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Habitat-Related Variations in Brain and Body Size of Pocket Gophers

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With 3 Figures and 2 Tables; 1 Appendix

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Abstract: Cranial capacities were measured in two sets of genetically-related pocket gophers, one from desert shrubland, the other from an irrigated alfalfa field. The two sets differed in sex ratio and in age structure, but both showed the strong sexual dimorphism characteristic of pocket gophers. After sorting by trapping site, sex and suture score (age), the covariations between brain weight, body length and cranial basilar length were calculated. The brains of the alfalfa field animals followed the same somatic scaling relations as those of the desert shrubland animals, all the differences in brain weight being explained fully by the sexual dimorphism in the somatic variables. The slopes defined by the means of brain and body weights of females and of males from the two sites were nearly equal, and were the same as the trajectories calculated from a geometric model based on the statistical characteristics of the samples. It is argued that these slopes define how much brain size must increase to serve a body of increased size, with no change in life style. The differences in age structure between males from the two sites provided evidence of a mechanism by which sexual dimorphism might develop and be enhanced in a nutritionally-enriched environment.

Key words: Allometry, Brain/body relations, Pocket gophers, Sexual dimorphism

Introduction

The well-documented mouse-to-elephant allometric relation $E = kP^\alpha$, where E = brain mass, k = scaling constant, P = body mass, and α = scaling slope, has long intrigued biologists. The scaling slope has been said to result from an overall constraint on brain mass ascribable to dimensional ($\alpha = 2/3$) or metabolic ($\alpha = 3/4$) factors, but neither the precise slope nor accompanying explanation has produced consensus. If either of these explanations were true, then the many large deviations from the overall constraint would require explanation. A fundamentally different view is that the overall mouse-to-elephant allometric relation reflects the mean evolutionary pathway among a large array of pathways from small to large body mass, the present position of any species in brain-body space reflecting its own unique evolutionary history. In their study of myomorph rodents, MANN et al. (1988) found that brain/body slopes of 30 species (samples of 20 or more specimens) ranged widely, from 0.20 to 0.59, with a mean slope of 0.334 ± 0.017 (\pm standard error). If those slopes reflect the increased amount of brain needed to operate a larger body, then some animals need relatively more brain than others to function at an increased body size. Furthermore, the genus slopes ranged from 0.29 to 0.79, proving that they are not simple extensions of species slopes. LANDE (1979)

calculated the brain/body slope of random genetic drift in murids at 0.36, but it is not known if this reflects the "required brain size" slope for the murid line. It may be informative to determine what happens to brain size when nutrition is greatly enhanced, that is, when somatic growth is markedly increased, due to an increased rate of cell division and an increased total number of cells (WINICK and NOBLE, 1967). But adult brain size is also influenced by programmed cell death (OPPENHEIM, 1991), which presumably adjusts the brain to its "required size". Thus, the brain/body slope along which a population moves under enhanced nutrition should reveal how much brain is needed to operate a body of a given size, with no change in life style.

In their thorough field study, DOBSON and KJELGAARD (1985 a, b) found that ground squirrels grew faster, matured more rapidly, and attained a larger adult body size than their control population, when high-protein horse feed was provided. Reproductive rate, litter size, and survival rate (especially of young and female animals) increased, thereby increasing the population size, changing its age structure, and to a lesser extent changing the sex ratio. COLE and BATZLI (1978) found similar changes in prairie voles after supplementing their normal diet with rabbit pellets. However, brain size was not measured in either study. PATTON and BRYLSKI (1987) found marked differences in body size between two sam-

ples of genetically-related pocket gophers, one from desert shrub habitat (the natural habitat for this species) and the other from an irrigated alfalfa field. Although they did not measure brain size directly, they determined that the different-sized skulls had similar shapes, leading them to conclude that cranial size varies with nutritional plane. To determine directly and quantitatively how brain mass varied with body mass, we measured the cranial volumes of the PATTON and BRYLSKI samples and related them to their measurements of body weight, body length and basilar length. Because the animals from these two sites were from the same genetic stock, they were ideal for determining the "basic" brain/body relation.

