonycteris*, fall above the frugivore line and most of the glossophagine and phyllostomatine nectarivores fall slightly below it.

Using the regression lines generated in Figure 2 as standards for comparison, we examined various families and subfamilies of bats as phylogenetic subsets. Figure 5 shows the family Pteropidae which is clustered around the regression line for frugivores, except that very large forms seemed to be displaced slightly below the

line as might be expected from allometric considerations (Jerison, 1973). *Hypsignathus monstrosus*, which fell below the line, has been reported to be partially carnivorous (Van Deusen, 1968), and this departure from frugivory may affect its displacement, although the teeth of this bat do not seem adapted for carnivory.

The larger species of the subfamily Stenoderminae and the family Vespertilionidae (Fig. 6) also are displaced slightly downward, but this may be a simple result of general allometric trends. Referring to Figure 6 the Vespertilionidae appears to be one of the most variable groups of all, and causes much of the scatter around the regression line for aerial insectivores in Figure 2. The genus *Myotis* is responsible for much of this scatter. Therefore we examined the genus *Myotis* more closely,

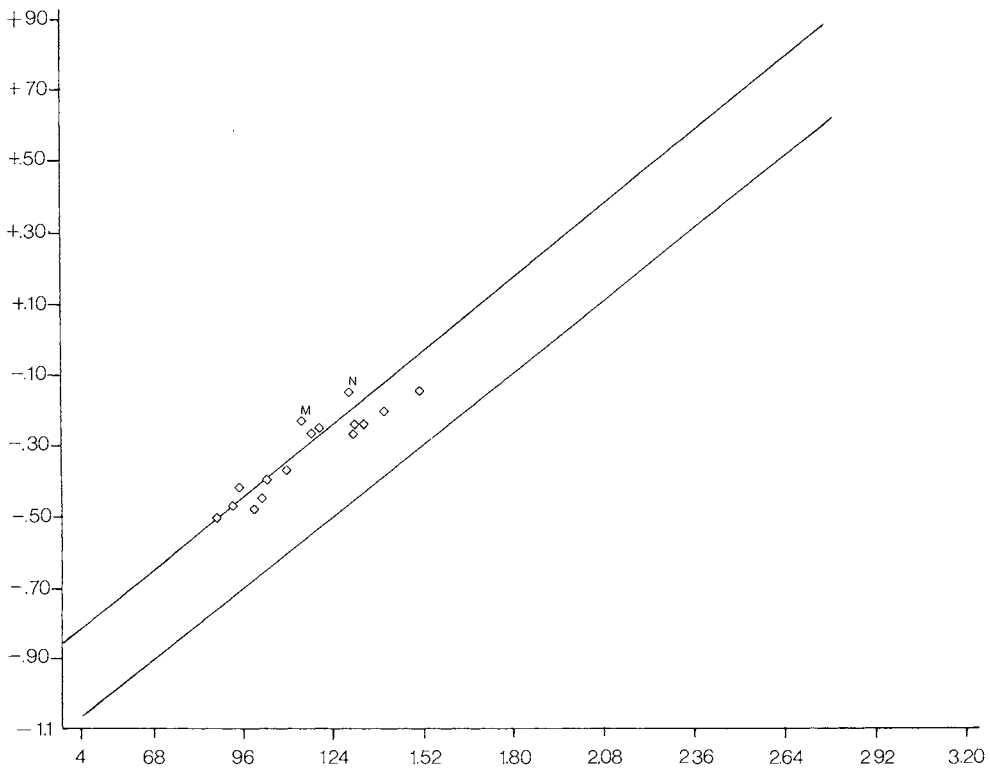


FIG. 4. Relative cranial volumes of nectarivorous bats plotted against the regression lines for frugivores and aerial insectivores from Fig. 2. M = *Megaloglossus*; N = *Nanonycteris*.

and we were fortunate to obtain the data set assembled by James S. Findley for his study of phenetics in the genus *Myotis* (Findley, 1973).

Findley (1973) suggested that one group of species in the genus *Myotis* might be adapted to "pick prey from various substrata, . . ." or, in our terminology, to glean foliage. All species in this group had high positive loadings for the first factor in his multivariate analysis and included *Myotis auriculus* and *M. thysanodes*, the two species farthest from the aerial insectivore line in Figure 6. These two species are rather small. Although Findley's factor I contains loadings for size, it also contains an entire suite of characters which are unrelated to size but do correlate with hovering flight. We regressed Findley's factor I scores against a ratio of cranial volume to body weight (\bar{x} wt. shot/ \bar{x} body

wt.) for nine species of *Myotis* to see if part of the cranial volume variation within the genus might be explained by morphological features which Findley thought reflected actual differences in feeding strategies. The results of that analysis indicate that there is a positive correlation ($r = 0.87$) between relative cranial volume and Findley's factor I phenetic measure. This relation strengthened our interpretation that the variation shown in Figure 6 is a reflection of different foraging strategies within the genus *Myotis*.

