

RELATIVE BRAIN SIZE AND DEMOGRAPHIC STRATEGIES IN DIDELPHID MARSUPIALS

JOHN F. EISENBERG AND DON E. WILSON

National Zoological Park, Smithsonian Institution, Washington, D.C.; National Fish and Wildlife Laboratory, National Museum of Natural History, Washington, D.C. 20560

Submitted July 11, 1979; Revised July 17, 1980; Accepted December 5, 1980

Moeller (1973) provided a provocative analysis of relative brain size trends within the Marsupialia. By regressing brain weight against body weight he demonstrated that the Didelphidae had the lowest brain-to-body-weight ratios of the four marsupial families studied. Furthermore, he demonstrated that the brain/body-weight ratios of marsupials were broadly overlapped by eutherians and that, indeed, some tenrecoïd insectivores and hedgehogs had lower ratios than did some comparably sized didelphids.

Our interest in the relative brain sizes of bats (Eisenberg and Wilson 1978) led us to conclude that convergently evolved large brains in certain bat families were broadly associated with different foraging strategies and processing of complex information. Specializations for nectar feeding, frugivory, and carnivory may involve selection for dependence on multisensory inputs to the brain. We speculated that foraging strategies demanding complex multisensory integration to locate and exploit energy-rich but widely dispersed food "patches" might result in selection for larger brains, with enhanced information storage and retrieval capacity.

The didelphid marsupials, however, have a rather uniform trophic strategy when compared with the bats. *Chironectes*, the water opossum, is aquatic and preys on small fish and crustacea; but other didelphids prey on small vertebrates, insects, and fruits. Arboreal ability varies widely (Hunsaker 1977), but the trophic strategies are not as divergent as has been noted for the Chiroptera. Rapid movement in trees involves the integration of input from several sets of sense organs, and we hypothesized that selection for arboreality might also result in selection for relatively large brains.

Moeller (1973) had only a limited number of didelphid specimens at his disposal (8 specimens from 2 species). We sought to measure a wide series of didelphid cranial capacities in order to confirm his initial conclusions. By comparing the didelphid cranial-volume-to-body-weight ratios with those ratios derived for other marsupials and tenrecoïd insectivores, we hoped to elucidate some valid generalizations concerning didelphid brain size relative to both the conservative eutherians and the extant marsupials of Australia.

We then examined the degree to which arboreal adaptation was associated with increased brain size. We reasoned that the fine motor coordination needed for arboreal life might enhance selection for a relatively larger brain size.

The cranial volumes of our didelphid sample showed considerable scatter when regressed against body weight. This offered us an opportunity to examine some earlier hypotheses concerning the relative brain size of edentates and insectivores (Eisenberg 1975). Eisenberg noted that relatively large adult brain size is associated with a syndrome of reproductive adaptations including increased life span, smaller litter size, slow development of the young, and protracted parental care. Gould (1977) expanded on this reproductive syndrome and linked it to the process of *K*-selection, which is pivotal to his hypothesis concerning the neotenic origin of the genus *Homo* (Gould 1977, pp. 349–351). The *K*-selection hypothesis as originally formulated by MacArthur and Wilson proposes that, in situations where a high density of interspecific competition exists, smaller clutch or litter sizes and increased parental investment will be favored (MacArthur and Wilson 1967). In the neotropics as many as eight species of didelphids may exist in macrosympatry, thereby maintaining the potential for strong trophic competition within this single family.

In an effort to evaluate the relative cranial capacities and life-history strategies of the nocturnal, arboreal didelphids, we chose to compare this group with the Old World prosimians. We chose prosimians because there is a remarkable convergence in trophic strategies between some didelphid marsupials and selected species of the genera *Microcebus*, *Arctocebus*, *Loris*, *Galago*, and *Perodicticus* (see Charles-Dominique 1975, 1977).

METHODS

Our study specimens were drawn from the collections at the National Museum of Natural History. Only specimens with an intact skull and field-recorded body weight (in grams) were selected. We used only males to eliminate the effects of sexual dimorphism and variations in body weight of females caused by pregnancy and lactation. We tried to select at least three specimens for each species, but failed in some cases. Species with less than two examples were deleted from further analyses. We used regression analysis to examine the structural relationships between various combinations of variables. These analyses are not intended to demonstrate the intensity of the relationships, more properly done by correlation analyses, nor do they imply a cause and effect relationship. Our rationale for such usage follows Simpson et al. (1960, p. 216). In some cases, we have used simple bivariate scattergrams to depict relationships.

Cranial volumes were determined as outlined in Eisenberg and Wilson (1978). The skull was weighed to the nearest 0.01 g. Number 10 dust shot was introduced through the foramen magnum and the skull was reweighed. The procedure was repeated after emptying out the original shot. Based on two measurements for each specimen, we calculated an average shot weight (Wt_s) for each specimen. This weight (Wt_s) was converted to volume (V) in cubic centimeters (cc) by using an empirically derived constant (K) and the formula $Wt \div K = V$. The constant for