Materials and Methods

The specimens of *Thomomys bottae perpes* used in this study were collected, prepared, and measured by J. L. PATTON and colleagues; we measured cranial volumes for this analysis. Specimens were made available to us by PATTON at the Museum of Vertebrate Zoology, University of California, Berkeley. Four groups were studied: Freeman Canyon females (FCf, n = 79) and males (FCm, n = 88), and Rose Valley Ranch females (RVRf, n = 169) and males (RVR, n = 72). Freeman Canyon consisted of Joshua tree shrubland located 1.6 mi below Walker Pass in Kern Co., CA, whereas Rose Valley Ranch was an alfalfa field monoculture located 2.5 mi north of Coso Jct in Inyo Co., CA, some 30 mi NNW of Freeman Canyon. Electrophoretic comparisons showed that the FC and RVR samples derived from the same genetic stock (PATTON and BRYLSKI, 1987).

Cranial volumes were measured by the shot-displacement method described by MANN et al. (1988). A 50:50 mixture of 8 and 9 ga shot was used to minimize the formation of lacunae while filling the cranium (lacunae can produce large errors). The cranial volumes were treated as equal to brain weight (E). Of the variables measured by PATTON and colleagues, the ones used here included body weight (P), body length (L = total length minus tail length), skull basilar length (Z = distance from posterior alveola of incisors to anterior margin of foramen magnum), and cranial suture score (S) as defined by DALY and PATTON (1987). The latter served for estimation of age structure of each sample and for age-specific analyses.

Means (X), standard deviations (SD), standard errors of the mean (SE) and coefficients of variation (CV = 100 SD/X) were calculated for each parameter for each group, and Pearson correlation coefficients (r) and reduced major axes (β) were computed for pairs of parameters for each group of animals. Slopes were also calculated from the mean values, such that

$$\hat{\nu} = (\ln E_{RVR} - \ln E_{FC}) / (\ln P_{RVR} - \ln P_{FC})$$

for each sex. A geometric method for estimating a trajectory corresponding to $\hat{\nu}$, but derived from the observed brain/body slope and the coefficient of correlation is described under Results.

Results

The sample was partitioned by trapping site, sex and suture score (age) for analysis; the relevant data are recorded in Appendix I. The samples differed in age

structure, as well as in body size; hence, both will be reviewed. DALY and PATTON (1987) found that a suture score boundary between 4.0 and 4.5 adequately distinguished juveniles from adults. This criterion was applied in the analysis: all specimens with $S > 4.0$ were classed as adults and those with $S \leq 4.0$ were classed as juveniles. The adult/juvenile ratios were: 1.82 for FC females; 1.75 for FC males; 3.33 for RVR females; 1.25 for RVR males. The adult FC females and males were present in nearly equal numbers; the adult RVR females outnumbered the adult RVR males nearly 8 to 3.

Brain and body sizes. Because the brain nearly fills the cranium and has a density near that of water, its volume in milliliters may be treated as equivalent to brain weight in grams. The mean weights of adult RVR brains were 9.1% (females) and 13.9% (males) larger than those of the corresponding adult FC brains, but the mean weights of the juvenile brains were nearly equal in the two samples (Appendix I). The distributions of brain weight for all groups were positively skewed and platykurtic, and they had similar coefficients of variation, ranging from 5% for adult RVR females to 8% for juvenile RVR males. The distributions of body weight showed these same characteristics, with sexual dimorphism being greatly increased in the RVR adults (σ/ϕ : RVR, 1.41; FC, 1.22). Body weights of RVR adults were 64.7% (females) and 91.0% (males) larger, whereas those of juveniles were 30.3% and 17.4% larger. The coefficients of variation were three times larger than those for brain weight, ranging from 14% for adult RVR females to 25% for juvenile RVR males. The distributions of body length and basilar length also showed these same characteristics, but with coefficients of variation similar to those of brain weight (Appendix I).

