

Brain-Body Size Relations in Grasshopper Mice

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Key Words

Brain allometry · Body size · Dimorphism ·
Encephalization · Mammals · Rodents · Grasshopper
mice

Abstract

Cranial volumes were measured on museum specimens of two species of grasshopper mice, *Onychomys leucogaster brevicaudus* and *Onychomys torridus pulcher*. These were compared with body weights and body lengths, as recorded on the museum tags. On average, females were heavier and slightly longer than males, but they had smaller cranial volumes by about 3%. Statistically, the differences were marginally significant (with no difference in body length for one species), but the pattern of differences was the same in both species, and therefore probably real. This casts suspicion on the common notion that a larger body size requires a larger brain. It also questions the real meaning of encephalization quotients.

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Introduction

One usually thinks of rodents as foragers for seeds, foliage, fruits, and insects, not as active predators. Their nervous systems drive their preferences and create the self-selective pressures that result in successful individual survival and reproduction. Among rodents, relative brain size varies with food preference, being smallest in folivores, larger in granivores, still larger in insectivores, and largest in generalists [Mace et al., 1981; Mace and Eisenberg, 1982; Mann et al., 1988]. Yet all satisfy their preferences by foraging, even the insectivores, which show a more opportunistic than stalking style. But grasshopper mice stalk, attack, kill and eat deer mice, pocket mice, and voles [Horner et al., 1964; Timberlake and Washburne, 1989], and even cotton rats three times their own weight [Ruffer, 1968]. Even so, mammals make up only 10% of their diet. Their main food (80%) consists of arthropods, mainly scorpions, grasshoppers and beetles, so much so that they have evolved a special gastric pocket to protect the glandular tissues from the chitinous materials they ingest [Horner et al., 1964]. Their coronoid processes are extended to provide a large insertion for the temporal muscle, their incisors are shortened, and their three molars are sub-optimal for grinding seeds and foliage. Rodents are killed by a bite to the head or by throttling [Egascue, 1960]. Timberlake and Washburne [1989] found that caged Northern grasshopper mice, when offered a cricket,

¹ Dr. Towe passed away on October 8, 2002.

attacked, killed, and began eating within 8.8 ± 1.7 (SE) s. The three deer mouse species tested were less aggressive, averaging attack latencies of 24, 129 and 140 s, with two of the 18 animals failing to kill at all.

A carnivorous life style implies a large territory, hence low density, so it is no surprise that grasshopper mice are extremely aggressive and lethal to their congeners. They live as couples in established territories within a 2–3 hectare home range. According to Ruffer [1965], they ‘invariably’ make their own burrows, with the male digging and the female helping. He notes that ‘females neither established nor helped defend territories,’ and that in encounters with other species, the male grasshopper mouse kills the intruder within 3 h of initial contact, while the female remains in or near the burrow. In same-sex encounters between two grasshopper mice, the intruder has a 70% chance of being killed the first day, 100% within three days.

A striking behavior of these mice involves one of their vocalizations, a loud, pure-tone call (9–14 kHz) produced most often by males while standing upright with head erect [Hafner and Hafner, 1979]. When recorded and played at slow speed the call is reminiscent of a wolf howl.

To complete the picture, one might expect males to be larger than females, a condition reported by Pinter [1970] in laboratory-reared mice, but denied by van Cura and Hoffmeister [1966] on the basis of field samples. However, the sample studied by Mann et al. [1988] suggested that reverse sexual size dimorphism might occur in *Onychomys*. It is generally held that a larger body implies a larger brain. This notion is drawn from cross-species comparisons, but if true, it should hold when comparisons are made within a species. If it does and if there is a reverse sexual dimorphism in grasshopper mice, then females should have larger brains than the males. However, the present analysis shows that average male cranial capacity is larger than that of females. Not only does this call into question the relationship between body and brain size, but it also questions the utility of encephalization quotients in brain size comparisons.

