

ADAPTIVE PHYSIOLOGY

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Abstract.—Herein we examine and analyze the available data for the genus *Peromyscus* that relate to energy metabolism, water metabolism, and the interrelationships between these variables, approaching our study from an allometric perspective. The genus is nearly ubiquitous in North America, and there appears to be a well-defined geographic gradation in body mass, with the largest species in the tropical south and smaller species at higher latitudes. Allometric comparisons of basal metabolism, evaporative water loss, and water regulatory efficiency with other rodents indicate that *Peromyscus* typically are intermediate between dietary specialist granivores and herbivores; this is in keeping with their intermediate dietary position of omnivory. Thus, *Peromyscus* species may be viewed as physiological generalists. Their frequent success in surviving physically stressful environmental conditions, we propose, is made possible through the intermittent use of torpor until the stress is moderated. We propose further that torpor is a generalized syndrome of small (less than 40 grams) species of *Peromyscus*, and that selection has favored smaller size in those species inhabiting more stressful (more northerly) regions, where torpor provides the added margin for survival.

In 1983, R. W. Hill and R. E. MacMillen published companion papers on energy regulation (Hill, 1983) and water regulation (MacMillen, 1983a) in *Peromyscus* in an attempt to compensate for the absence of a chapter devoted to physiology in King's (1968) book, *Biology of Peromyscus (Rodentia)*. As these papers effectively brought the topic of adaptive physiology of *Peromyscus* up to the present and because the purpose of this volume is to update information accrued on the biology of *Peromyscus* since 1968, we were faced with the dilemma of merely reiterating a topic already updated and addressed in detail, or of attempting a new and different approach based on some of the same information. We elected the latter and will confine our comments to consideration of two metabolic variables that are of major regulatory importance and hence should be subject to environmentally related selective pressures. These are: 1) basal (or standard) metabolic rate (BMR), a major component of energy metabolism; and 2) evaporative water loss (EWL), the major avenue of water loss of most terrestrial mammals and therefore a major component of water metabolism. We will also consider in detail the information that is available on the interrelationships between energy and water metabolism.

With regard to water regulatory capabilities, MacMillen (1983a) concluded that *Peromyscus* were intermediate in nearly all aspects of their water economies compared to other similar-sized rodents and

that this intermediacy reflected their intermediate dietary position, omnivory. Because dietary choices dictate qualitatively and quantitatively both water intake and energy intake, we hypothesize that omnivorous *Peromyscus* should be intermediate in energy metabolism when compared to similar-sized rodents having more specialized diets (for example, granivorous, herbivorous, carnivorous). This notion that regulatory processes and diet should be interrelated in mammals is not a new one and is examined and supported in detail by McNab (1980). In addition, because so many features of the lives of animals are related to their sizes (that is, they are allometric; for example, Peters, 1983; Calder, 1984), we will stress the relationships between 1) the above-mentioned metabolic variables, 2) diet, and 3) body size (as expressed through mass) in *Peromyscus* compared to other rodents. Throughout this paper we will adhere to the more traditional taxonomic treatment of Rodentia as presented by Hall (1981), rather than that of Honacki *et al.* (1982). Except for analyses already available in the literature (and as cited below) all of the raw data employed in our analyses are provided along with their sources in Tables 1 and 2.

GEOGRAPHIC DISTRIBUTION OF BODY SIZE

“The genus *Peromyscus* is one of the most widespread and geographically variable of North American rodents . . .” occurring in almost every habitat from arctic America in the north to the tropics of extreme southern Panama, and from the Pacific to the Atlantic coasts (Hall, 1981). Within this distribution two discernible patterns of variation in body mass occur with latitude: 1) an overall negative relationship with larger species in the tropical south and small species at higher latitudes, the converse of Bergmann's rule (Fig. 1 and Table 1); and 2) with the possible exception of *Peromyscus californicus*, body mass within the genus is independent of latitude between about 30° and 50° N latitudes, as is particularly exemplified by populations of *P. maniculatus* that nearly span that range (Fig. 1 and Table 1). We must admit, however, that our body mass data are limited to those species and populations for which physiological data exist and we largely ignore *Peromyscus* from latitudes lower than 30° N. However, inspection of standard specimen measurements from Hall (1981) seems to confirm our contention that *Peromyscus* species are larger in size in tropical and subtropical regions of Central and North America, decreasing in size as one proceeds northward. More data on body mass (a seldom-published, yet the

TABLE 1.—Basal metabolic rates, body masses, climatic data, and latitude for *Peromyscus* populations.

Subspecies or population	Body mass (g)	BMR (ml O ₂ /g.h)	Precipitation (cm)	Mean July temp. (°C)	Desert index (°C/cm)	Latitude (°N)	Source
<i>P. boylii</i>	232	2.34	63.0	26.2	0.42	39.8	Mazen and Rudd, 1980
<i>P. californicus</i>							
<i>parasiticus</i>	496	1.17	58.7	16.4	0.28	37.9	McNab and Morrison, 1963
<i>insignis</i>	45.5	1.03	64.4	25.2	0.39	34.2	McNab and Morrison, 1963
Coastal	41.3	1.37	33.8	19.3	0.57	33.5	Mazen and Rudd, 1980
<i>P. crinitus</i>							
<i>stephensi</i>	15.9	1.58	12.3	30.1	2.45	36.2	McNab and Morrison, 1963
<i>pergracilis</i>	20.9	1.48	14.8	25.9	1.75	40.3	McNab and Morrison, 1963
<i>crinitus</i>	13.6	1.33					Kenagy and Vleck, 1982
?	23.1 ¹	0.92				30.0	McNab, 1968
<i>P. eremicus</i>							
Nevada	21.5	1.48	12.3	30.1	2.45	36.2	McNab and Morrison, 1963
New Mexico	19.9	1.60	23.4	25.3	1.12	31.8	McNab and Morrison, 1963
<i>eremicus</i>	24.2	1.45				33.3	Murie, 1961
<i>fraterculus</i>	17.4	1.56	47.1	23.2	0.49	34.1	MacMillen, 1965
Desert	18.4	1.32	12.1	31.3	2.59	34.2	Hulbert <i>et al.</i> , 1985
Intermediate	19.1	1.41	34.8	25.7	0.77	33.8	Hulbert <i>et al.</i> , 1985
<i>P. floridanus</i>	30.8	1.68	121.4	27.7	0.23	29.1	Glenn, 1970
<i>P. gossypinus</i>	21.5	1.72	124.7	27.1	0.22	29.6	Glenn, 1970
<i>P. leucopus</i>							
<i>leucopus</i>	21.2	1.66				42.5	Deavers and Hudson, 1981
<i>novaboracensis</i>	26.0	2.2					Hart, 1953
<i>P. maniculatus</i>							
<i>gambeli</i>	19.1	2.04	58.7	15.4	0.28	37.9	McNab and Morrison, 1963
<i>sonoriensis</i>	24.2	1.67	30.2	23.6	0.78	38.0	McNab and Morrison, 1963
<i>gambeli</i>	20.5	2.55	58.7	15.4	0.28	37.9	Murie, 1961
<i>sonoriensis</i>	20.8	2.28				37.3	Murie, 1961
<i>gracilis</i>	17.0	1.8				44.4	Brower and Cade, 1966
<i>nebrascensis</i>	19.0	2.1	46.7	15.8	0.36	45.2	Hayward, 1965
<i>austerus</i>	19.5	2.0	106.8	17.4	0.16	49.2	Hayward, 1965
<i>sonoriensis</i>	20.0	2.0	14.0	23.2	1.66	37.7	Hayward, 1965
<i>artemisiae</i>	23.0	2.0	29.9	21.1	0.71	49.2	Hayward, 1965
<i>oreas</i>	25.0	1.8	145.2	12.2	0.08	49.2	Hayward, 1965
<i>coolegei</i>	20.8	1.82	7.4	31.1	4.20	28.9	Abbott, 1974
<i>sonoriensis</i>	19.6	1.88	13.3	28.8	2.17	34.6	Abbott, 1974
<i>gambeli</i>	18.5	2.13	32.7	22.1	0.68	33.7	Abbott, 1974
<i>rubidus</i>	19.7	2.26	98.3	15.6	0.16	39.5	Abbott, 1974
<i>austerus</i>	17.3	2.36	62.6	14.0	0.22	48.0	Abbott, 1974
?	16.7	1.74					Kenagy and Vleck, 1982
Chico, CA	17.2	2.56	63.0	26.2	0.42	39.8	Mazen and Rudd, 1980
<i>P. megalops</i>	66.2	1.37				17.6	Musser and Shoemaker, 1965
<i>P. pirrensis</i>	138.0	0.88				9.1	Hill, 1975
<i>P. polionotus</i>	12.0	1.79	135.5	27.3	0.20	29.2	Glenn, 1970
<i>P. sithensis</i>	28.0	1.65	126.1	13.9	0.11	53.3	Hayward, 1965
<i>P. thomasi</i>	110.8	1.12				17.6	Musser and Shoemaker, 1965
<i>P. truei</i>							
<i>truei</i>	33.2	1.53	30.2	23.6	0.78	38.0	McNab and Morrison, 1963
<i>gilberti</i>	33.3	1.88	58.7	16.4	0.28	37.9	McNab and Morrison, 1963

¹Judging from the published body weight, this population was probably misidentified as *P. crinitus*; it was not included in the *P. crinitus* species average value.