Larger mammals generally have a lower brain to body weight value than do smaller ones. The allometry of brain to body weight ratios as a function of size has been analyzed by Jerison (1973). In his analysis of the class Mammalia he determined that the slope for the regression of \log_{10} brain weight against \log_{10} body weight was

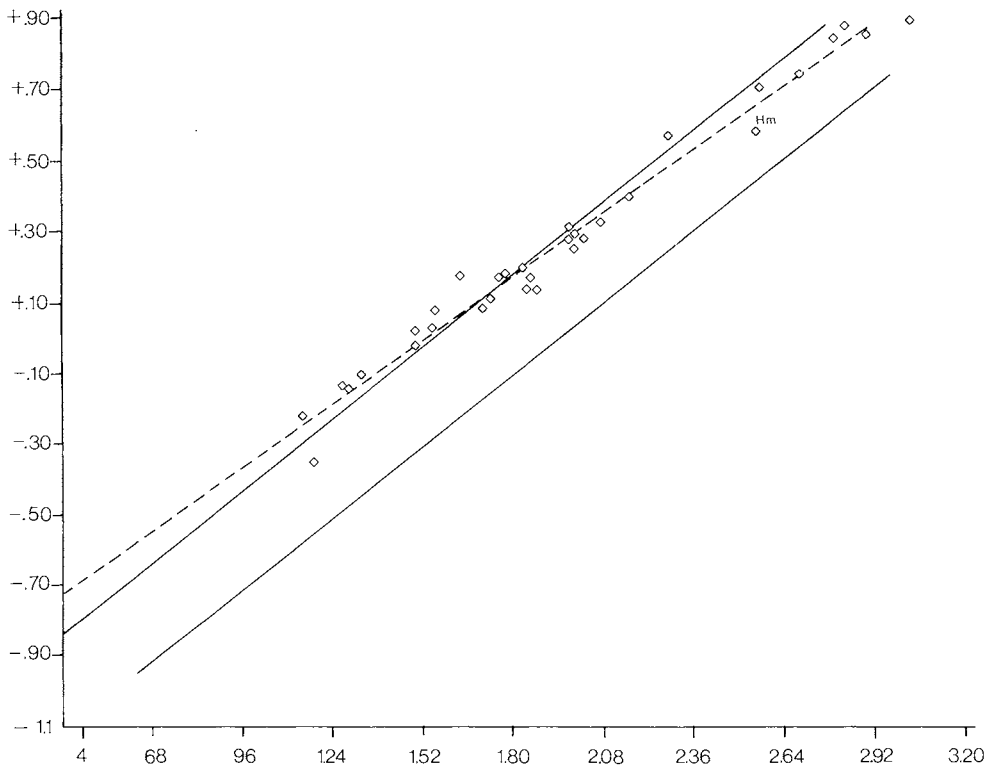


FIG. 5. Cranial volumes for the Pteropidae shown with the regression lines for frugivores and aerial insectivores from Fig. 2. The dotted line is the regression for the Pteropidae. Hm = *Hypsignathus monstrosus*.

0.66. His sample had few bats. Using our series of bats and other mammal data collected by Eisenberg (unpubl.), we recalculated a regression for the entire class Mammalia which gave a slope of 0.74 and an intercept of $\log_{10} = -1.26$. We then recalculated encephalization quotients (EQ) for each species of the Chiroptera and for those members of the Insectivora for which we had data. EQ is the ratio between the observed brain volume and expected brain volume. EQ values were determined using the general formula from Jerison (1973) with our newly determined values for the mammalian regression line. The expected volume (Ev) is calculated from the known mean body weight ($Wt.$) and the formula: $Ev = 0.055: Wt^{0.74}$. Table 3 presents the EQ average values for four insectivore families

and 15 chiropteran families. Utilizing EQ values, we avoid the effects of negative allometry when comparing large and small forms. Clearly the Pteropidae, Phyllostomatidae, and Thyropteridae have relatively large cranial volumes. The Megadermatidae, Nycteridae and Natalidae are not far behind. The bat families with the lowest EQ values are far in advance of the values for the "basal insectivores" and higher than most insectivore families with the exception of the fossorial and semi-aquatic Talpidae.