Materials and Methods

Analyses were carried out on 35 female and 45 male Northern grasshopper mice (*Onychomys leucogaster breviceaudus*) that had been collected in California in the woods of Lassen county, in high Alpine county, and in the dense brush of Mono county during different years in May and early June, and some in early July. Analyses were also carried out on 22 female and 36 male Southern grasshopper

mice (*Onychomys torridus pulcher*) that had been collected in the desert scrub of Inyo, San Bernardino, and Riverside counties of California during late April and May. Cranial volumes (C) of the 138 specimens housed at the University of California Museum of Vertebrate Zoology at Berkeley were measured by filling each cranium with 9-gauge shot and then aligning the shot in a shot-counter tray calibrated in 0.01 ml units [details recorded in Mann et al., 1988]. Head and body length in centimeters (L) and body weight in grams (P) were recorded from each specimen tag. An index of habitus [$H = (P)^{1/3}/L$] was calculated for each specimen in order to test the adequacy of the samples and identify possible outliers. All juveniles were excluded from the analyses on the basis of dental condition and $|H - \langle H \rangle| > 2SD_H$. Standard statistical analyses were carried out on all the variables. As in the study by Mann et al. [1988], cranial volume (C) will be regarded as an adequate index of brain mass (E).

Results

The upper half of table 1 records the statistical results for *Onychomys leucogaster breviceaudus*: the females were heavier than the males but of the same length. However, they had smaller brains. The coefficients of variation (CVs) were normal, with body weight CVs about three times body length CVs, and with cranial volume varying as a one-dimensional organ. Even so, body weight CVs were distinctly larger for females than for males. Indeed, comparison of the variances yielded an $F = 2.183$, $dfn = 34$, $dfd = 44$ associated with a $p = 0.0076$. The scatter plots of figure 1, with linear regressions superimposed, show that the female (solid dots) and male distributions (open squares) strongly overlapped, although the points for females were shifted down and to the right. The male body length distribution shows an accumulation around the 10-cm value, which may explain the similarity in body length but difference in body weight between the sexes. However, other factors may contribute to this finding. Table 1 says that the seemingly modest difference in brain size was probably real ($p = 0.018$). It also says that the females were, on average, bulkier than the males ($\langle H_F \rangle = 0.312$ and $\langle H_M \rangle = 0.305$). To be equally bulky, males would have to have averaged 9.53 cm in body length. Table 2 formalizes what is evident in figure 1, namely, that the correlation values between cranial volume and body weight and body length were modest. It also shows that, except for female cranial volume on body weight, the slopes probably differed from zero.

The lower half of table 1 records the statistical results for *Onychomys torridus pulcher*: the females were heavier and longer than the males, but their cranial volumes were on average smaller, although not significantly so. The pattern of differences was similar to that of the northern