TABLE 1
BODY WEIGHT AND CRANIAL VOLUME DATA FOR THE DIDELPHIDAE

Species	<i>n</i>	\bar{X} Body (g) Weight \pm SD	\bar{X} Cranial Volume (cc) \pm SD	E. Q. (M)	E. Q. (D)
1. <i>Caluromys philander</i>	3	170 \pm 61	2.69 \pm .22	1.09	1.27
2. <i>Caluromys derbianus</i>	6	295 \pm 51	3.56 \pm .31	.96	1.21
3. <i>Caluromys lanatus</i>	2	356	3.53	.91	1.06
4. <i>Monodelphis brevicaudata</i> ..	12	84 \pm 29	.91 \pm .11	.62	.66
5. <i>Marmosa cinerea</i>	14	107 \pm 23	1.55 \pm .13	.89	.97
6. <i>Marmosa fuscata</i>	4	40 \pm 7	.89 \pm .09	1.06	1.01
7. <i>Marmosa mexicana</i>	4	57 \pm 6	1.00 \pm .05	.91	.91
8. <i>Marmosa murina</i>	8	54 \pm 13	1.03 \pm .04	.98	.98
9. <i>Marmosa noctivaga</i>	3	62 \pm 8	1.15 \pm .12	.99	1.01
10. <i>Marmosa ocellata</i>	3	41 \pm 3	.93 \pm .04	1.08	1.05
11. <i>Marmosa robinsoni</i>	8	116 \pm 28	1.32 \pm .12	.72	.80
12. <i>Philander opossum</i>	8	330 \pm 67	3.72 \pm .41	.93	1.18
13. <i>Metachirus nudicaudatus</i>	5	342 \pm 38	2.81 \pm .19	.68	.88
14. <i>Lutreolina crassicaudata</i>	2	504	3.41	.62	.84
15. <i>Didelphis marsupialis</i>	11	1,161 \pm 294	7.13 \pm .48	.70	1.06
16. <i>Didelphis virginiana</i>	8	2,015 \pm 308	7.55 \pm .51	.50	.80
17. <i>Chironectes minimus</i>	3	764 \pm 131	5.54 \pm .55	.74	1.06

NOTE.—E. Q. (M) = Encephalization quotient calculated from the regression line for the class Mammalia; E. Q. (D) = Encephalization quotient calculated from the regression line for the family Didelphidae.

no. 10 shot is 6.0. Encephalization quotients (E. Q.) were then calculated for each species. Since actual brain weight corresponds rather closely to the cranial capacity as measured by our technique (Eisenberg and Wilson 1978), we consider the regression of cranial volume in cubic centimeters against body weight in grams will correspond to an actual regression of brain weight against body weight. The E. Q. is the ratio between observed (E_o) brain size and the expected size (E_v) following Jerison (1973). The expected volume was calculated from the known mean body weight (W_{t_b}) and the formula $E_v = 0.055 \cdot W_{t_b}^{0.74}$ (see Eisenberg and Wilson 1978). This E. Q. value is derived from a regression of brain against body weight for some 300 species of mammals and is referred to as E. Q. (M). An E. Q. value can also be calculated from the didelphid regression which is useful for intrafamilial comparisons. This latter E. Q. value, E. Q. (D), was calculated according to the formula: $E_v = 0.094 \cdot W_{t_b}^{0.61}$. Table 1 presents the data tabulations and E. Q. values for 17 species of didelphid marsupials.

RESULTS

We regressed \log_{10} brain volume against \log_{10} body weight for our sample of 17 species of didelphids ($n = 106$; see table 1). First we selected only those species whose cranial volume was greater than 1 cc and for which we had at least three specimens (12 species; $n = 77$). The slope was 0.606 and the intercept was -1.027 . The coefficient of determination was 0.96. If we extended the sample to include the smaller species and the larger species for which we had at least two specimens,

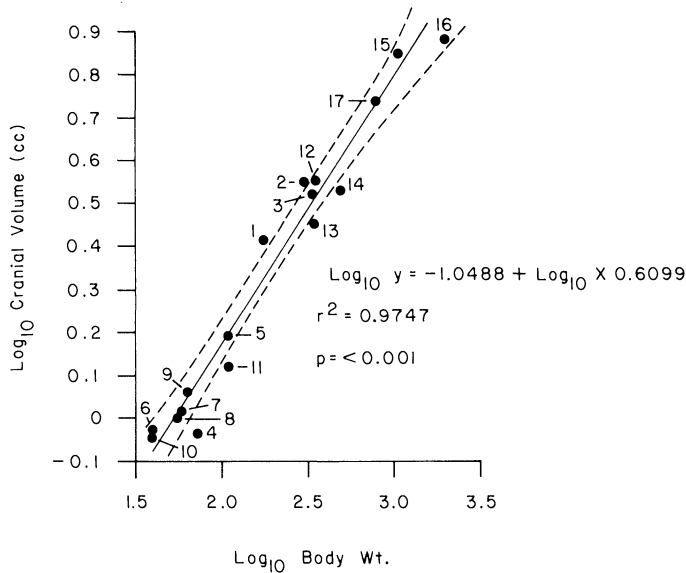


FIG. 1.—Regression of \log_{10} mean cranial volume (cc) against \log_{10} mean body weight in grams for the data presented in table 1. Dotted lines demarcate 95% confidence limits of any value of X for a predicted value of Y .

yielding an increased sample of 17 species of didelphids, then the slope was 0.6099 and the intercept -1.0488 with a coefficient of determination of 0.97. (See fig. 1). In conformity with Moeller, our data suggest that the Didelphidae, as a taxonomic unit, have a slightly lower ratio of cranial capacity to body weight than do the other Marsupialia, but there is considerable scatter.

Using the E. Q. values (table 1), we then examined the relationship between degree of arboreality and relative cranial volume. To determine the degree of arboreal adaptation, we employed a bivariate analysis. The length of the tail relative to the head and body length is a rather good indicator of arboreal ability in small mammals (Horner 1955; Lemen 1980). These ratios are presented in table 2. We then plotted these ratios against the percentage of arboreal catches as recorded by Handley (1976) and O'Connell (1979). Handley recorded the place of capture (i.e., ground vs. trees) for the mammals collected in Venezuela by the Smithsonian Venezuela Project. Arboreal catches were then expressed as percentages of total catches. Since the relative sampling effort in terms of arboreal versus terrestrial "sets" are not recorded, there are definite sampling errors inherent in using his data. Nonetheless there was a positive covariation (fig. 2). O'Connell's data were derived from grid trapping with a fixed number of arboreal and terrestrial traps. Plotting the tail-to-head-and-body ratio against her proportion of arboreal catches from Guatopo National Park in Venezuela yielded a close, positive covariation (see fig. 2). On the strength of these plots we infer the degree of arboreal adaptation for the didelphid data set from the ratios of tail to head and body. Figure 3 indicates that a high ratio of tail to head and body length and, by inference, a high preference for arboreal activity appear to be positively associated with a relatively large brain.