Table 4 presents the average EQ value for each trophic role as defined by Wilson (1973). In composing this table we included those species which seemed to fall unequivocally in a given trophic role. In conformity with the regression analysis, nectarivores and frugivores have the high-

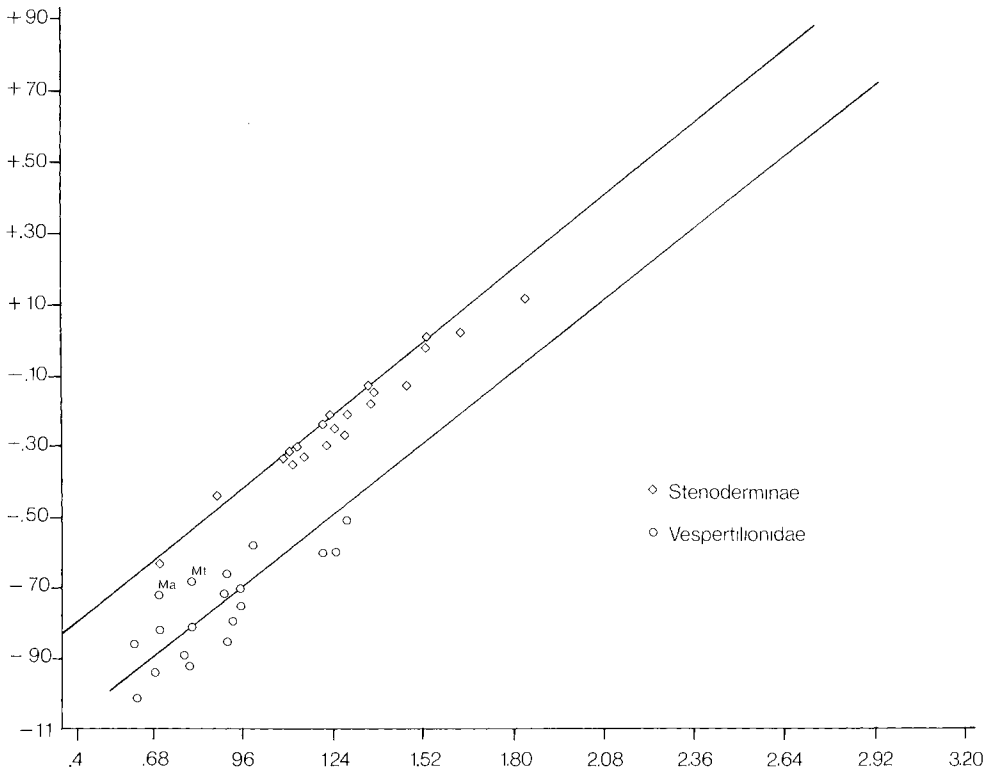


FIG. 6. Relative cranial volumes of the Stenoderminae and Vespertilionidae plotted against the regression lines for frugivores and aerial insectivores from Fig. 2. Note the scatter in the Vespertilionidae. Ma = *Myotis auriculus*; Mt = *Myotis thysanodes*.

est EQ values closely followed by the sanguivores. Carnivores come next followed by foliage gleaners and piscivores. The aerial insectivores have the lowest encephalization quotients.

The classification scheme of Wilson was based on a survey of the literature combined with first hand knowledge of some phyllostomatids and vespertilionids. The scatter around the regression lines and the standard deviations for EQ values suggest some diversity of feeding strategies by the species of selected genera or subfamilies.

Encephalization quotients when calculated for the subfamilies of the Phyllostomatidae indicate that the Phyllostomatinae fall near the mean for foliage gleaners. *Mimon crenulatum* ($EQ = 0.86$) and *Tonatia sylvicola* ($EQ = 0.92$) are thought to be foliage gleaners (Wilson, 1973; Gard-

ner, 1977). *Micronycteris megalotis* ($EQ = 1.28$) is thought to be a frugivore (Goodwin and Greenhall, 1961). The Desmodontinae have encephalization quotients nearly as high as the frugivores.

The Emballonuridae and Molossidae have EQ values near those of the aerial insectivores but some emballonurids with high EQ values may well be foliage gleaners, e.g. *Taphazous longimanus* ($EQ = 0.88$) and *Diclidurus isabellus* ($EQ = 0.85$). The Rhinolophidae have EQ values near the aerial insectivore average, but the Mormoopidae and Hipposideridae are somewhat higher. Some members of the Hipposideridae may forage in a manner similar to classical foliage gleaners such as *Hipposideros cyclops* ($EQ = 0.86$).