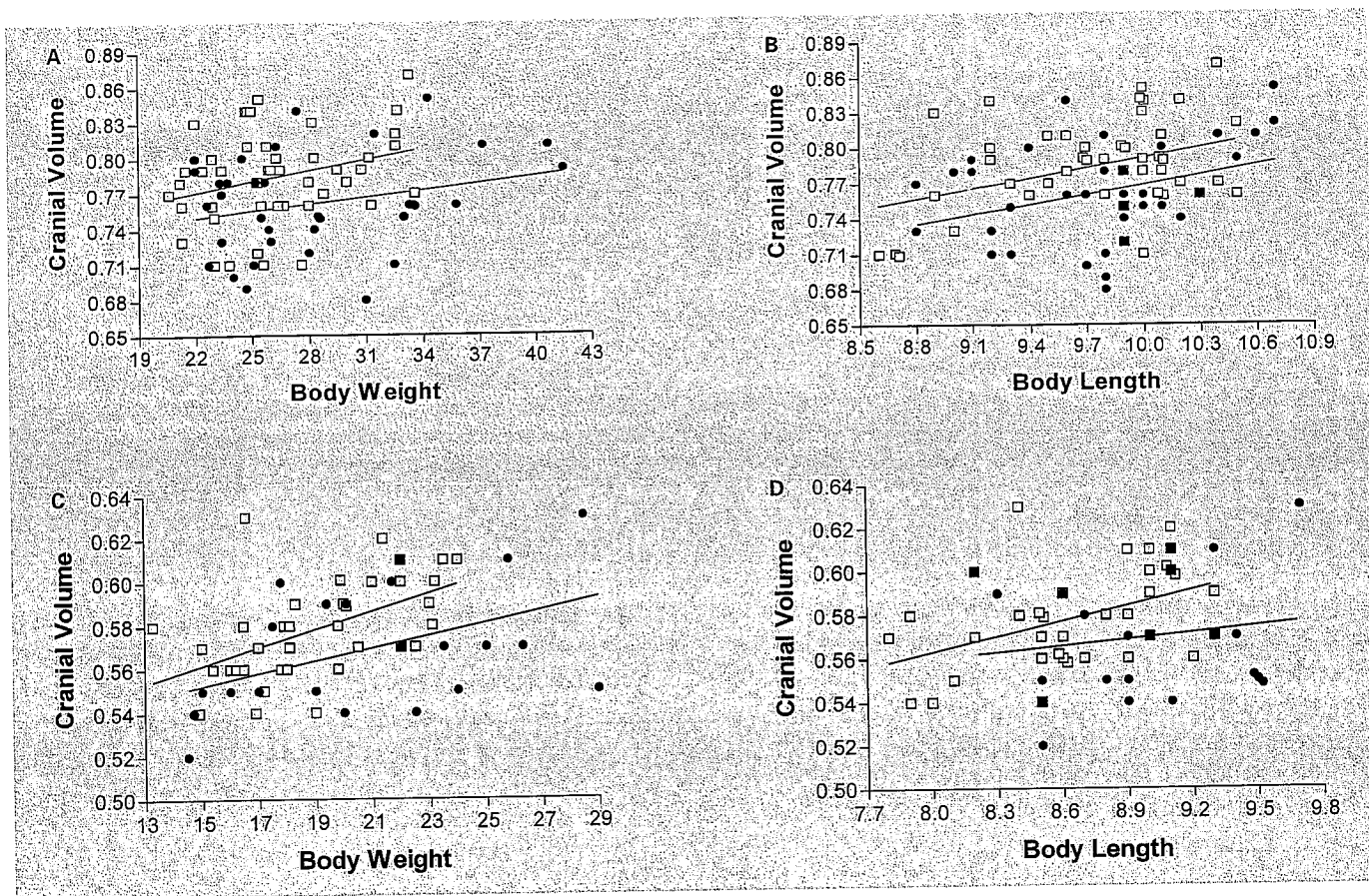


Fig. 1. Graphs of cranial volume as a function of body weight (**A**) and body length (**B**) for 35 females (solid dots) and 45 males (open squares) of *Onychomys leucogaster brevicaudus*. Graphs of cranial volume as a function of body weight (**C**) and body length (**D**) for 22 females and 36 males of *Onychomys torridus pulcher*. Identical values for same sex are shown staggered, and for both sexes are shown as solid squares. Regression lines as stated in table 2.

Table 1. Statistical description, including median (Mdn), mean, standard error (SE), coefficient of variation (CV%), and probability that the females and males were drawn from the same population (p), by sex for both species

	Females				Males				t test* p
	Mdn	Mean	SE	CV%	Mdn	Mean	SE	CV%	
<i>O.l.b.</i>									
P (g)	26.30	28.42	0.860	18.8	25.80	26.35	0.531	13.5	0.042
L (cm)	9.80	9.77	0.086	5.2	9.90	9.75	0.075	5.1	0.848
C (ml)	0.760	0.762	0.007	5.5	0.790	0.784	0.006	5.0	0.016
<i>O.t.p.</i>									
P (g)	20.90	20.97	0.927	20.7	18.65	19.07	0.473	14.9	0.049
L (cm)	8.95	8.97	0.091	4.7	8.60	8.66	0.069	4.8	0.010
C (ml)	0.570	0.569	0.006	5.0	0.580	0.579	0.004	3.9	0.174

O.l.b. = *Onychomys leucogaster brevicaudus*; *O.t.p.* = *Onychomys torridus pulcher*.

* df = 56 in every case for *O.l.b.*; df = 78 in every case for *O.t.p.*; 2-tailed unpaired test.

P = Body weight; L = head and body length; C = cranial volume.