TABLE 2
TROPIC COMPETITION ANALYSIS AND TAIL-TO-BODY RATIOS FOR THE
VENEZUELAN DIDELPHIDAE

Species	No. of Collecting Sites	NO. OF ASSOCIATED SPECIES		Tail ÷ Head and Body* $\bar{X} \pm SD$
		Range	$\bar{X} \pm SD$	
<i>Didelphis marsupialis</i>	40	0-7	2.46 ± 1.71	1.05 ± .07
<i>Marmosa robinsoni</i>	21	0-7	2.24 ± 1.92	1.35 ± .07
<i>Monodelphis breviceaudata</i>	22	0-7	2.77 ± 1.76	.62 ± .10
<i>Marmosa fuscata</i>	12	0-6	2.75 ± 1.69	1.21 ± .06
<i>Caluromys philander</i>	15	1-6	3.67 ± 1.45	1.57 ± .08
<i>Caluromys lanatus</i>	8	2-5	3.75 ± 1.08	1.53 ± .07
<i>Marmosa murina</i>	15	1-7	4.07 ± 1.53	1.49 ± .22
<i>Marmosa cinerea</i>	12	2-7	4.08 ± 1.38	1.41 ± .10
<i>Philander opossum</i>	10	2-6	4.20 ± 1.17	1.10 ± .07
<i>Metachirus nudicaudatus</i>	5	3-6	4.40 ± 1.02	1.29 ± .09
<i>Chironectes minimus</i>	3	0-4	2.33 ...	1.26 ...
<i>Lutreolina crassicaudata</i>	1	...	4.00 ...	1.05 ...

* n = 8.

In an attempt to assess the degree of potential competition to which a species of the Didelphidae is exposed as a result of living in sympatry with other didelphids, we performed the following analysis. We omitted the aquatic *Chironectes* as well as the Andean and Falcon Peninsula endemics from the data set of Handley. The twelve remaining species were then studied to determine the number and identity of associated species at each collecting locality. Table 2 resulted from this analysis. An examination of this table indicates that some species such as *Didel-*

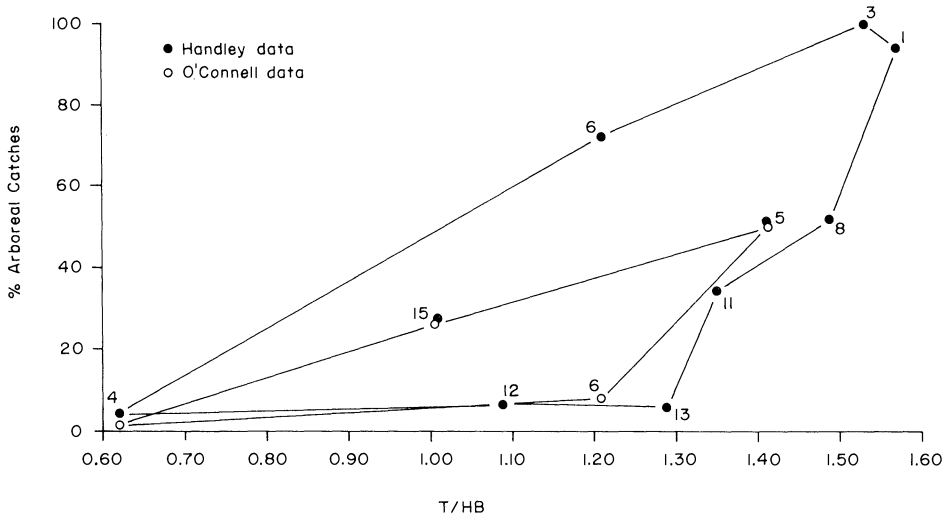


FIG. 2.—Bivariate scattergram showing relation between ratio of tail length to head and body length and the percentage of arboreal catches for Venezuelan didelphids. Numbers keyed to table 1.

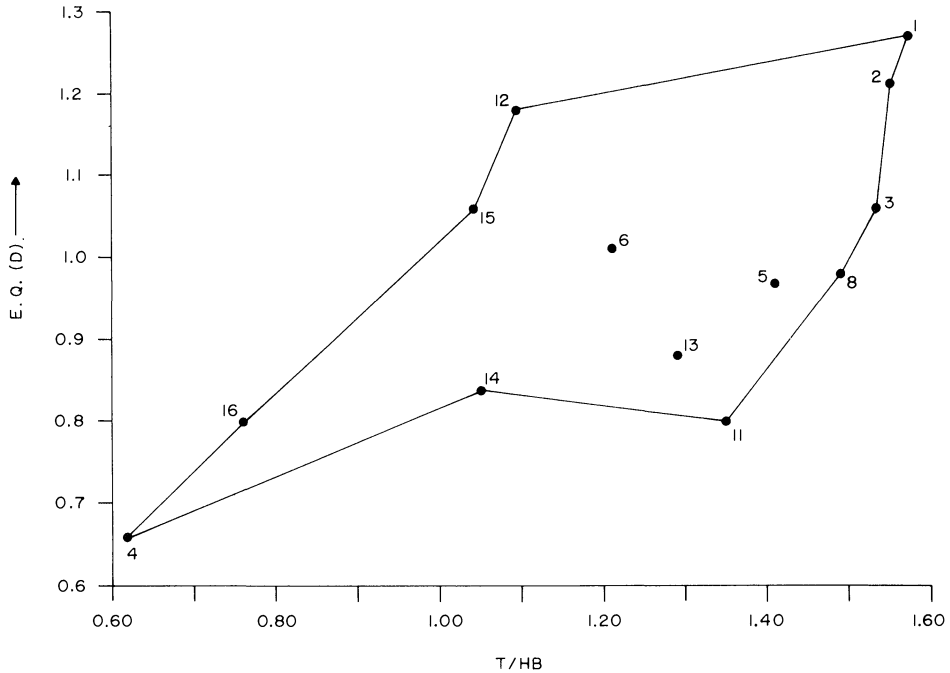


FIG. 3.—Bivariate scattergram showing relation between encephalization quotient and the ratio of tail length to head and body length for didelphid marsupials. Numbers keyed to table 1.