Table 1. Reduced major axis slopes (β) and coefficients of correlation (r) for brain weight on body weight (E/P) and on body weight minus brain weight (E/(P-E)), and for the cube root of brain weight on body length (E^{1/3}/L) and on cranial basilar length (E^{1/3}/Z) for adult female (f) and male (m) pocket gophers trapped in Freeman Canyon (FC) and at Rose Valley Ranch (RVR). Number in each group (N) is given in last column.

	E/P		E/(P-E)		E ^{1/3} /L		E ^{1/3} /Z		N
	β	r	β	r	β	r	β	r	
FCf	0.420	0.55	0.415	0.55	0.395	0.62	0.585	0.65	51
RVRf	0.347	0.30	0.344	0.30	0.397	0.38	0.542	0.51	130
FCm	0.311	0.68	0.307	0.68	0.367	0.70	0.421	0.76	56
RVRm	0.473	0.55	0.470	0.55	0.413	0.53	0.439	0.65	40

The pattern of covariation between paired variables was the same in all groups. Table 1 records how adult brain weight varied with body weight and with

body weight minus brain weight. It also records how the cube root of brain weight (dimensional adjustment) varied with body length and with basilar length. The correlations averaged about 0.60, but all were lower for the FC than for the RVR animals and were highest between brain weight and basilar length. Among the juveniles, all corresponding slopes were lower and correlations higher, but, again, the latter were highest between brain weight and basilar length. Table 1 also shows that including brain weight on both sides of the allometric equation introduces a negligible error (brain weight is a small fraction of total body weight).

Graphs of mean brain weight by suture score were similar to the graphs of mean basilar length by suture score plotted by PATTON and BRYLSKI (1987) on an "age in months" scale. The apparent "spurt" of growth in basilar length between suture scores 4.0 and 5.0 in the RVR male group was also apparent in brain weight. Fig. 1 shows how brain weight and body weight varied jointly, each point derived from animals with the same suture score. Suture scores (ages) increase from left to right along the curve. The symbols, which locate the four sex-by-site groups, reveal that all animals followed the same joint growth function. The modified Gompertzian function,

$$E = 0.36 \exp(1.17[1 - \exp(-0.05P)]) + 0.0019P,$$

plotted as the continuous curve in Fig. 1, describes the relationship well (the root mean square error with respect to E was 0.045 g). The figure also shows

that both brain and body continue to grow throughout adult life and maintain the same relative growth rates after attaining maturity. It was this continued growth which forced the modification of the normal Gompertz function which has a plateau value.

Geometric similarity. If body conformation were maintained across all sizes, then body length would vary directly with basilar length, and both body length and basilar length would vary directly with the cube root of body weight. But such was not the case: adult body length increased considerably more rapidly than adult basilar length, and more rapidly in females ($\beta_{L/Z} = 1.48$ for FCf and 1.38 for RVRf) than in males ($\beta_{L/Z} = 1.15$ for FCm and 1.07 for RVRm). These differences were not so apparent in the juvenile animals. On the other hand, adult body length varied almost directly with the cube root of adult body weight ($\beta_{L/P^{1/3}} = 1.05$ for FCf; 0.89 for RVRf; 0.86 for FCm; 1.14 for RVRm), whereas adult basilar length increased more slowly ($\beta_{Z/P^{1/3}} = 0.70$ for FCf; 0.65 for RVRf; 0.74 for FCm; 1.07 for RVRm). This latter difference was also not so apparent in juveniles. Thus, the juveniles showed geometric similarity with respect to all variables, but the adults showed geometric similarity only between body length and body weight. Basilar length was relatively shorter in the larger animals.