Table 2. Correlation (r), regression slope (a), intercept (Y_0), and probability that the slope was zero (p), for pairs of variables, by sex for both species

	Females				Males			
	r	a	Y_0	p	r	a	Y_0	p
<i>O.l.b.</i>								
C/P	0.243	0.0019	0.7081	0.160	0.287	0.0031	0.7018	0.056
C/L	0.326	0.0273	0.4950	0.056	0.359	0.0284	0.5075	0.015
L/P	0.667	0.0639	7.953	0.0001	0.502	0.0692	7.924	0.0004
<i>O.t.p.</i>								
C/P	0.438	0.0029	0.5093	0.042	0.521	0.0042	0.4992	0.001
C/L	0.148	0.0099	0.4803	0.511	0.435	0.0238	0.3730	0.008
L/P	0.427	0.0417	8.093	0.047	0.514	0.0755	7.224	0.001

O.l.b. = *Onychomys leucogaster brevicaudus*; *O.t.p.* = *Onychomys torridus pulcher*.
P = Body weight; L = head and body length; C = cranial volume.

mice. Figure 1 shows that the distributions for the two sexes overlapped extensively, although data points for the females were shifted down and to the right. Table 1 shows that the coefficients of variation were normal, although the variation in female body weight was rather large. It also shows that the females and males were equally bulky ($\langle H_F \rangle = 0.307$ and $\langle H_M \rangle = 0.308$). The lower half of table 2 shows that all correlation values were modest, and that, except for female cranial volume on body length, all the slopes differed from zero. Thus, the southern mice showed substantially the same pattern of brain/body relationships as did the northern mice.

The tail length of the northern subspecies, *O.l. brevicaudus*, adhered to its name, for it averaged 27.8% of total body length: $\langle 3.77 \rangle \pm 0.29$ cm in females, and $\langle 3.73 \rangle \pm 0.40$ cm in males. By contrast, the tail length of the southern subspecies, *O.t. pulcher*, averaged 33.9% of total body length: $\langle 4.58 \rangle \pm 0.36$ cm in females, and $\langle 4.50 \rangle \pm 0.39$ cm in males.

Discussion

The adult body weights and lengths found in this study are similar to those reported by others, but they suggest a reverse sexual size dimorphism. Hafner and Hafner [1979] concluded from their small sample of Northern grasshopper mice that the males are larger than the females. The study by Pinter [1970] on the growth of Northern and Southern grasshopper mice bred and reared in the laboratory also showed the adult males to be heavier than the adult females, although they did not differ in body length. But she concluded with the remark that 'the

results obtained in the present laboratory investigation cannot be strictly applied to *Onychomys* under natural conditions.' Neither Pinter [1970], nor van Cura and Hoffmeister [1966], nor Horner and Taylor [1968] found significant length differences between the sexes. The present study found a one-in-twenty chance that males do not differ systematically from females in body weight (a one-in-forty chance that females are not heavier than males). Body length presented a different problem: no difference was found in the northern species, but a clear difference was found in the southern species. Two factors make the data for the northern species suspect: 40% of the length values were found in the interval 9.9–10.1 and the difference in habitus. If males are as bulky as females, then one would predict $L_M = P^{1/3}/H_F = 9.53$ cm for mean male body length, much less than the observed value of 9.75 cm.

Cranial volumes present a different picture: they appear to be larger in the males. This is apparent in the sample of Northern grasshopper mice, where females were significantly heavier than males, but males had significantly larger cranial volumes. The sample of Southern grasshopper mice shows the same relations, although cranial volumes had a one-in-five (or six) chance of being the same between the sexes. This finding presents an interesting problem for the concept of 'encephalization.' The 'Theory of Brain Size' elaborated by Jerison [1963, 1973] partitions observed brain mass (E_o) into two interconnected, possibly commingled components – one that manages the internal and external affairs of the body (housekeeping functions) and the other associated with 'intellectual' functions. The former is defined as expected mass (E_e) which, when stated as a quotient of total brain mass (E_o/E_e), yields an index of encephalization. However, the way

in which expected brain mass is derived determines the magnitude of the encephalization quotient for each species (a large literature concerns this issue). As for grasshopper mice, the housekeeping functions may involve a large portion of the brain. Perhaps the best way to find an expected brain mass, E_e , for the grasshopper mouse is to use its relatives as reference. The data of Mann et al. [1988] yield $E_e = 0.066P^{0.673}$, which leads to encephalization quotients of 1.21 and 1.31 for female and male *O.L. brevicaudus*, and to 1.11 and 1.21 for *O.t. pulcher*. That is, the male quotients are about 8.3% larger than the female quotients. Because the housekeeping functions involve about the same amount of brain in each sex, the 8% difference in encephalization quotients must reflect the 'intellectual functions' of Jerison.