phis marsupialis, *Marmosa robinsoni*, *Marmosa fuscata*, and *Monodelphis brevicaudata* may occur alone or with many associated species. They have a low mean number of associated didelphids (2.24–2.77) and a high variance. This reflects their adaptability and range of habitat tolerance. All four have a high mean litter size (6–10, O'Connell 1979). All species are terrestrial or scansorial.

The species which are strongly arboreal, *Caluromys lanatus*, *Caluromys philander*, *Marmosa cinerea*, and *Marmosa murina*, occur on the average with 3.6–4.0 other didelphid species. The scansorial *Philander opossum* in Venezuela is also associated with an average of 4.2 didelphids in microsympatry. An inspection of figure 4 indicates that species with a low E. Q. (D) tend to have a low number of associated sympatric species of didelphids. The extreme cases of species habitually associated with high numbers of sympatric species tend to have high E. Q. (D) values. There is, however, considerable scatter. *Metachirus nudicaudatus* appears highly aberrant.

The number of young produced by females during a breeding season can be highly variable. Some species are adapted to reproduce once or twice in a lifetime; others may have the potential to reproduce over a period of several annual cycles. In spite of such variations, the mean litter size is a useful indicator of reproductive potential (Eisenberg 1981). The determination of litter size for didelphid marsupials presents some difficulties. The problems derive from the fact that a female didelphid gives birth to extremely altricial young after a gestation of some 14 days

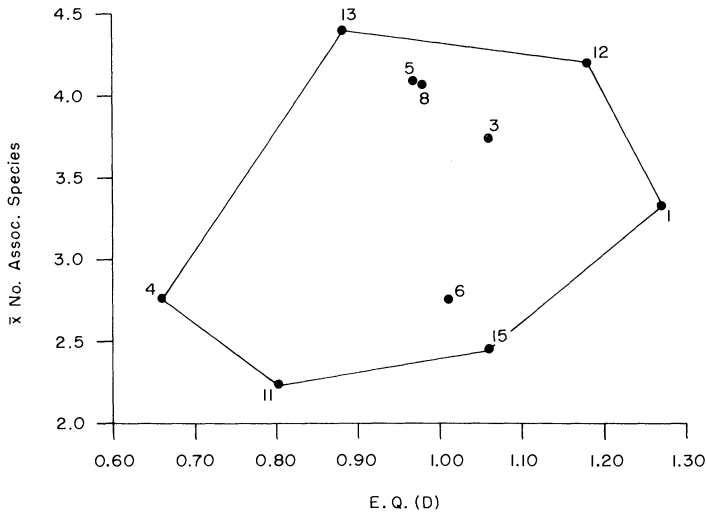


FIG. 4.—Bivariate scattergram indicating the relation between mean number of associated species and the encephalization quotient for Venezuelan didelphids. Data from table 2; numbers keyed to table 1.

(Collins 1973). The young attach to nipples for some 7–9 wk and then undergo a nest phase where the female returns to nurse them for a variable interval prior to weaning and dispersal (Eisenberg 1975). Loss of young during the teat attachment phase is common, and comparable to intrauterine mortality in eutherians (Eisenberg 1981). Some standardization is necessary for comparing litter sizes from the literature for didelphids. Furthermore, by any measure litter sizes may vary within species when one compares populations across altitudinal or latitudinal gradients (O'Connell 1979).

Teat number can give an index of the maximum litter size attainable. Table 3 lists what we know concerning the teat number and litter size for a series of didelphids from Venezuela and neighboring areas of the neotropics. Roughly, the mean litter size for attached young is 0.54 the number of mammae. Whether we consider mean number of attached young or nipple number, the E. Q. covaries negatively with "litter size" or "potential litter size" (see fig. 5). Because resting metabolic rate varies widely among the didelphid marsupials (McNab 1978), we have indicated deviant metabolic rates in figure 5. There is no evident relationship between metabolic rates and litter size or E. Q. value.

A plot of E. Q. values against mean body weight for prosimians, didelphid marsupials, and tenrecoid insectivores is shown in figure 6. The tenrecoid insectivores, which are typified by a rather "basic" brain structure (Bauchot and Stephan 1966), have even lower brain-to-body-weight ratios than do the majority of didelphids. This should lay to rest the notion that marsupials are characterized by relatively small brains when compared with eutherians.