TABLE 2.—Basal metabolic rates and body masses of rodent species.

Species	Body mass (g)	BMR (ml O ₂ /g.h)	Source
CRICETINAE (28 species)			
<i>Akodon azarae</i>	23.5	1.70	Haysen and Lacy, 1985
<i>Baiomys taylori</i>	7.3	1.95	Hudson, 1965
<i>Neotoma albigula</i> ¹	161.8	0.735	
High desert	173.0	0.74	Brown and Lee, 1969
Low desert	150.6	0.73	Brown and Lee, 1969
<i>Neotoma cinerea</i> ¹	262.6	0.728	
Coastal	299.0	0.78	Brown and Lee, 1969
Colorado highland	288.9	0.70	Brown and Lee, 1969
California highland	261.0	0.63	Brown and Lee, 1969
High desert	201.3	0.80	Brown and Lee, 1969
<i>Neotoma fuscipes</i>	186.7	0.79	Brown and Lee, 1969
<i>Neotoma lepida</i> ¹	116.4	0.767	
Coastal	138.5	0.72	Brown and Lee, 1969
Intermediate desert	110.3	0.79	Brown and Lee, 1969
Low desert	100.4	0.79	Brown and Lee, 1969
<i>Ochrotomys nuttali</i>	19.5	1.39	Haysen and Lacy, 1985
<i>Onychomys torridus</i>	19.1	1.55	Whitford and Conley, 1971
<i>Peromyscus boylii</i>	23.2	2.34	Mazen and Rudd, 1980
<i>Peromyscus californicus</i> ¹	45.5	1.19	McNab and Morrison, 1963; Hulbert <i>et al.</i> , 1985
<i>Peromyscus crinitus</i> ¹	16.8	1.463	McNab and Morrison, 1963; Kenagy and Vleck, 1982
<i>Peromyscus eremicus</i> ¹	20.1	1.47	Murie, 1961; McNab and Morrison, 1963; Hulbert <i>et al.</i> , 1985; MacMillen, 1965
<i>Peromyscus (Podomys) floridanus</i>	30.8	1.68	Glenn, 1970
<i>Peromyscus gossypinus</i>	21.5	1.72	Glenn, 1970
<i>Peromyscus leucopus</i> ¹	23.6	1.93	Hart, 1953; Deavers and Hudson, 1981
<i>Peromyscus maniculatus</i> ¹	19.9	2.058	Murie, 1961; McNab and Morrison, 1963; Hayward, 1965; Brower and Cade, 1966; Abbott, 1974; Mazen and Rudd, 1980; MacMillen, 1965
<i>Peromyscus megalops</i>	66.2	1.37	Musser and Shoemaker, 1965
<i>Peromyscus (Isthomys) pirrensis</i>	138.0	0.88	Hill, 1975
<i>Peromyscus polionotus</i>	12.0	1.79	Glenn, 1970
<i>Peromyscus sithensis</i>	28.0	1.65	Hayward, 1965
<i>Peromyscus (Megadontomys) thomasi</i>	110.8	1.12	Musser and Shoemaker, 1965
<i>Peromyscus truei</i> ¹	33.3	1.705	McNab and Morrison, 1963
<i>Reithrodontomys megalotis</i> ¹	8.8	2.455	
<i>megabitis</i>	9.0	2.50	Pearson, 1960
<i>longicaudus</i>	7.9	2.63	Thompson, 1985
<i>ravus</i>	9.5	2.235	Thompson, 1985
<i>Sigmodon alleni</i>	137.8	1.475	Bowers, 1971
<i>Sigmodon fulviventer</i>	137.8	1.505	Bowers, 1971

TABLE 2.—(Continued).

Species	Body mass (g)	BMR (ml O ₂ /g.h)	Source
<i>Sigmodon hispidus</i>	139.3	1.654	Bowers, 1971
<i>Sigmodon leucotis</i>	128.6	1.450	Bowers, 1971
<i>Sigmodon ochrognathus</i>	115.1	1.340	Bowers, 1971
MICROTINAE (25 species)			
<i>Apodemus agrarius</i>	21.0	2.27	Deavers and Hudson, 1981
<i>Apodemus flavicolis</i>	30.0	2.28	Deavers and Hudson, 1981
<i>Apodemus sylvaticus</i>	22.0	2.60	Deavers and Hudson, 1981
<i>Arvicola terrestris</i>	97.5	1.16	Deavers and Hudson, 1981
<i>Clethrionomys gapperi</i> ¹	23.4	2.84	
	22.1	2.3	Deavers and Hudson, 1981
	22.9	4.7	Deavers and Hudson, 1981
	23.3	2.08	Deavers and Hudson, 1981
	24.0	3.14	Deavers and Hudson, 1981
	24.9	1.96	Deavers and Hudson, 1981
<i>Clethrionomys glareolus</i> ¹	18.9	2.85	
	17.4	3.2	Deavers and Hudson, 1981
	20.4	2.5	Deavers and Hudson, 1981
<i>Clethrionomys rufocanus</i>	27.5	2.1	Deavers and Hudson, 1981
<i>Clethrionomys rutilus</i>	28.0	2.75	Hayssen and Lacy, 1985
<i>Dicrostonyx groenlandicus</i> ¹	54.0	1.785	
	61.0	1.6	Deavers and Hudson, 1981
	47.0	1.97	Casey <i>et al.</i> , 1979
<i>Lemmus sibiricus</i>	64.0	2.47	Casey <i>et al.</i> , 1979
<i>Microtus arvalis</i>	23.9	2.5	Deavers and Hudson, 1981
<i>Microtus californicus</i>	44.0	1.55	Bradley, in Wunder, 1975
<i>Microtus longicaudus</i> ¹	33.4	2.185	
	25.3	2.67	Deavers and Hudson, 1981
	41.4	1.70	Kenagy and Vleck, 1979
<i>Microtus mexicanus</i>	29.0	1.63	Bradley, in Wunder, 1975
<i>Microtus minutus</i>	8.7	5.0	Hayssen and Lacy, 1985
<i>Microtus montanus</i>	30.8	2.65	Deavers and Hudson, 1981
<i>Microtus nivalis</i>	32.8	2.47	Hayssen and Lacy, 1985
<i>Microtus ochrogaster</i> ¹	46.6	1.693	
	38.5	2.16	Wunder <i>et al.</i> , 1977
	47.4	1.74	Wunder <i>et al.</i> , 1977
	54.0	1.18	Bradley, in Wunder, 1985
<i>Microtus oeconomus</i>	32.0	3.15	Casey <i>et al.</i> , 1979
<i>Microtus pennsylvanicus</i> ¹	35.3	2.21	
	39.0	1.93	Bradley, in Wunder, 1985
	35.6	2.5	Deavers and Hudson, 1981
	31.2	2.2	Deavers and Hudson, 1981
<i>Microtus pinetorum</i>	25.0	1.98	Bradley, in Wunder, 1985
<i>Microtus richardsoni</i>	51.0	1.74	Bradley, in Wunder, 1985
<i>Microtus townsendi</i>	52.2	1.64	Kenagy and Vleck, 1982
<i>Ondatra zibethicus</i> ¹	873.0	0.883	
	1100.0	0.97	Hart, 1962
	869.0	0.80	Fish, 1979
	649.0	0.88	Fish, 1982
<i>Pitymys pinetorum</i> ¹	24.4	2.58	
	22.5	2.6	Deavers and Hudson, 1981
	26.3	2.56	Deavers and Hudson, 1981

TABLE 2.—(Continued).