Allometric relations. The ϑ slopes defined by the mean values for the FC to RVR adults are shown in Table 2. For females, $\vartheta_{E/P} = 0.174$, with 95% confidence interval of 0.145–0.195 and intercept of 0.62. For males, $\vartheta_{E/P} = 0.201$, with 95% confidence interval

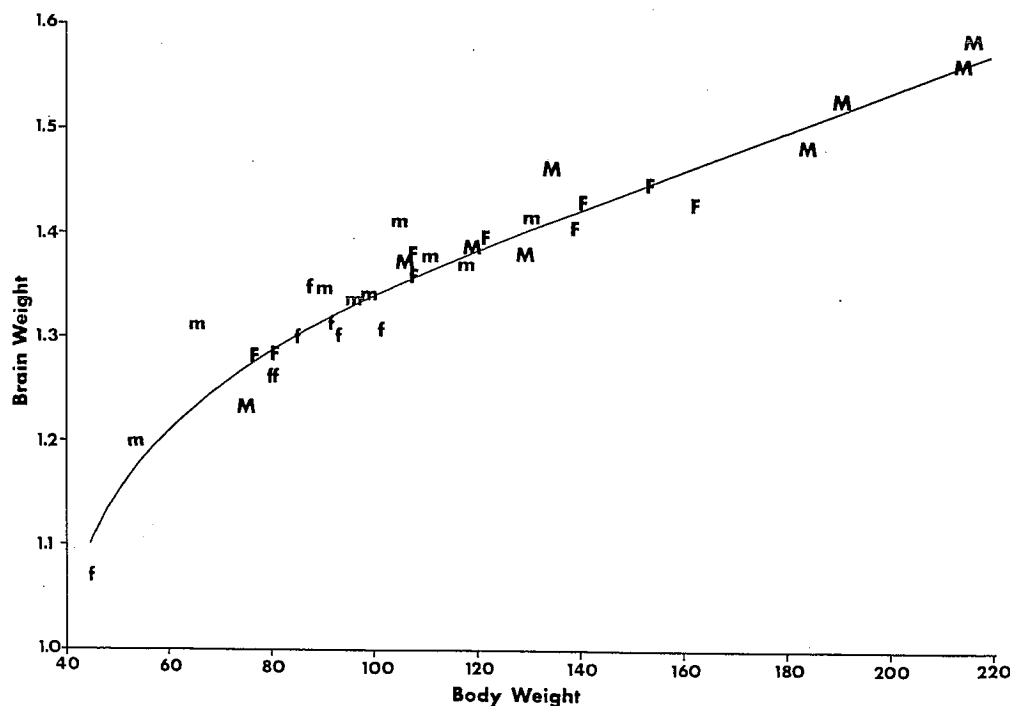


Fig. 1. Relation of brain weight (E) to body weight (P) during growth and into maturity, as indicated by mean values for suture-score groups. FC females (f); FC males (m); RVR females (F); RVR males (M). Solid curve: best-fit Gompertzian function modified to allow the function to increase throughout the body weight range (see text).

of 0.164–0.252 and intercept 0.52. Thus, the two slopes were statistically indistinguishable.

Table 2. Observed slopes ($\hat{\theta}$), predicted slopes (p') based on FC statistical characteristics, predicted mean brain weight (pE) of adult RVR pocket gopher and difference in standard errors from observed mean brain weight (ΔSE), calculated for brain weight on body weight (E/P) and body weight minus brain weight ($E/(P-E)$), and for cube root of brain weight on body length ($E^{1/3}/L$) and cranial basilar length ($E^{1/3}/Z$). Asterisk marks highly deviant prediction.