The maximum age attained in captivity was then plotted against body size for didelphids and prosimians (fig. 7). The slow-reproducing prosimians show greater potential longevity than do the didelphids for all weight classes. The genus

TABLE 3
LITTER SIZE FOR SELECTED DIDELPHIDAE

Species	n	LITTER SIZE			Teat No.	Authorities
		\bar{X}	Range	SD		
1. <i>Didelphis marsupialis</i>	...	7.5	3-10	...	13	Osgood 1921; O'Connell 1979
2. <i>Marmosa robinsoni</i>	...	8.0	6-15	...	19	Hunsaker 1977; O'Connell 1979
3. <i>Monodelphis brevicaudata</i>	3	7.0	O'Connell 1979
4. <i>Marmosa fuscata</i>	1	6.0	9	O'Connell 1979; Tate 1933
5. <i>Caluromys philander</i>	3	6.0	O'Connell 1979
6. <i>Caluromys derbianus</i>	...	3.0	Hunsaker 1977
7. <i>Marmosa murina</i>	4	5.8	4-7	± 1.1	11	Husson 1978; Tate 1933
8. <i>Marmosa cinerea</i>	11	Tate 1933
9. <i>Philander opossum</i>	7	3.4	4-5	± 1.9	7	Husson 1978; Osgood 1921
10. <i>Metachirus nudicaudatus</i>	4	5.0	1-9	...	9	Husson 1978; Osgood 1921
11. <i>Chironectes minimus</i>	3	3.3	2-5	Hunsaker 1977
12. <i>Lutreolina crassicaudata</i>	9	Osgood 1921

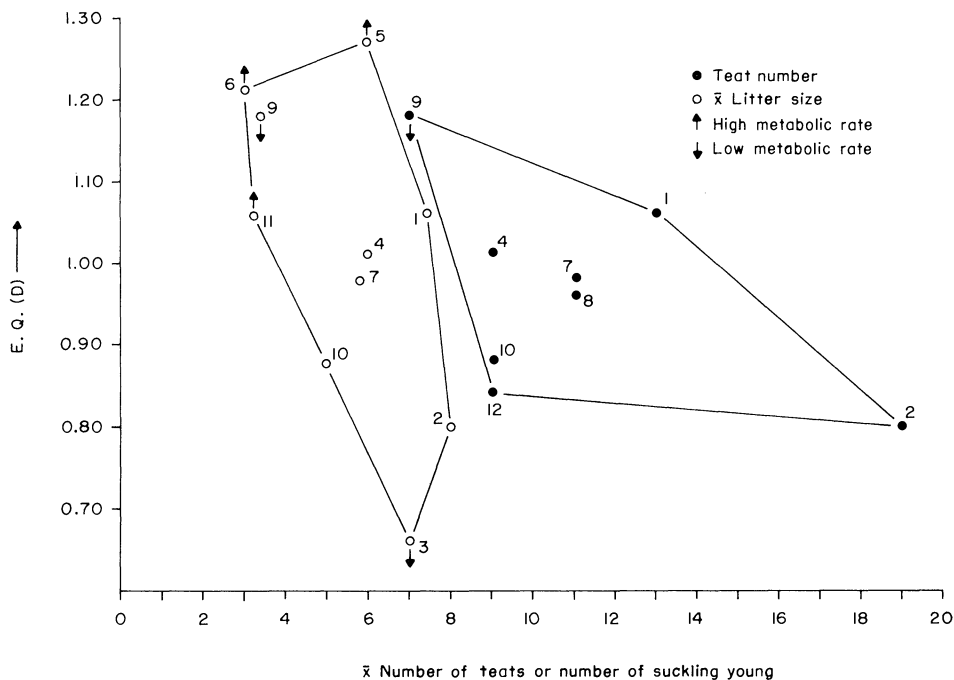


FIG. 5.—Scattergram of mean litter size or mean teat number against encephalization quotient. Data from table 3; relative metabolic rates from McNab (1978). Higher litter size and teat number are associated with low EQ values. There is no discernible trend with metabolic rates. Numbers keyed to table 3.

Caluromys is an exception among the didelphids (fig. 7). It is relatively long lived, has a small litter size (fig. 5), high metabolic rate, and is well adapted for arboreal life.

DISCUSSION

The genus *Caluromys*, the woolly opossums, has high E. Q. (D) values compared to other didelphids. All three species of *Caluromys* have E. Q. (M) values near unity (table 1). They are also among the most arboreal of the Didelphidae (Handley 1976). Their small litters (1–6) and higher metabolic rates are also exceptional among didelphids. Maximum recorded longevity is 62 mo for *Caluromys derbianus* (Hunsaker 1977). *Caluromys derbianus* is widely distributed in Central America and northern South America. *Caluromys philander* occurs from northern South America to south-central Brazil (Hunsaker 1977). The genus is basically frugivorous but does take a variety of other foods (Hunsaker 1977). The only movement data available are for *Caluromys philander* in Brazil, where they appeared to be relatively sedentary (Davis 1945).

The short-tailed opossums of the genus *Monodelphis* have a low E. Q. (D) value (table 1). They show low arboreality (4%) and large litters (8–14). The metabolic rate is low, and unfortunately sufficient longevity data are unavailable. The genus