Species	Body mass (g)	BMR (ml O ₂ /g.h)	Source
HETEROMYIDAE (21 species)			
<i>Dipodomys agilis</i>	60.6	1.050	Hayssen and Lacy, 1985
<i>Dipodomys deserti</i>	104.7	0.898	Hinds and MacMillen, 1985
<i>Dipodomys merriami</i>	35.8	1.257	Hinds and MacMillen, 1985
<i>Dipodomys microps</i>	55.7	1.080	Hayssen and Lacy, 1985
<i>Dipodomys ordii</i>	46.8	1.372	Hinds and MacMillen, 1985
<i>Dipodomys panamintinus</i>	64.2	1.157	Hinds and MacMillen, 1985
<i>Dipodomys anomalus</i>	69.3	1.450	Hayssen and Lacy, 1985
<i>Heteromys desmarestianus</i>	75.8	1.308	Hinds and MacMillen, 1985
<i>Liomys irroratus</i>	44.9	1.341	Hinds and MacMillen, 1985
<i>Liomys salvini</i>	42.7	1.314	Hinds and MacMillen, 1985
<i>Microdipodops megacephalus</i>	11.0	2.743	Hinds and MacMillen, 1985
<i>Microdipodops pallidus</i>	15.2	1.300	Hayssen and Lacy, 1985
<i>Perognathus baileyi</i>	29.1	1.187	Hinds and MacMillen, 1985
<i>Perognathus californicus</i>	22.0	0.970	Hayssen and Lacy, 1985
<i>Perognathus fallax</i>	19.6	1.370	Hinds and MacMillen, 1985
<i>Perognathus flavus</i>	8.3	2.085	Hinds and MacMillen, 1985
<i>Perognathus hispidus</i>	32.0	1.434	Hinds and MacMillen, 1985
<i>Perognathus intermedius</i>	14.6	1.070	Hayssen and Lacy, 1985
<i>Perognathus longimembris</i>	8.0	1.759	Hinds and MacMillen, 1985
<i>Perognathus parvus</i>	19.2	1.719	Hayssen and Lacy, 1985
<i>Perognathus penicillatus</i>	16.0	1.400	Hayssen and Lacy, 1985

¹Calculated (unweighted) average value. For *Peromyscus* species, individual subspecies or populations are listed in Table 1.

most revealing size dimension) of species of the genus clearly are needed to delineate and confirm this suspected relationship between body mass and latitude in *Peromyscus*.

BASAL METABOLIC RATES

The basal metabolic rate (BMR) of an endothermic animal is the rate of metabolism of a fasting adult animal at rest in its thermal neutral zone (Bartholomew, 1982a). Basal rate has long been known to vary in a predictable manner with body mass (Kleiber, 1932) and rather fixed relationships exist between BMR, rate of increase in metabolism below thermal neutrality, and the lower limit of thermal neutrality, which are functions of insulative capacity and physical principles of heat exchange (Scholander *et al.*, 1950a, 1950b, 1950c). In addition, the daily energy expenditure of an animal in nature is definable as BMR plus additives (specific dynamic action, thermoregulation, activity, production), and thus BMR offers an

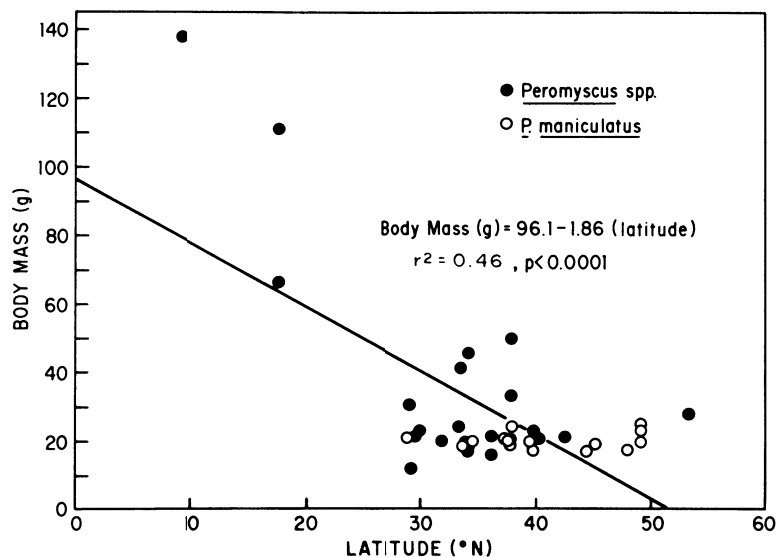


FIG. 1.—Relationship between body mass and latitude in *Peromyscus* populations ($N = 39$ of which 16 are *P. maniculatus*) for which physiological data are available. The line is fit to the data by least-squares regression analysis. The highly significant regression is due to the inclusion of the three largest species.

essential baseline from which to evaluate the rates of energy metabolism that actually exist under natural conditions of stress or activity (Bartholomew, 1982a). As such, BMR is a meaningful index of the metabolic or energetic intensity at which an endotherm lives.

In order to determine the relation of BMR of *Peromyscus* to that of other rodents, we have examined this variable in detail in the murid rodent subfamily Cricetinae to which *Peromyscus* belongs, as well as in the subfamily Microtinae and the family Heteromyidae (Table 2). In many North American habitats representatives of at least two of these three taxa co-occur, resulting in potentially competitive interactions. Figure 2 depicts the allometric relationship between BMR and body mass in these three taxonomic groups. The regression lines are from analysis of covariance, which showed that slopes did not differ significantly among taxa ($P > 0.063$), but all intercepts (elevations) did differ significantly ($P < 0.009$). Using a pooled slope of -0.266 ± 0.057 (± 95 percent confidence interval), intercepts are 5.62 for Microtinae, 3.93 for Cricetinae, and

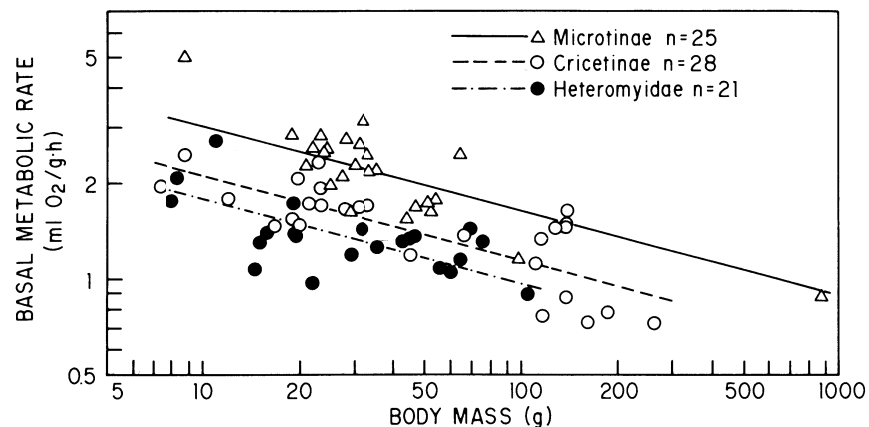


FIG. 2.—Double logarithmic plot of mass-specific basal metabolic rate regressed on body mass in three rodent taxa. Each point represents an average value from the literature for a single species (see Table 2). Regression lines are from analysis of covariance.

3.32 for Heteromyidae. Separate allometric equations for the three taxa are $[BMR (ml O_2/g \cdot h) = \text{Body Mass (g)}^b]$:

$$\text{Microtinae, } 7.61 \div / \times 1.452 M^{-0.351 \pm 0.101}, r^2 = 0.69$$

$$\text{Cricetinae, } 3.59 \div / \times 1.402 M^{-0.243 \pm 0.085}, r^2 = 0.57$$

$$\text{Heteromyidae, } 2.74 \div / \times 1.564 M^{-0.210 \pm 0.129}, r^2 = 0.38$$

Coefficients are followed by 95 percent confidence intervals. The equation for the 14 species of *Peromyscus* ($n = 14$, using species means from Table 2), is $4.21 \div / \times 1.645 M^{-0.288 \pm 0.141}, r^2 = 0.62$.