	Females				Males			
	$\hat{\theta}$	p'	pE	ΔSE	$\hat{\theta}$	p'	pE	ΔSE
E/P	0.174	0.178	1.443	0.77	0.201	0.191	1.550	-0.94
$E/(P-E)$	0.173	0.174	1.443	0.84	0.199	0.188	1.549	-1.05
$E^{1/3}/L$	0.189	0.206	1.447	1.43	0.239	0.231	1.553	-0.40
$E^{1/3}/Z$	0.227	0.219	1.432	-0.94	0.226	0.290	1.620	3.55*

Geometric model. In linear space, the major axis of a normal bivariate distribution is defined by the ratio of standard deviations ($\alpha = SD_y/SD_x$), and the two least-squares slopes are found by multiplying the major axis slope by $r_{x:y}$ for $y = f(x)$ or dividing by $r_{x:y}$ for the inverse slope $y = f^{-1}(x)$. However, normal mammalian growth yields positively skewed body size distributions, a condition that is usually corrected by transformation to logarithmic space. In logarithmic space, the analogous descriptors become the ratio of the coefficients of variation ($B = CV_x/CV_y$), and $p = \text{atan}(\hat{\theta}_B - \hat{\theta}_{b^2_B})$ for $y = f(x)$ and $e = \text{atan}(\hat{\theta}_B + \hat{\theta}_{b^2_B})$ for $y = f^{-1}(x)$, where $\hat{\theta}_B = \text{atan } B$ and $b^2 = (1-r)/(1+r)^1$. In both linear and logarithmic cases, the least-squares slopes provide the best estimate of the value of y (or x) for any given value of x (or y).

This description is illustrated by the two graphs of brain weight (E) on body weight (P) plotted in Fig. 2 in logarithmic coordinates. Taking $r = 0.6$ (a typical value) and taking $B = 0.36$ (the slope of random

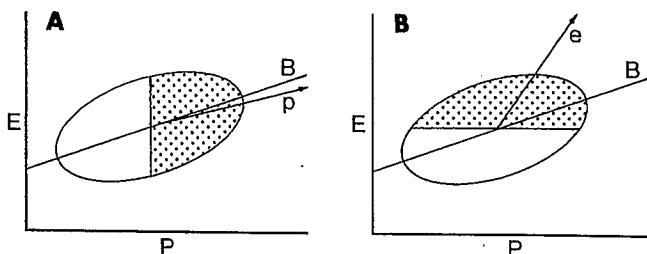


Fig. 2. Correlation ellipses ($r = 0.6$) centered on mean E and P , with major axis at slope $B = CV_E/CV_P$. Graph A: least-squares slope p shows trajectory if selection is for increased body size (P); Graph B: least-squares slope e shows trajectory if selection is for increased brain size (E). See text for details.

¹ Because we are interested in the minor/major axis ratio (a/b), we set $a = 1$, such that $b^2 = (1-r)/(1+r)$, and correlation ellipse is of degree $\text{asin } b$.

genetic drift), a 30° “correlation” ellipse is generated, centered on the means of E and P , and tilted 19.8° ($\text{atan } 0.36$). (The degree of the ellipse and its tilt will vary from species to species; these values are examples.) Slope p , the least-squares slope on $E = f(P)$, is the expected trajectory under selection for increased body weight (dotted area in Fig. 2 A), and slope e , the least-squares slope on $E = f^{-1}(P)$, is the expected trajectory under selection for increased brain size (dotted area in Fig. 2 B)². Here, $p = 0.26$ and $e = 1.41$. This statistical approach estimates the trajectory of brain/body evolution of a species under a known selection pressure.

In the case of PATTON and BRYLSKI’s pocket gophers of the alfalfa field, the pressure was for increased body size with brain size changing only as a correlated trait, in other words, along a p slope in this model. Because body weights were increased by nutritional factors rather than selective breeding, the correlation ellipse had to be replaced by a “determination” ellipse, where $b^2 = (1-r^2)/(1+r^2)$, to reflect the amount of variance in brain weight ascribable solely to variance in body weight (r^2 estimates that variance). In the case shown in Fig. 2 A, that slope is $p' = 0.18$ (10°), the slope that should describe the amount by which brain weight must increase to serve a body that is larger by some given amount, but that behaves in the same way as its smaller congeners.