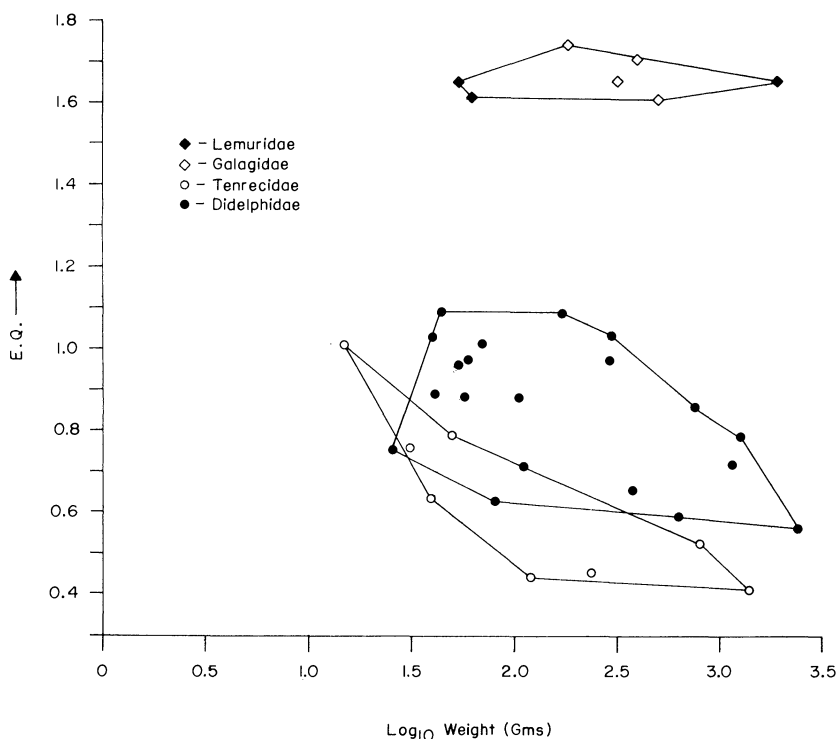


FIG. 6.—Scattergram plotting encephalization quotients against body size for a set of basal insectivores (the Tenrecidae), the didelphid marsupials, and a series of prosimians. Primate and teat number are associated with low E.Q. values. There is no discernible trend with but that the didelphid marsupials are partially overlapped by the tenrecid insectivores.

ranges from Panama southward to Argentina (Hunsaker 1977). Although omnivorous, they may be more carnivorous than some other didelphids and thus have larger home ranges and lower densities (O'Connell 1979).

Species of the genus *Marmosa*, the mouse opossums, are quite variable in E. Q. (D) values, ranging from 0.80 in *Marmosa robinsoni* to 1.05 in *Marmosa ocellata*. *Marmosa cinerea* and *Marmosa murina*, both having intermediate E. Q. values, apparently spend equal amounts of time on the ground and in the trees. *Marmosa robinsoni* also has relatively large litters (8–11), and *Marmosa fuscata* with a high (1.01) E. Q. (D) has small litters (6). Most species of *Marmosa* are mainly insectivorous, but a variety of foods are taken (Hunsaker 1977). *Marmosa robinsoni* appears to have small home ranges and moderate population densities (Fleming 1972; O'Connell 1979). Average captive longevity is less than 2 yr (Collins 1973). Some didelphid marsupials, such as *Marmosa robinsoni*, show a rapid population turnover. Barnes and Barthold (1969) noted that females of *Marmosa robinsoni* show ovarian senescence by 14 mo. Large litters and short life spans characterize some small marsupials in both the families Didelphidae and Dasyuridae (Braithwaite and Lee 1979).

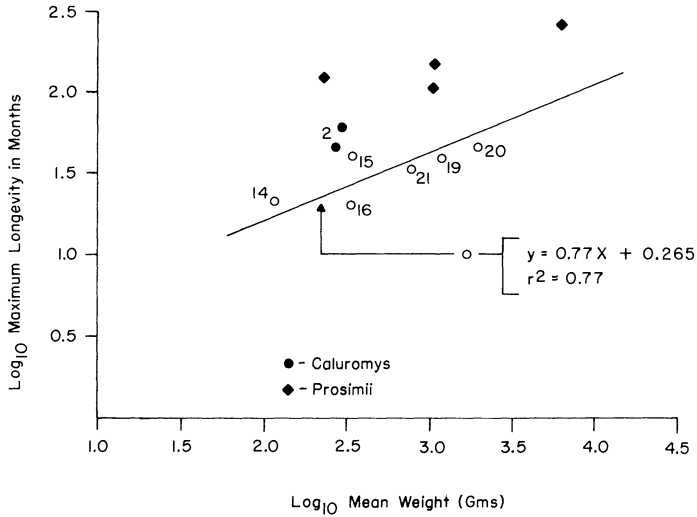


FIG. 7.—Longevity in months (\log_{10}) plotted against \log_{10} mean body weight for prosimians and didelphid marsupials. Note the extended longevity of the prosimians relative to the didelphids. *Caluromys* (2) is intermediate and has high E. Q. values for the Didelphidae. Longevities from Collins (1973) and M. L. Jones (in litt.). Numbers keyed to table 1.

Philander opossum is unique because it has a relatively high E. Q. value (0.93), yet seems to be strongly terrestrial in Venezuela. In our experience, they are somewhat scansorial and tend to forage through the undergrowth as well as on the ground. They also forage more rapidly and appear more alert while foraging than most other didelphids. They have relatively small litters (4–5), and a low metabolic rate (fig. 5). The maximum longevity is 42 mo (Hunsaker 1977).

Metachirus nudicaudatus, although superficially resembling *Philander opossum*, has a low E. Q., and Handley's (1976) data show them to be strongly terrestrial. The litter size is moderate at a mean of 5. Maximum reported longevity is 22 mo, but Hunsaker (1977) has suggested a life span of 3–4 yr.

Lutreolina crassicaudata has a low E. Q., and is mainly terrestrial. Litter size is unknown and maximum longevity is 3 yr (M. L. Jones, in litt.). Except for *Chironectes*, this species is probably more aquatic than the rest of the family.

Didelphis is characterized by a moderate to low E. Q. (D) and has mainly terrestrial habits, with large litters (5–10) and moderate longevity (42 mo). The genus is widely distributed throughout North and South America. The low E. Q. (D) value for *D. virginiana* may be a reflection of their occurrence in the temperate zone where the rigors of climate cause them to develop appreciable layers of body fat, resulting in higher body weights than congeners.

The faunal distributions for Venezuela are reasonably well known (Handley 1976; Eisenberg and Redford 1979). An examination of the assemblages of didelphids for each of Handley's collection localities indicates a range from one to eight species. Since many species are limited altitudinally a collection area of several square kilometers can yield eight species in macrosympatry, but in microsympatry

six species appear to be the maximum. If we exclude the Andean and the arid Falcon Peninsular areas, which harbor several endemic species (Eisenberg and Redford 1979), from the remaining discussion, then the Amazonian, Llanos, and North Coast Range biotic regions may be compared (definitions from Eisenberg and Redford 1979). Allowing for accidents of climate and biogeography which have resulted in some noticeable disjunctions in mammal distributions in the northern neotropics, it seems fair to say that within the multistratal, tropical evergreen forests, competition within trophic levels has been rather intense. In brief, species with a long history of adaptation to strong competition may exhibit attributes of *K*-selection (MacArthur 1972).