The Natalidae fall near the foliage gleaner average and the Rhinopomatidae

TABLE 3. *Encephalization quotients for insectivores and bats.*

	Range	$\bar{x} \pm SD$
Chiroptera		
Megachiroptera		
Pteropidae	0.95-1.47	1.20 \pm 0.16
Microchiroptera		
Rhinopomatidae	0.59-0.62	0.61 \pm 0.01
Emballonuridae	0.64-1.23	0.76 \pm 0.13
Noctilionidae	0.74-0.93	0.84
Nycteridae	0.94-1.28	1.08
Megadermatidae	0.93-1.14	1.06 \pm 0.11
Rhinolophidae	0.73-0.93	0.79 \pm 0.09
Phyllostomatidae	0.79-1.41	1.13 \pm 0.13
Vespertilionidae	0.39-1.00	0.66 \pm 0.14
Molossidae	0.47-0.88	0.65 \pm 0.09
Hipposideridae	0.54-1.31	0.82 \pm 0.21
Natalidae	—	1.00
Furipteridae	—	0.84
Thyropteridae	—	1.20
Mormoopidae	0.75-0.87	0.81 \pm 0.05
Insectivora		
Solenodontidae	0.55-0.69	0.59 \pm 0.08
Tenrecidae	0.31-0.98	0.53 \pm 0.20
Soricidae	0.37-0.80	0.61 \pm 0.13
Talpidae	0.78-1.34	1.02 \pm 0.26
"Basal" Insectivora		
<i>Tenrec ecaudatus</i>		0.42
<i>Hemicentetes semispinosus</i>		0.43
<i>Setifer setosus</i>		0.45
<i>Echinops telfairi</i>		0.40
<i>Sorex murinus</i>		0.47
<i>Sorex minutus</i>		0.55
<i>Sorex araneus</i>		0.62
<i>Erinaceus europeus</i>		0.51

fall near the low range for the aerial insectivores. The Noctilionidae contains two quite different feeding strategies. *Noctilio leporinus* feeds on fish and its *EQ* is 0.928. *Noctilio albiventris* (= *labialis*) on the other hand, is a known aerial in-

TABLE 4. *Encephalization quotients and trophic role.*

Trophic role*	<i>EQ</i>	
	Range	Mean \pm SD
Carnivore	0.8-1.20	1.05 \pm .13
Sanguivore	1.10-1.22	1.17
Piscivore	0.74-1.20	0.94 \pm .20
Foliage Gleaning	0.61-1.13	0.93 \pm .21
Frugivore	0.81-1.47	1.18 \pm .14
Nectarivore	0.88-1.43	1.22 \pm .14
Aerial Insectivore	0.39-1.1	0.70 \pm .14

* According to Wilson, 1973.

sectivore (Wilson, 1973), and its *EQ* value is also as expected (0.74). In the Furipteridae, *Furipterus horrens* was suspected by Wilson (1973) to be an aerial insectivore, but its *EQ* value (0.845) suggests that it is a foliage gleaner. *Thyroptera tricolor* (Wilson, 1973) is an aerial insectivore, but its high *EQ* (1.26) is at variance with other members of this trophic class. This apparent contradiction may be due to the unusual roosting habits of this species. These bats roost in the rolled leaves of *Heliconia* plants and are forced to change roosts about every night (Findley and Wilson, 1974). Thus, the searching behavior used in censusing the environment for developing leaves to be used as future roosts may be similar to that of a frugivore censusing fruit trees.

DISCUSSION

Findley (1969), who measured the chiropteran cranial capacity from a sample almost equivalent to ours, established a correlation between cranial capacity and the area of the foramen magnum. His published plots are not directly comparable with our data, but he could find no specific trends with respect to cranial capacity and phylogeny. Eisenberg (1975) noted that the cranial capacities of bats exceeded those of "basal" insectivores of a comparable weight, but the data plotted in his Figure 4 exaggerate the statement because they were all drawn entirely from the Phyllostomatidae. At the time he prepared the figure, it was not appreciated how unique the phyllostomatid bats were with regard to the remainder of the Microchiroptera.

Jerison (1973) briefly considers the Chiroptera, but he included no specific treatment of the trends in brain-body weight correlations for this taxon. His admirable survey of the class Mammalia permitted the conclusion that through time the phylogenetic trend has been an increase in relative brain size for all higher taxa of mammals on the contiguous continental land masses.