Thus, if the animals follow the theoretical trajectory (i.e., if $p' \approx \hat{\theta}$), then p' tells the rate at which brain must increase in size to adequately serve a body of increased size, with no change in life style. Table 2 shows the estimated mean brain weights (pE) and how much these estimates differed from the observed RVR mean brain weights, expressed in standard errors of the mean (SE). The geometric method clearly provides adequate estimates, and subtracting brain weight from body weight makes little difference to the final result. However, the estimate of brain weight from basilar length for adult RVR males missed by 3.55 SE error. This may have been due to the rather high correlation between basilar length and the cube root of brain weight ($r = 0.76$) in the adult FC males, produced by a couple outliers (the average correlation of 0.64 yields an extremely accurate estimate), but it more likely was due to the peculiar scaling of basilar length.

Age structure. The age structures for the females and males from Freeman Canyon, expressed in cumula-

² The line (s) p (e) passes through the center of the ellipse and the centroid of the right (upper) half of the ellipse, dividing it into symmetrical halves, and is, therefore the line of least-squares.

tive frequency histograms, were nearly identical (Fig. 3-1), whereas those from Rose Valley Ranch differed markedly (Fig. 3-2). The RVR females and males started out along nearly parallel paths, but diverged sharply after a suture score of 3.5, the males lagging the females. On the assumption that the sex ratios at birth were the same at both trapping sites, only three adult RVR males were found for every eight expected, suggesting that many RVR males either died or left the alfalfa field as they became sexually mature, in the suture score range from 3.5 to 4.5.

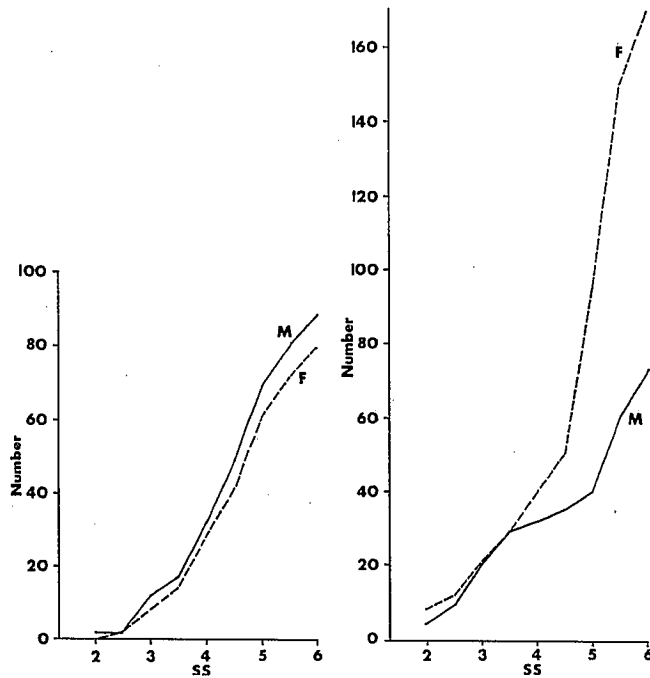


Fig. 3. Age structures, expressed as cumulative distributions of number of animals by suture score (SS). Graph 1: FC females (F) and males (M); Graph 2: RVR females (F) and males (M).

Adult RVR females were, on average, 165% heavier than adult FC females, whereas adult RVR males were 191% heavier than adult FC males. However, if the lighter RVR juveniles disappeared from the alfalfa field, through death or emigration, then the heavier half of the adult FC males may be used to predict the condition of the adult RVR males. The statistical properties of the heavier half ($E = 1.42$, $P = 128.4$, $\beta_{E/P} = 0.423$, $r_{E:P} = 0.50$, $p' = 0.153$) predicted a mean adult RVR male brain weight of 1.53 g, 1.90 SE below the observed mean. The heavier half also predicted, from $\beta_{E^{1/3}/Z} = 0.454$, $r_{E:Z} = 0.68$ and $p' = 0.267$, that the adult RVR mean brain weight would be 1.57 g, 0.5 SE above the observed mean. Also, the adult RVR males were only 164% heavier than the heavier half of the adult FC males, the same percentage increase as the females. By contrast, the juvenile RVR males did not dif-

fer from other juveniles, thus reinforcing the idea that the adult RVR males represent a subset of the RVR male population selected as those animals attained sexual maturity.