It is apparent (Fig. 2) that the metabolic intensity of cricetines is intermediate to that of the largely granivorous heteromyids, which is lower, and the nearly exclusively herbivorous microtines, which is higher. Although most of the cricetine BMRs are for *Peromyscus* species, which are omnivorous, also included are representatives of several other genera: *Onychomys* (carnivorous-insectivorous), *Baiomys* and *Reithrodontomys* (probably also omnivorous), and *Neotoma* and *Sigmodon* (herbivorous) (Fig. 3). Thus, either within the genus *Peromyscus* or cricetine genera collectively, most of the dietary items sought by rodents are included in the diets of cricetines. If a relationship exists between diet and BMR, the allometric relationship for BMR of cricetines should not differ from that of rodents in general, regardless of taxonomic affinity; such in fact is the case (Fig. 3). It is interesting to note, however, that of the two chiefly

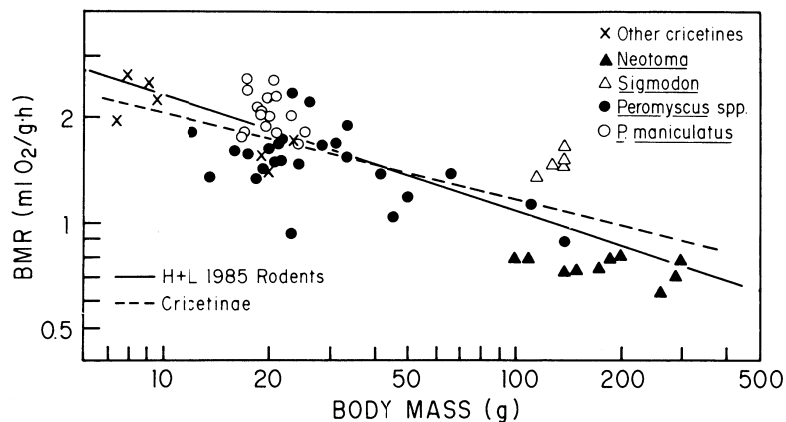


FIG. 3.—Double logarithmic plot of BMR regressed on body mass for species or populations of cricetine rodents. Solid regression line is from Hayssen and Lacy's (1985) equation for 122 species of rodents. Dashed line is the regression for 28 species of Cricetinae (see text).

herbivorous cricetine genera depicted, one (*Neotoma*) has species whose BMRs are rather low and similar to those of heteromyids, whereas the other (*Sigmodon*) apparently exhibits BMRs that are unusually high and similar to those of microtines (Figs. 2, 3). Nevertheless the BMRs of the omnivorous *Peromyscus* are intermediate to those of the dietarily more specialized rodents with whom they co-occur and potentially interact (Fig. 3).

The *Peromyscus* populations for which BMR data are available divide readily into two groups: 1) *Peromyscus maniculatus*, with significantly ($P < 0.0001$) elevated BMRs, and 2) other *Peromyscus* species with lower BMRs (Fig. 4, Table 1). The regression lines are from analysis of covariance, which showed that slopes did not differ significantly for *P. maniculatus* populations ($n = 17$) versus other *Peromyscus* populations ($n = 25$) but the former had significantly higher BMRs ($P = 0.0001$). Using a pooled slope of -0.208 ± 0.121 (± 95 percent confidence interval), intercepts are 3.80 for *P. maniculatus* and 2.93 for other *Peromyscus*. The equation for all *Peromyscus* populations ($n = 42$) is:

$$\text{BMR} = 4.38 \div / \times 1.549 M^{-0.301 \pm 0.135}, r^2 = 0.34$$

The relevance of these intergroup differences in terms of ecological energetics and diet are unclear to us, but *P. maniculatus*, the most ubiquitous species of the genus, appears to operate at a level

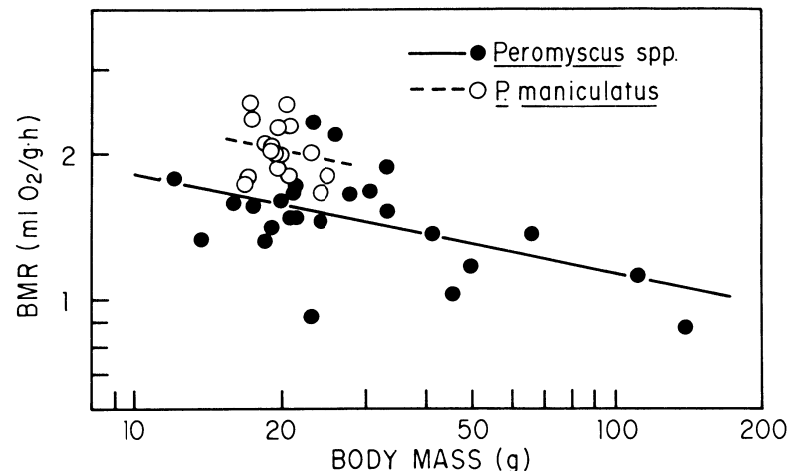


FIG. 4.—Double logarithmic plot of BMR regressed on body mass in *Peromyscus*. Regression lines are from analysis of covariance.

of metabolic intensity that exceeds that of most other species of the genus.

In addition to the strong relationship between body mass and BMR in rodents, climatic conditions, particularly aridity, have been postulated as ultimate (evolutionary) determinants of reduced BMR, especially in burrowing rodents (for example, Hinds and MacMillen, 1985; MacMillen and Lee, 1970; McNab, 1966). McNab and Morrison (1963), in particular, have contended that desert-dwelling *Peromyscus* have reduced BMRs, proposing that the extent of physiological adaptation to desert conditions in *Peromyscus* (the sum of the percentage reduction from allometric expectations of surface-specific thermal conductance and BMR) is sensitive to mean annual rainfall and mean July (summer) temperature, either separately or collectively. As a collective index of aridity McNab and Morrison (1963) proposed the use of a Desert Index [= mean July temperature ($^{\circ}\text{C}$)/mean annual rainfall (cm)]. To determine the relative influences of body mass and geographic or climatic factors, or both on BMR, we conducted a multiple regression analysis of BMR on body mass, mean annual precipitation, mean July temperature, the McNab-Morrison Desert Index, and latitude for 31 populations representing 10 species of *Peromyscus*, from localities between 29° and 53° N latitude and with body mass between 12 and

TABLE 3.—Alternative multiple regression equations for 31 *Peromyscus* populations (data from Table 1).

Dependent variable	Independent variables (% of variance explained) (significance level)
$\text{Log}_{10} \text{BMR} = -\text{Log}_{10} \text{Body mass (28.4) + Precipitation (3.8)}$	(0.0016) (0.2193)
$\text{Log}_{10} \text{BMR} = -\text{Log}_{10} \text{Body mass (28.4) - Temperature (20.8)}$	(0.0001) (0.0021)
$\text{Log}_{10} \text{BMR} = -\text{Log}_{10} \text{Body mass (28.4) - Desert index (11.1)}$	(0.0004) (0.0315)
$\text{Log}_{10} \text{BMR} = -\text{Log}_{10} \text{Body mass (28.4) + Latitude (11.2)}$	(0.0009) (0.0305)

50 grams (Table 1). Precipitation and temperature data were taken from climatic summaries for the weather station nearest to the collecting locality, as given in the following sources: British Columbia Dept. Agriculture (1975), U.S. Dept. Agriculture (1941), and Hastings and Humphrey (1969).

As expected, the single most important correlate of BMR in this analysis is body mass, explaining 28.4 percent of the variability (Table 3). After entering body mass into the multiple regression, an additional significant negative correlation accounting for 20.8 percent of the variability exists between mean July temperature and BMR. Also significantly correlated with BMR are the Desert Index (negative) and latitude (positive), each explaining about 11 percent of the variation. The partial correlation between precipitation and BMR is not significant. If body mass and temperature are entered first into a multiple regression, neither the Desert Index nor latitude (nor precipitation) explains a significant amount of the remaining variance in BMR.

Thus energy metabolism in *Peromyscus* as reflected in BMR appears to be sensitive to high summer temperatures, at least within the intermediate latitudinal range represented by available data. That the reduction in BMR with high midsummer temperature is not actually attributable to aridity rather than temperature per se is demonstrated by the weak and nonsignificant correlation with precipitation. The weak correlation with the Desert Index likely is attributable exclusively to the influence of the temperature component in the index. The results of our analysis are in contrast to those of McNab and Morrison (1963), and we emphasize that the adaptive significance of reduced BMR under conditions of high ambient tem-

perature has yet to be elucidated experimentally. It should be stressed that our analysis and most other studies of relationships between metabolic characteristics and climatic factors have employed only coarse meteorological variables, which may not accurately reflect actual microclimatic conditions encountered by the animals (Gates, 1980).