Given the differences in relative cranial volume and presumed brain size, we might ask how these differences reflect variations in the relative size of discrete brain structures. As early as 1903 Dräseke noted that the brain of a megachiropteran resembled that of a strepsirhine primate and differed markedly from the brains of other chiropterans. Henson (1970) wrote that the microchiropterans have enlarged the eighth cranial nerve and all major subcortical ganglia associated with it. This specialization correlates with the evolution of their echolocating ability. On the other hand, the Megachiroptera show little specialization of the structures associated with the eighth cranial nerve, but do show a high development of the visual and olfactory centers. Lutgemeier (1962) indicates that the optic system accounts for about 9.4% of the brain stem in *Pteropus*

but only 5.8% in *Pipistrellus*. Mann (1963a) pointed out that the olfactory bulbs accounted for 57% of the "fundamental encephalon" in *Pteropus*, but only 21.6% in *Myotis*. *Artibeus* was intermediate with a value of 49%. Nevertheless, reduction in the relative size of neuronal structures associated with olfaction and vision in the Microchiroptera does not imply that these sensory modalities are uninvolved in orientation (Suthers, 1970). What is implied is that vision and olfaction are supplementary to echolocation.

As a general rule, the Megachiroptera show a well developed cerebellum compared with most microchiropterans although the Phyllostomatidae show a trend toward an enlarged cerebellum (Henson, 1970), especially the Stenoderminae and Desmondontinae (McDaniel, 1976). It seems possible then to conceive of the chiropteran brain evolving in a mosaic fashion as natural selection acts on the various populations. Where feeding strategies converge, we find morphological convergence in brain structure and relative size.

Although the relatively large size of the brain found in the Pteropidae and Phyllostomatidae may be related to the need for maintenance of a large mass of neural tissue devoted to olfaction and vision, one may well ask if the neocortex shows any trends in relative size across taxa. Wirz (1954) noted that the neocortex of the Microchiroptera was better developed than that of the "basal" insectivores. Mann (1963b) noted that the neocortex of the Pteropidae as well as of the phyllostomatid genera *Artibeus* and *Desmodus* was far better developed than that of the insectivorous Microchiroptera which he studied. The insectivorous phyllostomatid genera *Mimon* and *Lonchorina* have the least modified brain structure of the family Phyllostomatidae (McDaniel, 1976).

Large cranial volumes with their larger brain size imply a relatively large amount of neocortex, and these data further suggest that any departure from aerial insectivory as a trophic strategy may be accompanied not only by modifications in the

visual and olfactory projection areas but also in the relative amount of neocortex itself. Stephan and Pirlot (1970), who made discrete volumetric measurements on the brains of several chiropterans, concluded that, although the neocortex was somewhat advanced relative to the basal insectivores in the Hipposideridae, Molossidae, Rhinolophidae and Vespertilionidae, the neocortex showed profound enlargement in the Pteropidae, Phyllostomatidae and the Noctilionidae. Again, it is suggested that a relatively large brain is not only a correlate of large olfactory bulbs or relatively large eyes but also of a relatively larger neocortex.

Relatively large cranial volumes and larger brains with a large neocortical volume have evidently evolved independently several times within the order Chiroptera. The stenodermine and glossophagine bats have replicated a trend in brain structure comparable to that of the Pteropidae. The most specialized chiropterans for flight, the Molossidae and some Vespertilionidae, do not exhibit profound increases in relative brain size when compared to the non-volant Insectivora. Either such specialized aerial insectivores have been under selective pressure to maintain a reduced organ mass (including the brain) to facilitate active flight or specialization for echolocation as the principle means of locating aerial prey does not require a large mass of neocortical material. Thus, such specialization permits a reduction in relative brain tissue devoted to connections and projections from the other sensory inputs compared to foliage gleaners and other trophic specialists. We submit that a foraging strategy based on locating relatively large pockets of energy-rich food that are unpredictable in temporal and spatial distribution necessitates the use of a complicated information storage and retrieval system involving input from several sense organs. The enlarged neocortex and associated subcortical structure reflects this adaptive strategy for nectarivores, frugi-

vores, carnivores, piscivores, and sanguivores.

SUMMARY

Brain weights were estimated from the cranial volumes of 225 species of Chiroptera. The log of the average cranial volume was regressed against the log of the average body weight and the results analyzed for correlations with phylogenetic affinity and foraging strategy. It is concluded that the family Phyllostomatidae shows a strong convergence of brain to body weight ratios toward the patterns shown by the Pteropidae. Foraging strategies involving the location of rich food resources which are isolated in small pockets seem to require a large brain weight relative to body mass. If we assume the ancestral chiropteran had a brain structured more like a terrestrial insectivore, then the highly specialized aerial insectivores with the lowest relative brain to body weight ratios of the extant chiroptera reflect an evolutionary tendency to maintain the brain mass at a minimum weight.

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