The Llanos has experienced extreme aridity during the glacially controlled interpluvial periods of the Pleistocene. Its mammalian fauna is all derived from higher altitude Pleistocene refugial areas. Its reduced semideciduous tree cover favors colonist species which are not strongly adapted to a multistratal, evergreen tropical forest. Typically *Marmosa robinsoni* and *Didelphis marsupialis* are the didelphids of the Llanos, one moderately arboreal, the other scansorial.

In the North Coast Ranges of Venezuela a common assemblage is the semiaquatic *Chironectes minimus*, the terrestrial *Monodelphis breviceaudata*, the scansorial set of *Marmosa fuscata* and *Didelphis marsupialis*, and the strongly arboreal *Caluromys philander* and *Marmosa cinerea* (O'Connell 1979).

In the Amazonas region a terrestrial species *Monodelphis breviceaudata* is frequently associated with the scansorial set of *Philander opossum* and *Didelphis marsupialis*. The common arboreal set is either *Caluromys philander*, *Caluromys lanatus*, *Marmosa cinerea* and *Marmosa murina* or *Metachirus nudicaudatus*, *Marmosa cinerea* and *Marmosa murina*. *Marmosa fuscata* replaces *Marmosa murina* at higher altitudes (Handley 1976).

Judging from the distribution maps constructed from Handley's efforts, some species occur over a wide range and in many different microhabitats (e.g., *Monodelphis breviceaudata* and *Didelphis marsupialis*). Others are restricted to multistratal tropical evergreen forest. In this latter habitat are found the arboreal specialists *Caluromys*, *Metachirus*, and some species of *Marmosa*. The arboreal set is graded in size with a ratio of mean body weight for species pairs ranging from 0.63 (*Marmosa cinerea*:*Caluromys philander*) to 0.31 (*Marmosa cinerea*:*Metachirus nudicaudatus*); see also table 1.

Johnson (1977), in noting the convergent evolution of marsupial and eutherian brains, stated that "it is impressive how little marsupial brains differ from those of placental brains in their structure and function" (p. 261). Marsupial behavior patterns also show convergences to those of the eutherians (Eisenberg and Golani 1977; Eisenberg et al. 1975). Relatively large cranial capacities and correspondingly large brains evolve under a multiplicity of selective pressures. Selection for certain complex feeding strategies may promote relatively large brain size (Eisenberg and Wilson 1978). Perhaps an arboreal existence also promotes large brain size and a correspondingly large cerebellum. What emerges from these data is further evidence that selection for relatively large brains appears to be linked with an adaptive syndrome which includes increased longevity, decreased litter size, and perhaps an increased percentage of the juvenile life span spent in a social

learning situation. This trend also has been identified in edentates and insectivores (Eisenberg 1975) and is expanded elsewhere (Eisenberg 1981).

Two species appear to be exceptions to the general hypotheses: *Metachirus nudicaudatus* and *Philander opossum*. *Philander* is scansorial, yet has a relatively large brain. In conformity with its large brain size, it shows a reduced litter size, and longer potential longevity, suggesting trophic competition has favored successive reproduction and a complex foraging strategy. *Philander* in Venezuela occurs with a high number of trophic competitors and is almost always associated with *Didelphis*, which is a pioneer genus in terms of its geographic range and broad tolerance for a variety of habitat types. We may broadly think of *Philander* as *K*-selected relative to *Didelphis*.

Metachirus appears to be strongly adapted for arboreal life but it often occurs in brushy, transitional habitats (Hunsaker 1977). In Venezuela, *Metachirus* does not often occur in microsympatry with the like-sized *Caluromys lanatus* (Handley 1976). Indeed the low co-occurrence of *Metachirus* and *Caluromys* suggests a long-term competitive axis and a corresponding adaptation on the part of *Metachirus* to edge habitats. The lower reproductive potential of *Caluromys* implies that this genus is *K*-selected relative to *Metachirus*.

It appears then that adaptation to a strongly arboreal existence can involve selection for relatively larger brains. Adaptation to climatically stable, complex rainforests favors arboreality but also may result in increased competition at the same trophic level both between closely related and distantly related taxa. A consequence of such competition can be *K*-selection which favors adult survival over the survival of offspring, and increased parental care of offspring under certain conditions (Wilbur et al. 1974). Litter sizes are reduced and the potential reproductive "life span" of the adult is increased. The genus *Caluromys* appears to have undergone such a process of *K*-selection as a consequence of its adaptation for structurally complex rainforests. In this respect, the genus has converged in life-history strategy toward the life histories of some Prosimians.

We submit that adaptation to an arboreal habitus is generally accompanied by selection favoring a larger brain relative to a comparably sized terrestrial form, but we also contend that in the didelphids the adaptation to an arboreal way of life may have exposed a given species to severe trophic competition from other didelphids in the climax rainforests. Surely *K*-selection, with its positively co-varying factors of increased longevity, decreased annual reproductive capacity, and larger relative brain size, is confounded with adaptation for arboreal foraging in the climax rainforest, and a diffuse approach (e.g., Wilbur et al. 1974) may be useful. We cannot untangle the variables, but suggest that the perspective may be useful to students of primate phylogeny.

SUMMARY

Mean cranial volumes were established for 17 species of didelphid marsupials. The variability in mean cranial capacity for any given weight class was examined. Arboreal preference is associated with a relatively large brain except in the case of *Philander opossum*. Among didelphid opossums those with relatively large cranial

capacities are characterized by a relatively longer life span and lower litter sizes. When compared to prosimians, didelphids generally exhibit shorter life spans, smaller relative cranial capacities, and larger litters. It is concluded that some didelphid marsupials (e.g., *Caluromys*) have undergone selection toward a demographic strategy which is in part convergent with the extant nocturnal prosimians.