It is commonly assumed that a larger body requires a larger brain. In a recent article Seyfarth and Cheney [2002] stated, 'Across the animal kingdom, brain size increases with increasing body size.' The fact that this comment was offered without attribution points to its general acceptance. Theoretical treatments, such as the geometric model of Towe and Mann [1995], are often built upon such an assumption (although the one referenced does not require it). To be sure, the general notion of a direct relationship between body size and brain size is usually derived from cross-species comparisons. Nonetheless, it makes no sense to apply it to sexual dimorphism above the species level. Though this is perhaps a 'comfortable' notion, it is by no means necessarily correct. Both a larger cutaneous surface and a larger muscle mass would seem to require a larger body, but if cutaneous receptive fields get larger and motor units get larger, the body could become larger without a change in brain size. Clearly, on average *Onychomys* females control their larger bodies without a concomitant increase in brain size, at least if males are taken as the standard of comparison. It seems difficult to reconcile *Onychomys* with a general 'Theory of Brain Size' [Jerison, 1963, 1973].

The encephalization quotient, often used for comparison of brains of different species, is only as good as the determination of the expected brain size (E_e). The goodness of that determination depends upon the standard of comparison. Large changes in results can occur with small changes in that standard. For example, Jerison [1973] determined the slope of the brain-body relation for a wide sample of mammals to be 0.67. Martin [1981], using a larger sample (which included mostly smaller mammals), obtained a value of 0.76. Encephalization quotients calculated from these regression lines can be quite different. Table 3 provides the encephalization quotients for the

Table 3. Encephalization quotients* calculated for animals of the current study using brain-body relationships

Study	<i>Onychomys leucogaster brevicaudus</i>		<i>Onychomys torridus pulcher</i>	
	Female	Male	Female	Male
Mann et al. [1988]	1.21	1.31	1.11	1.21
Jerison [1973]	0.70	0.75	0.63	0.69
Martin [1981]	1.20	1.12	0.96	1.05

* $EQ = E_o/E_e$, where EQ = encephalization quotient, E_o = observed brain size, E_e = expected brain size.

animals of this study calculated using the brain-body relationships for myomorph rodents [Mann et al., 1988], for contemporary mammals [Jerison, 1973] and for placental mammals [Martin, 1981]. Clearly, the values are dissimilar. Values calculated using Stephan and Andy's [1969] basal insectivore standard would be even more deviant. One may reasonably ask what constitutes the 'proper' standard of comparison.

The high metabolic demand of brain tissue leads to the idea that brain size is minimal. Hence, some obvious factors must be at work in forming the male brain. The variations in body mass associated with developmental, dietary, seasonal, and reproductive states may be reduced by confining the study to adult animals trapped in similar environments in the same season. Because these conditions were largely met in the present samples, the results – statistical statements about populations of grasshopper mice – may be taken as descriptive. However, not enough is known about the lives of grasshopper mice to identify the factors responsible for the observed differences. Most behavioral differences have been examined in the laboratory. Whether sex-specific stresses in the field lead to hormonal effects on brain growth is moot, though laboratory manipulations of meadow voles [Whaling et al., 1990] suggest that this is possible. Sexual dimorphisms are not uncommon in the CNS [Tobet and Fox, 1988], but all are small, and could hardly add up to a 3% difference in brain mass. Some other factors must be at work, putting different demands on males than on females. We do not know how the behavioral differences between the genders outlined in the introduction may be related to these differences in brain and body size. Perhaps there are other species with similar brain-body relations, and a key to understanding them may lie in the similarities to grasshopper mice.

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