EVAPORATIVE WATER LOSS

The major avenue of water loss in rodents is by evaporation from the lungs and skin, termed evaporative water loss (EWL; Chew, 1951; Schmidt-Nielsen and Schmidt-Nielsen, 1951). Measurements of EWL in *Peromyscus* are limited to only a few species and are equivalent to, or higher than, those for other rodents of similar size (MacMillen, 1983a). Moderate to rather high rates of EWL in *Peromyscus* are in keeping with their omnivorous diet, which includes a high intake of succulent foods (herbage, fruit, insects), so long as such foods can be found, thereby promoting both positive energy and water balance. The available data on EWL in *Peromyscus* are plotted for comparison with the more extensive data for other mammalian groups in Figure 5. Only measurements made between ambient temperatures of 5° and 25° C are used, because it is within this temperature range that EWL remains nearly constant (Hinds and MacMillen, 1985). The regression line for Eutheria relating mass-specific EWL to body mass is based on 23 species and 40 populations (including three species and five populations of *Peromyscus*), ranging in mass from 16 grams (pallid bat, *Antrozous pallidus*) to 3630 kilograms (Asian elephant, *Elephas maximus*) (from Chew, 1965, as computed by Hinds and MacMillen, 1985). The regression line for heteromyid rodents represents 13 species ranging from 8 to 105 grams (Hinds and MacMillen, 1985). Obviously heteromyids have unusually low rates of EWL, whereas *Peromyscus* species have unusually high rates of EWL, higher even than might be expected given their omnivorous diet. We must emphasize, however, that the data available for *Peromyscus* are largely for populations of *P. maniculatus*, whose BMRs are unusually elevated for *Peromyscus* (Fig. 4). Clearly many more data are required for a variety of species and sizes of *Peromyscus* before meaningful generalizations and comparisons may be made concerning mass-specific rates of evaporative water loss in this group of mammals. Because pulmonary water loss and oxygen consumption ($\dot{V}O_2$) are inter-related in the respiratory process, another commonly-used expression is the ratio of EWL to $\dot{V}O_2$, when the two variables are measured simulta-

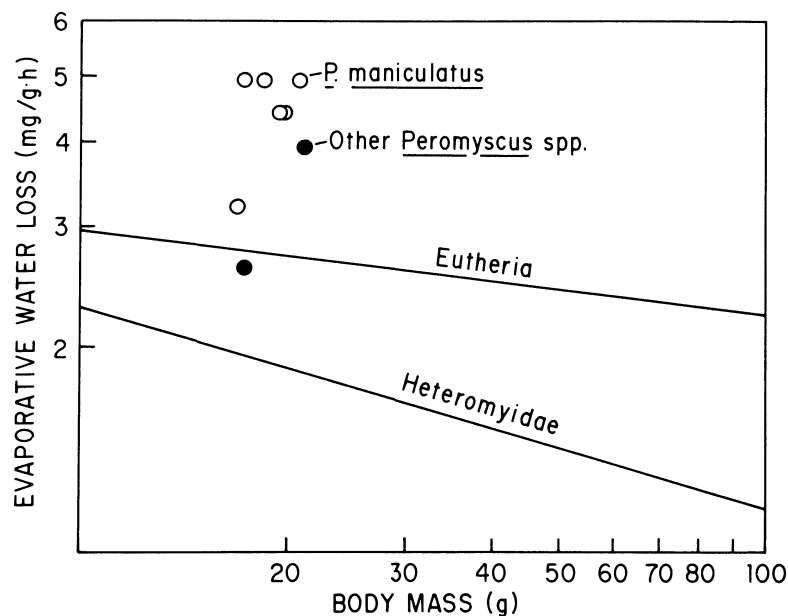


FIG. 5.—Relationship between evaporative water loss (expressed as a function of body mass) and body mass in *Peromyscus* and other mammals. The *Peromyscus* species are given in Table 4. The regression lines are fit to the data for eutherian mammals ($EWL = 3.90 \text{ g}^{-0.122}$) given by Chew (1965), as computed by Hinds and MacMillen (1985), and for heteromyid rodents ($EWL = 4.51 \text{ g}^{-0.295}$) given by Hinds and MacMillen (1985).

neously and across a broad range of ambient temperature (T_a). The regression line (Fig. 6) calculated by MacMillen and Grubbs (1976) for the relation between EWL to $\dot{V}O_2$ ratio and T_a for 23 species representing four families of rodents, which ranged broadly across the spectrum of dietary specialization, included only a single species of *Peromyscus* (*P. eremicus*). For comparison, a separate regression line fit to the data now available for *Peromyscus* (*P. eremicus*, *P. leucopus*, and six subspecies of *P. maniculatus*) is also shown in Figure 6. Again, *Peromyscus* have rather high rates of EWL, about 35 percent greater than those of other rodents. At moderate to high temperatures, the rates of EWL in *P. maniculatus* subspecies are conspicuously higher than those in the other two *Peromyscus* species. If there were a fixed ratio of EWL to $\dot{V}O_2$ for all rodents, the data points should cluster around the regression line for combined rodents in Figure 6. That *Peromyscus* generally fall on or above that

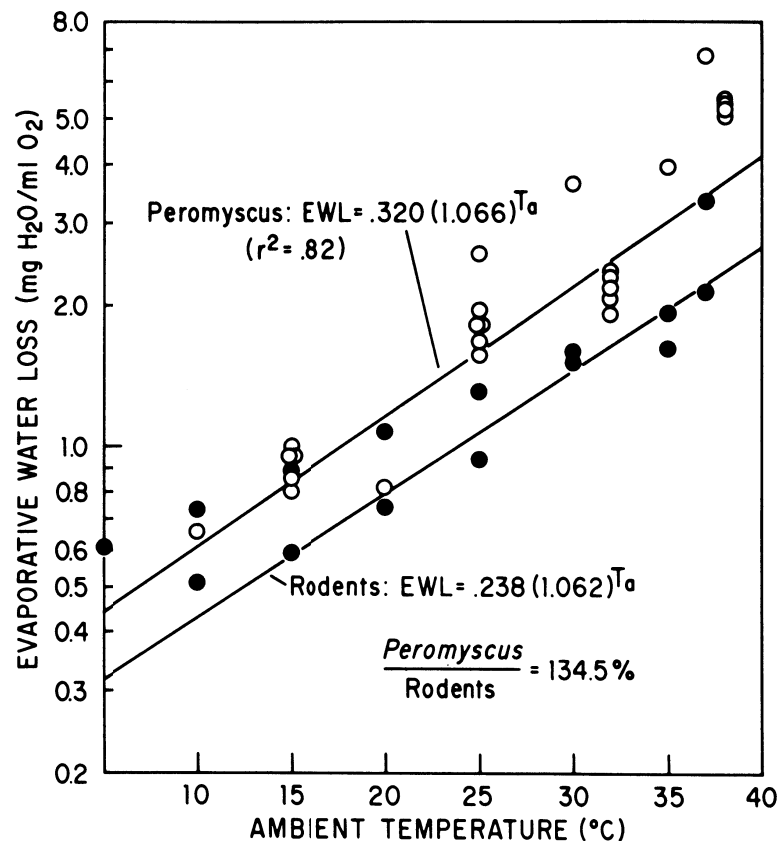


FIG. 6.—Relationship between evaporative water loss (expressed as a function of oxygen consumption) and ambient temperature in *Peromyscus* and other rodents. The regression line for *Peromyscus* is fit by the method of least squares; that for other rodents is from MacMillen and Grubbs (1976). The hollow circles represent measurements for subspecies of *P. maniculatus*, and the filled circles for other *Peromyscus* species as indicated in Table 4.

line is indicative that not only may $\dot{V}O_2$ be elevated, as in *P. maniculatus* (Fig. 4), but that EWL must be disproportionately elevated. Because at least half of these populations of *Peromyscus* are from desert or semi-desert habitats, we conclude that among normothermic rodents *Peromyscus* are quite liberal with regard to water expenditures from evaporative routes.