ACKNOWLEDGMENTS

We thank Ronald Giegerich, who assisted with the volumetric measurements; C. O. Handley, Jr., who generously made the Smithsonian Venezuela Project collection available to us; and M. A. Bogan, A. Gardner, G. Mace, and P. Harvey, who provided editorial criticism.

LITERATURE CITED

- Barnes, R. D., and S. W. Barthold. 1969. Reproduction and breeding behavior in an experimental colony of *Marmosa mitis* Bangs (Didelphidae). *J. Reprod. Fertil.* 6:477-482.
- Bauchot, R., and H. Stephan. 1966. Données nouvelles sur l'encephalisation des Insectivores et des Prosimiens. *Mammalia* 30:160-196.
- Braithwaite, R. W., and A. Lee. 1979. A mammalian example of semelparity. *Am. Nat.* 113:151-155.
- Charles-Dominique, P. 1975. Nocturnality and diurnality: an ecological interpretation of these two modes of life by an analysis of the higher vertebrate fauna in tropical forest ecosystems. Pages 69-88 in W. P. Luckett and F. S. Szalay, eds. *Phylogeny of the Primates*. Plenum, New York.
- . 1977. Ecology and behaviour of nocturnal Primates. Columbia University Press, New York.
- Collins, L. R. 1973. *Monotremes and marsupials*. Smithsonian, Washington, D.C.
- Davis, D. E. 1945. The home range of some Brazilian mammals. *J. Mammal.* 26(2):119-127.
- Eisenberg, J. F. 1975. Phylogeny, behavior and ecology in the Mammalia. Pages 47-68 in W. P. Luckett and F. S. Szalay, eds. *Phylogeny of the Primates*. Plenum, New York.
- . 1981. *The mammalian radiations: a study in evolution and adaptation*. University of Chicago Press, Chicago.
- Eisenberg, J. F., L. R. Collins, and C. E. Wemmer. 1975. Communication in the Tasmanian devil (*Sarcophilus harrisii*) and a survey of auditory communication in the Marsupialia. *Z. Tierpsychol.* 37:379-399.
- Eisenberg, J. F., and I. Golani. 1977. Communication in Metatheria. Pages 575-599 in T. Sebeok, ed. *How animals communicate*. Indiana University Press, Bloomington.
- Eisenberg, J. F., and K. Redford. 1979. A biogeographic analysis of the mammalian fauna of Venezuela. Pages 31-36 in J. F. Eisenberg, ed. *Vertebrate ecology in the northern neotropics*. Smithsonian, Washington, D.C.
- Eisenberg, J. F., and D. E. Wilson. 1978. Relative brain size and feeding strategies in the Chiroptera. *Evolution* 32(4):740-751.
- Fleming, T. H. 1972. Aspects of the population dynamics of three species of opossums in the Panama Canal Zone. *J. Mammal* 53(3):619-623.
- Gould, S. J. 1977. *Ontogeny and phylogeny*. Belknap, Cambridge, Mass.
- Handley, C. O., Jr. 1976. Mammals of the Smithsonian Venezuela Project. *Brigham Young Univ. Sci. Bull. Biol. Ser.* 20(5):1-91.
- Horner, E. 1955. Arboreal adaptations of *Peromyscus* with special reference to use of the tail. *Contrib. Lab. Vert. Biol. Univ. Mich.* 61:1-84.
- Hunsaker, D. D. 1977. Ecology of New World marsupials. Pages 95-158 in D. Hunsaker, II, ed. *The biology of marsupials*. Academic Press, New York.
- Husson, A. M. 1978. *The mammals of Suriname*. Brill, Leiden.
- Jerison, H. 1973. *The evolution of the brain and intelligence*. Academic Press, New York.

- Johnson, J. I., Jr. 1977. Central nervous system of marsupials. Pages 157–278 in D. Hunsaker, II, ed. *The biology of marsupials*. Academic Press, New York.
- Lemen, C. 1980. Relationship between relative brain size and climbing ability in *Peromyscus*. *J. Mammal.* 61:360–364.
- MacArthur, R. H. 1972. *Geographical ecology*. Harper & Row, New York.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, N.J.
- McNab, B. K. 1978. The comparative energetics of neotropical marsupials. *J. Comp. Physiol. B.* 215:115–128.
- Moeller, H. 1973. Zur Evolutionshöhe des Marsupialiergehirns. *Zool. Jahrb. (Anat.)* 91:434–448.
- O'Connell, M. A. 1979. The ecology of didelphid marsupials from northern Venezuela. Pages 73–87 in J. F. Eisenberg, ed. *Vertebrate ecology in the northern neotropics*. Smithsonian, Washington, D.C.
- Osgood, W. H. 1921. A monographic study of the American marsupial *Caenolestes*. *Field Mus. Nat. Hist. Publ. Zool. Ser.* 14(1):1–162.
- Sacher, G. A. 1975. Use of zoo animals for research on longevity and aging. Pages 191–198 in *Research in zoos and aquariums*. National Academy of Science, Washington, D.C.
- Simpson, G. G., A. Roe, and R. C. Lewontin. 1960. *Quantitative zoology*. Harcourt Brace, New York.
- Tate, G. H. H. 1933. A systematic revision of the marsupial genus *Marmosa*. *Bull. Am. Mus. Nat. Hist.* 66(1):1–250.
- Wilbur, H. M., D. W. Tinkle, and J. P. Collins. 1974. Environmental certainty, trophic level, and resource availability in life history evolution. *Am. Nat.* 108:805–817.