Discussion

Brain/body allometries. When sorted by site, suture score (age) and sex, the pocket gophers were found to be geometrically similar with respect to body weight and body length, but not cranial basilar length. The latter increased slower than body length, especially among females. Even so, the correlation of brain weight with basilar length was slightly stronger than with body length or body weight. PATTON and BRYLSKI (1987) found that the animals from the alfalfa field (RVR) were larger and more sexually dimorphic than those from the desert shrubland site (FC). We found that despite these differences, the brains of the RVR animals maintained the same scaling relationships with body weight, body length and basilar length as the FC animals and that the females followed the same brain/body size trajectories as the males. Therefore, the sex difference in brain size is due entirely to the sex difference in body size. That is, when account is taken of body size, no sexual dimorphism exists with respect to brain size.

This is an important outcome, when viewed in terms of the ideas of "proper brain size" (JERISON, 1977) and "selective cell death" (OPPENHEIM, 1991). During growth and development, the overproduction of nerve cells, coupled with paring and shaping through selective cell death, is presumed to produce a brain the "proper" size for the body with which it is associated. If true, then the between-site trajectories (θ) reveal the slope of required brain/body change for pocket gophers: brain must increase as roughly the 2/11 power of body size to remain in "proper" proportion. This is much slower than the overall mammalian brain/body slope of roughly 7/10, which means that in evolving from small to large forms within any genetic line, new demands on brain size have been at work. The geometric model not only describes the observed brain/body response to enhanced nutrition quite well, but it also says that if selection for increased brain size has been as frequent and intense as selection for increased size of other body organs, then the values associated with Fig. 2 predict that a mean slope of $\beta = 0.69$ (the result of evaluation of the expression, $\tan [0.5 \{ \tan e + \tan p \}]$) will be observed. This is the overall slope that MANN et al. (1988) found in their study of myomorph rodents.

Furthermore, the model suggests that species, such as those of the genus *Peromyscus* in the data of MANN et al. (1988), which have steep E/P relations (β around 0.79)³ may have been under strong pressure to increase brain size (e slope). Conversely, species, such as those of the genus *Rattus*, which have shallow E/P relations (β around 0.29) may have been under little or no pressure to increase brain size, the predominant evolutionary pressure having been to increase body size (p slope). Genera with intermediate slopes may have been under mixed pressures to increase body size and, independently, brain size.

Age structures and sexual dimorphism. PATTON and BRYLSKI (1987) found female and male pocket gophers in equal numbers in Freeman Canyon, but they found twice as many females as males in Rose Valley. Their age distributions, as estimated from suture scores, showed no sex differences in Freeman Canyon, but striking sex differences in the Rose Valley population. The survival rate (as indicated by trapping rate) of the females was uniformly high, whereas the Rose Valley males showed a sharp drop in survival rate as they became sexually mature. Apparently, the smaller males either died or emigrated during that time, leaving the larger males in possession of the alfalfa field. This increased the index of sexual dimorphism for body weight, from 1.22 in desert shrubland to 1.41 in the alfalfa field. However, using only the heavier half of the FC males - mimicking the condition of the RVR population - yields an index of sexual dimorphism of 1.42. The heavier half of the FC males proved to be better than the whole FC male sample in predicting of the observed values of brain size for the adult RVR males. Thus, we propose that one mechanism by which sexual dimorphism might develop depends on the nutritional resources of the habitat and their effect on reproductive rate, population density and competition for mating space. It is also clear that the enhanced dimorphism in RVR animals is due to effects on the male not on the female animals as it is in some primates (MARTIN et al., 1992).