INTERRELATIONSHIPS BETWEEN ENERGY AND WATER METABOLISM

Metabolic water production (MWP) represents a major component of the water requirements of at least certain granivorous rodents (Howell and Gersh, 1935). MacMillen (1972) was among the first to point out clearly in rodents that 1) at ambient temperatures (T_a) below thermal neutrality, MWP (as translated directly from measures of oxygen consumption = energy metabolism) is negatively related to T_a ; 2) EWL, the chief avenue of water loss, is either positively related to or is independent of T_a ; and 3) for each species a T_a exists at which MWP equals EWL, resulting in positive water balance. These relationships were further refined by MacMillen and Grubbs (1976) who analyzed data for all rodents for which simultaneous measures of $\dot{V}O_2$ (translatable into MWP) and EWL existed. They concluded that differences in T_a at which MWP equals EWL did not exist between desert and non-desert species and that every species of rodent possesses the capacity for preformed water independence (that is, exclusive reliance upon MWP) at some moderate to low T_a , depending upon the species and the composition of the energy source being oxidized. More recently, MacMillen and Hinds (1983) applied this concept to representative species of all genera of the chiefly granivorous family Heteromyidae and demonstrated that these dietary specialists on seeds achieve equality of MWP and EWL at relatively high T_a s. Heteromyids, therefore, commonly meet their water needs under laboratory conditions from MWP while oxidizing carbohydrate-rich seeds, augmented by the small amount of preformed water they contain. MacMillen and Hinds (1983) defined as an index of water regulatory efficiency as that T_a at which MWP equals EWL, based upon the compositional ratio (protein:lipid:carbohydrate) of the oxidative substrate and the metabolic water yield of that composition. Species with a higher T_a at which MWP equals EWL are more efficient than those with a lower T_a at which MWP equals EWL.

If there is a strict relationship between the degree of dietary specialization and water regulatory efficiency as defined above and as suggested by MacMillen (1983a), we would anticipate that omnivores such as *Peromyscus* would be less efficient than granivorous heteromyids but more efficient than strict herbivores or insectivore-carnivores that subsist on succulent diets. By the same token we would anticipate that water regulatory efficiency in *Peromyscus* would compare closely with that of rodents in general, for the latter represent a broad range of diets (that is, equivalent to omnivory).

The EWL data from Figure 6 for *Peromyscus* can be transformed into the ratio MWP to EWL by assuming oxidation of a standard seed, for example, millet (13.5 percent protein, 5.1 percent lipid, 81.4 percent carbohydrate) from which the consumption of 1 milliliter of oxygen yields 0.62 milligrams of metabolic water (MacMillen and Hinds, 1983). Regression lines for the limited data available for *Peromyscus*, the more extensive data for heteromyids (MacMillen and Hinds, 1983), and data for 23 species in other rodent groups (MacMillen and Grubbs, 1976) are shown in Figure 7. These three groups rank in water regulatory efficiency as follows: heteromyids (T_a at MWP = EWL = 19.8°C) are greater than rodents in general (T_a at MWP = EWL = 16.1°C) which are greater than *Peromyscus* (T_a at MWP = EWL = 10.3°C). That *Peromyscus*

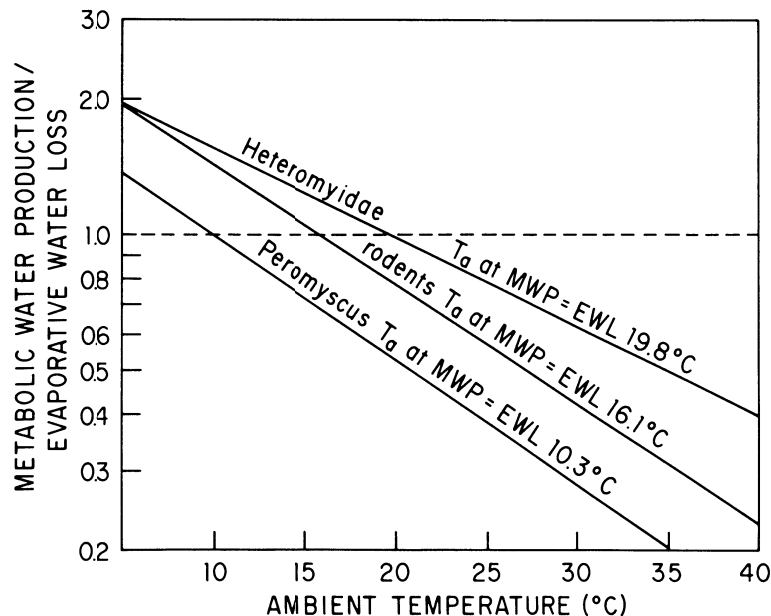


FIG. 7.—Relationship between metabolic water production (MWP)/evaporative water loss (EWL) and ambient temperature (T_a) in heteromyid rodents [MWP/EWL = 2.493(0.955) T_a ; MacMillen and Hinds, 1983], rodents in general [MWP/EWL = 2.618(0.942) T_a ; MacMillen and Hinds, 1976], and *Peromyscus* species as indicated in Table 4 [MWP/EWL = 1.932(0.938) T_a]. The index of water regulatory efficiency for each group is defined as that T_a at which the regression line intercepts the line of unity (dashed line) at which MWP = EWL.

appear to be less efficient than rodents in general may well be a sampling artifact, as very few dietary specialists on succulent foods were available for rodents in general, and data for the most efficient *Peromyscus*, *P. crinitus* (MacMillen, 1983a), were not available. However, the fact that *Peromyscus* appear to have relatively high rates of EWL (Fig. 5) but intermediate rates of metabolism (Fig. 3) suggests that they may have as a genus low indices of water regulatory efficiency among rodents. Clearly *Peromyscus* are not highly efficient with regard to water regulation while subsisting on a dry-seed diet. In addition, their relative inefficiency is in keeping with their typically omnivorous diet that normally provides the necessary preformed water input to compensate for rather high rates of water loss. As a cautionary note, only heteromyids (MacMillen and Hinds, 1983) have had critical analysis of the relationship between MWP and EWL, requiring simultaneous measurements of $\dot{V}O_2$ and EWL. Although there are measurements of $\dot{V}O_2$ for many rodent species, few investigators have bothered to obtain the easily-made measurements of EWL. In particular, the available data for *Peromyscus* are insufficient for broad comparisons, and simultaneous measurements of $\dot{V}O_2$ and EWL are almost completely lacking for such rodent specialists on succulent diets as *Microtus*, *Neotoma*, and *Onychomys*.

In heteromyid rodents, MacMillen and Hinds (1983) demonstrated not only an unusually high degree of water regulatory efficiency, but also that the index of water regulatory efficiency (T_a at MWP = EWL) scales negatively with body mass, especially among quadrupedal species. This scaling regression equation for heteromyids is T_a at MWP = EWL = $29.682g^{-0.137}$. Comparisons of water regulatory efficiency of individual *Peromyscus* populations with the heteromyid regression line relating the index of water regulatory efficiency to body mass (Fig. 8, Table 4) demonstrate that even when body mass is accounted for, *Peromyscus* are still far less efficient in water regulation than heteromyids. The relative inefficiency with regard to water regulation in *Peromyscus* is even more apparent when the individual regression lines relating the quotient of MWP and EWL to T_a in *Peromyscus* are compared to those of heteromyids (Fig. 9, Table 4). Even the most efficient *Peromyscus* (a desert population) is a poorer water regulator than the least efficient heteromyid (a tropical population). We must reiterate, however, that data on water regulatory efficiency are not available for *P. crinitus*, whose ability to tolerate water deprivation while subsist-

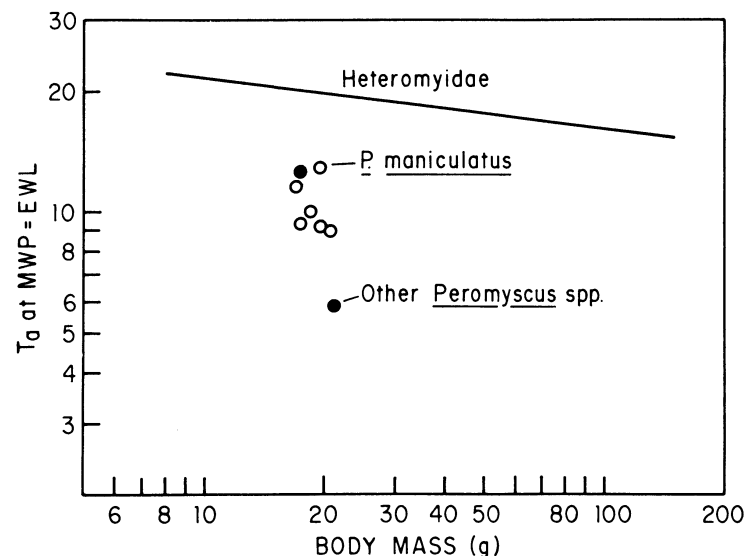


FIG. 8.—Relationship between the index of water regulatory efficiency (T_a at MWP = EWL) and body mass in heteromyid rodents (solid line; based on MacMillen and Hinds, 1983) and in species of *Peromyscus* listed in Table 4.

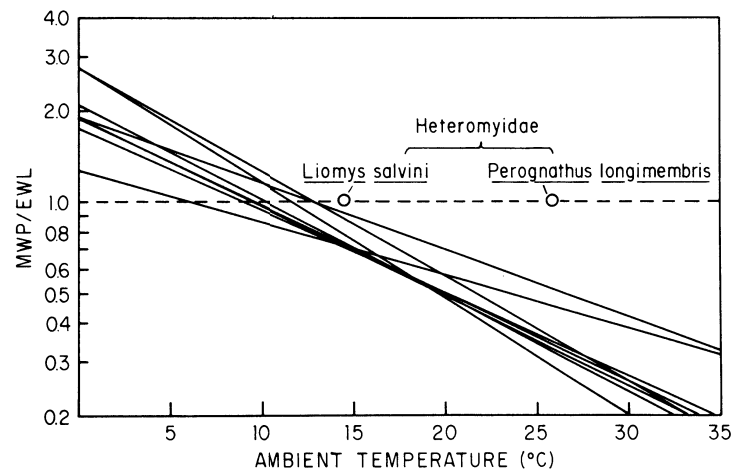


FIG. 9.—Relationship between MWP/EWL and T_a in *Peromyscus* and in the least efficient (*L. salvini*) and most efficient (*P. longimembris*) heteromyid rodents. Equations for the regression lines fit to the *Peromyscus* data are given in Table 4. The horizontal dashed line represents unity between MWP and EWL. Hollow circles represent the indices of water regulatory efficiency (T_a at MWP = EWL) for the two heteromyids.

TABLE 4.—Body mass, index of water regulatory efficiency (T_a when $MWP = EWL$), and regression equations relating MWP/EWL to T_a in *Peromyscus* and two heteromyid species (see Figs. 8 and 9).

Species	Body mass (g)	T_a when $MWP = EWL$ (°C)		Regression equation	Source
		T_a	$MWP = EWL$		
CRICETIDAE					
<i>Peromyscus eremicus</i>	17.4	12.7		$MWP/EWL = 1.887(0.951) T_a$	MacMillen, 1965
<i>P. leucopus</i>	22.1	5.7		$MWP/EWL = 1.247(0.962) T_a$	Deavers and Hudson, 1981
<i>P. maniculatus austerus</i>	17.3	9.4		$MWP/EWL = 1.849(0.937) T_a$	Abbott, 1974
<i>P. m. coolegei</i>	20.8	9.0		$MWP/EWL = 1.749(0.940) T_a$	Abbott, 1974
<i>P. m. gambelii</i>	18.5	10.0		$MWP/EWL = 2.040(0.931) T_a$	Abbott, 1974
<i>P. m. gracilis</i>	17.0	11.6		$MWP/EWL = 2.774(0.916) T_a$	Brower and Cade, 1966
<i>P. m. rubidus</i>	19.7	9.2		$MWP/EWL = 1.842(0.936) T_a$	Abbott, 1974
<i>P. m. sonoriensis</i>	19.6	12.9		$MWP/EWL = 2.776(0.924) T_a$	Abbott, 1974
HETEROMYIDAE					
<i>Liomys satzumi</i>	42.7	14.4		$MWP/EWL = 2.021(0.952) T_a$	MacMillen and Hinds, 1983
<i>Perognathus longimembris</i>	8.0	25.8		$MWP/EWL = 4.521(0.942) T_a$	MacMillen and Hinds, 1983

ing on air-dry millet far exceeds that of other *Peromyscus* that have been studied and is equivalent to that of some of the more efficient heteromyids (MacMillen, 1983a).

In summary, in regard to water regulatory efficiency as herein defined, *Peromyscus* species appear to be rather inefficient compared to rodents in general. Their lack of well-developed physiological capacities for efficient water regulation is compensated for by an omnivorous diet which ensures adequate inputs of both energy and water. However, because of insufficient data for species that subsist on more succulent diets, it remains to be positively demonstrated that *Peromyscus* are actually intermediate among rodents in general with regard to water regulatory efficiency.

CONCLUSIONS

With respect to metabolic rate and evaporative water loss, both being physiological variables useful in gauging levels of regulatory efficiencies, *Peromyscus* are rather unspectacular among rodents, being neither extremely efficient nor extremely inefficient. This apparent physiological intermediacy is consistent with an omnivorous diet that provides substantial flexibility in meeting both energy and water needs, even under restrictive situations imposed by climate, competitive interactions, or both. It likely is this flexibility that helps explain the paradox of the ubiquity in North America of this unspecialized genus, whose species inhabit virtually every terrestrial situation regardless of degree of environmental rigor and often co-occur with other rodents (for example, *Dipodomys* and *Perognathus* spp.) whose physiological specializations are credited for their survival under demanding circumstances. In this regard *Peromyscus* are spectacular examples of the success of physiologically unspectacular animals, demonstrating that such generalists are as capable of coping with rigorous circumstances as are rodents with greater physiological specializations.

We believe the success of *Peromyscus* in inhabiting harsh environments in the absence of apparent specializations may be attributed to their omnivorous diets and their employment of torpor to escape, either seasonally or for shorter times, periods of environmental stress. At least among the smaller species of *Peromyscus* (less than 40 grams) torpor provides temporary relief from demanding circumstances related either to energy or water regulation, and its utility is discussed in some detail in Hill (1983) and MacMillen (1983a). Torpor has been viewed historically as a physiological specialization in the extreme, but its common occurrence among

smaller mammalian and avian species of widely separated taxa (McNab, 1983) argues that it more likely is a general endothermic phenomenon associated with small body size. Torpor differs in various endothermic species both with regard to temporal patterns and depths of hypothermia (Bartholomew, 1982*b*), and the degree of complexity of this patterning we believe represents the specialization of this more general phenomenon. Torpor in *Peromyscus* appears to be of a very non-specialized nature, being basically limited to successive diurnal bouts and involving only moderate hypothermia; nevertheless, it provides effective relief from otherwise intolerable conditions (Hill, 1983; MacMillen, 1983*a*).

McNab (1983) proposed the concept of a minimal boundary curve for endothermy that relates BMR to body mass, with the notion that species falling below that curve frequently employ torpor. Among rodents, with the exception of microtines, nearly all species with masses less than 40 grams for which data exist have BMRs that fall below this minimal boundary curve. However, an equally valid and biologically reasonable interpretation is that in rodents, with the exception of microtines, a body mass threshold exists at about 40 grams, below which species may commonly employ torpor and above which torpor is far less commonly employed. In these small species having high mass-relative energy and water needs while normothermic, ecologically stressful periods may occur frequently enough to result in morbidity unless survival alternatives exist; torpor (or hypothermia) is such an alternative, reducing energy and water requirements to levels consistent with their availability during temporarily stressful periods.

The concept of a size-related threshold for torpor has been applied effectively to heteromyid rodents (MacMillen, 1983*b*; MacMillen and Hinds, 1983). Herein we apply the same concept to *Peromyscus*. We believe that larger (greater than 40 grams) *Peromyscus* species abundant in subtropical and tropical regions of greater resource (food and water) availability throughout the year, where normothermic survival is accompanied by few risk-related constraints with regard to energy and water regulation. In proceeding from tropical to subtropical settings with increasing seasonality, body mass of *Peromyscus* decreases consistently with seasonally-determined levels of energy and water production, assuming normothermia and physiological generalization. At about 30° N latitude, continuous normothermia becomes locally incompatible with seasonally-stressful periods (aridity, low temperatures, or both) in spite of reductions in body mass to less than 40 grams and accom-

panying reductions in absolute energy and water needs. At this point torpor provides the necessary physiological relief to ensure survival. Once the size threshold for torpor has been achieved, environmental conditions leading to energy and water stresses can be ameliorated by torpor without further reduction in body mass. This view is consistent with the apparent relationship between body mass and latitude in *Peromyscus* (Fig. 1), and with the ubiquity of this biologically generalized genus throughout North America. We propose this view not as a proven fact, but as an internally consistent hypothesis whose testing should bear fruitful results.