Pocket gophers living in alfalfa fields breed throughout the year, whereas those living in less favorable habitats breed seasonally (MILLER, 1946). As in many other rodents, an abundance of nutritious green forage facilitates breeding (DIXON, 1929), and such a diet is available in alfalfa fields through most of the year (the α -spinosterol in alfalfa may also increase the growth rate). The resulting large population may strain territorial limits, inducing conflicts that favor the larger males. Thus, the

smaller males may be killed, maimed or intimidated to leave the area in search of a less hostile neighborhood. Although male pocket gophers tolerate females in adjacent territories, they are not tolerant of other males during the breeding season (which may be close to 365 days in length in the alfalfa field), though outside the breeding season, a few males may share the same burrow system (HANSEN and MILLER, 1959). We suggest that competition for mating territories in the alfalfa field removes the smaller males, and that such persistent selective exclusion results in an enduring increase in mean body size.

Abbreviations

E, brain weight; P, body weight; α , scaling slope; k, scaling constant; L, body length minus tail length; Z, cranial basilar length; S, cranial suture score; X, parameter mean value; SD, standard deviation; SE, standard error of the mean; CV, coefficient of variation; r, Pearson correlation coefficient; β , reduced major axis; \hat{v} , slope derived from mean values; B, ratio of coefficients of variation; p, trajectory derived from B and r; p', trajectory derived from B and r^2 ; e, trajectory derived from B and r; pE, brain weight estimated from p' slope; FC, Freeman Canyon; RVR, Rose Valley Ranch; RVRf, Rose Valley Ranch females; RVRm, Rose Valley Ranch males; FCf, Freeman Canyon females; FCm, Freeman Canyon males.

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³ The values 0.79 and 0.29 here are genus slopes, based on limited samples. Weighted average species slopes, 0.46 and 0.28, also show the difference in E/P relations of these two groups.

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Appendix I

Means (X), standard deviations (SD), standard errors (SE) and coefficients of variation (CV) for brain weight (E), body weight (P), body length (L) and cranial basilar length (Z) of female (f) and male (m) pocket gophers trapped at Freeman Canyon (FC) and Rose Valley Ranch (RVR). Number of adults/juveniles: FCf 51/28; RVRf 130/39; FCm 56/32; RVRm 40/32.

		Adults				Juveniles			
		X	SD	SE	CV	X	SD	SE	CV
E	FCf	1.32	0.092	0.013	7.0	1.26	0.097	0.018	7.7
	RVRf	1.44	0.068	0.006	4.7	1.36	0.090	0.014	6.7
	FCm	1.37	0.091	0.012	6.6	1.35	0.088	0.016	6.5
	RVRm	1.56	0.098	0.016	6.3	1.37	0.110	0.019	8.0
P	FCf	90.4	15.0	2.10	16.6	80.3	17.6	3.32	21.9
	RVRf	148.9	20.3	1.78	13.6	104.7	21.1	3.38	20.2
	FCm	109.9	23.5	3.09	21.4	94.8	19.8	3.50	21.0
	RVRm	210.0	27.8	4.40	13.2	111.3	28.4	5.02	25.5
L	FCf	13.6	0.79	0.110	5.8	12.8	0.87	0.165	6.8
	RVRf	15.8	0.64	0.056	4.0	14.2	0.89	0.142	6.2
	FCm	14.3	0.88	0.117	6.1	13.7	0.82	0.145	6.0
	RVRm	17.1	0.86	0.136	5.0	14.4	1.16	0.204	8.0
Z	FCf	2.95	0.115	0.016	3.9	2.81	0.177	0.033	6.3
	RVRf	3.34	0.098	0.009	2.9	2.98	0.199	0.032	6.7
	FCm	3.13	0.167	0.022	5.3	2.97	0.156	0.028	5.2
	RVRm	3.80	0.179	0.028	4.7	3.04	0.261	0.046	8.6