A question arises, however, concerning the positioning of this size threshold for torpor in both *Peromyscus* and heteromyids at about 40 grams, particularly considering the frequent use of torpor by sciurids that exceed (often considerably) 40 grams in mass. We have no answer based on experimental evidence to this question, but propose that the difference lies in the capacity of sciurids to store fat, often to the point of obesity, as an energy reserve to draw upon during the torpor period. *Peromyscus* and heteromyids lack this conspicuous fat storage capacity and must rely upon lower-energy food stores in or near nest chambers. These relationships between body mass, use of torpor, and quantity, quality, and site of storage of energy reserves drawn upon during the torpor period merit further investigation.

Finally, we should emphasize that, because of their generalized biological characteristics and success in occupying a wide range of habitats, *Peromyscus* are ideal mammalian models to employ in investigations of many of the questions in physiological ecology that remain unsolved. Frequently such questions have arisen in studies of more specialized rodents whose degrees of specialization together with frequent rarity and limited distributions make them less tractable for study. Following are some of the problems that could be addressed profitably by employing *Peromyscus* as model study organisms. First, what is the relationship between basal metabolic rate, as commonly measured in laboratory studies, and daily energy expenditures (DEE) in the field, as determined using doubly-labelled water techniques? Do species with a high BMR, such as *P. maniculatus*, necessarily have a high DEE? Conversely, does a low BMR necessarily translate into low total energy requirements in nature? Similarly, what is the relationship between "basal" evaporative water loss and actual field water-turnover rates? What is the functional significance of basal metabolic rate? Does a correlation,

perhaps indicating a causal or at least a permissive relationship, exist between BMR and 1) maximal rates of oxygen consumption, which would have consequences for locomotor endurance; 2) summit metabolism, which would have consequences for thermoregulatory abilities; 3) rates of evaporative water loss; 4) reproductive and growth rates; 5) ability to detoxify plant secondary compounds or invertebrate toxins encountered in the diet. We suggest that examining such correlations in relation to ecological, life history, and phylogenetic factors would be fruitful not only in increasing our understanding of the biology of *Peromyscus* but of small mammals and their adaptive physiologies in general.

ACKNOWLEDGMENTS

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LITERATURE CITED

- ABBOTT, K. D. 1974. Ecotypic and racial variation in the water and energy metabolism of *Peromyscus maniculatus* from the western United States and Baja California, Mexico. Unpubl. Ph.D. dissert., Univ. California, Irvine, 155 pp.
- BARTHOLOMEW, G. A. 1982a. Energy metabolism. Pp. 46–93, in *Animal physiology, principles and adaptations* (Fourth ed.) (M. S. Gordon, ed.). Macmillan Publ. Co., New York, 635 pp.
- . 1982b. Body temperature and energy metabolism. Pp. 333–406, in *Animal physiology, principles and adaptations* (Fourth ed.) (M. S. Gordon, ed.). Macmillan Publ. Co., New York, 635 pp.
- BOWERS, J. R. 1971. Resting metabolic rate in the cotton rat: *Sigmodon*. *Physiol. Zool.*, 44: 137–147.
- BRITISH COLUMBIA DEPARTMENT OF AGRICULTURE. 1975. *Climate of British Columbia*. 85 pp.
- BROWER, J. E., AND T. J. CADE. 1966. Ecology and physiology of *Napaeozapus insignis* (Miller) and other woodland mice. *Ecology*, 47: 46–63.
- BROWN, J. H., AND A. K. LEE. 1969. Bergmann's rule and climatic adaptation in woodrats (*Neotoma*). *Evolution*, 23: 329–338.
- CALDER, W. A., III. 1984. *Size, function and life history*. Harvard Univ. Press, Cambridge, Massachusetts, 431 pp.
- CASEY, T. M., P. C. WITHERS, AND K. K. CASEY. 1979. Metabolic and respiratory

- responses of Arctic mammals to ambient temperature during the summer. *Comp. Biochem. Physiol.*, 64A: 331–341.
- CHEW, R. M. 1951. The water exchanges of some small mammals. *Ecol. Monogr.*, 21: 215–225.
- . 1965. Water metabolism in mammals. Pp. 43–178, in *Physiological mammalogy*. Vol. 2 (W. V. Mayer and R. G. Van Gelder, eds.). Academic Press, New York, 326 pp.
- DEAVERS, D. R., AND J. W. HUDSON. 1981. Temperature regulation in two rodents (*Clethrionomys gapperi* and *Peromyscus leucopus*) and a shrew (*Blarina brevicauda*) inhabiting the same environment. *Physiol. Zool.*, 54: 94–108.
- FISH, F. E. 1979. Thermoregulation in the muskrat (*Ondatra zibethicus*): the use of regional heterothermia. *Comp. Biochem. Physiol.*, 64A: 391–397.
- . 1982. Aerobic energetics of surface swimming in the muskrat *Ondatra zibethicus*. *Physiol. Zool.*, 55: 180–189.
- GATES, D. M. 1980. *Biophysical ecology*. Springer-Verlag, New York, 611 pp.
- GLENN, M. E. 1970. Water relations in three species of deer mice (*Peromyscus*). *Comp. Biochem. Physiol.*, 33: 231–248.
- HALL, E. R. 1981. *The mammals of North America*. John Wiley & Sons, New York, 1: xv + 1–600 + 90 and 2: vi + 601–1181 + 90.
- HART, J. S. 1953. Energy metabolism of the white-footed mouse, *Peromyscus leucopus leucopus*, after acclimation at various environmental temperatures. *Canadian J. Zool.*, 31: 99–105.
- . 1962. Mammalian cold acclimation. Pp. 203–213, in *Comparative physiology of temperature regulation*. Vol. 2 (P. Hannon and E. Viereck, eds.). Arctic Aeromedical Laboratory, Fort Wainwright, Alaska, 278 pp.
- HASTINGS, J. R., AND R. R. HUMPHREY. 1969. Climatological data and statistics for Baja California. Tech. Rept. on Meteorology and Climatology, No. 18. Univ. Arizona Inst. Atmospheric Physics, 96 pp.
- HAYSSEN, V., AND R. C. LACY. 1985. Basal metabolic rates in mammals, taxonomic differences in the allometry of BMR and body mass. *Comp. Biochem. Physiol.*, 81A: 741–754.
- HAYWARD, J. S. 1965. Metabolic rate and its temperature-adaptive significance in six geographic races of *Peromyscus*. *Canadian J. Zool.*, 43: 309–323.
- HILL, R. W. 1975. Metabolism, thermal conductance, and body temperature in one of the largest species of *Peromyscus*, *P. pirrensis*. *J. Thermal Biology*, 1: 109–112.
- . 1983. Thermal physiology and energetics of *Peromyscus*; ontogeny, body temperature, metabolism, insulation, and micro-climatology. *J. Mamm.*, 64: 19–37.
- HINDS, D. S., AND R. E. MACMILLEN. 1985. Scaling of energy metabolism and evaporative water loss in heteromyid rodents. *Physiol. Zool.*, 58: 282–298.
- HONACKI, J. H., K. E. KINMAN, AND J. W. KOEPL (EDS.). 1982. *Mammal species of the world*. Allen Press and Assoc. Syst. Collections, Lawrence, Kansas, 694 pp.
- HOWELL, A. B., AND I. GERSH. 1935. Conservation of water by the rodent *Dipodomys*. *J. Mamm.*, 16: 1–9.
- HUDSON, J. W. 1965. Temperature regulation and torpidity in the pygmy mouse, *Baiomys taylori*. *Physiol. Zool.*, 38: 243–254.
- HULBERT, A. J., D. S. HINDS, AND R. E. MACMILLEN. 1985. Minimal metabolism,

- summit metabolism and plasma thyroxine in rodents from different environments. *Comp. Biochem. Physiol.*, 81A:687–693.
- KENAGY, G. J., AND D. VLECK. 1982. Daily temporal organization of metabolism in small mammals: adaptation and diversity. Pp. 322–338, in *Vertebrate circadian systems* (J. Aschoff, S. Dean, and G. Groos, eds.). Springer-Verlag, Berlin, 363 pp.
- KING, J. A. (ED.). 1968. *Biology of Peromyscus* (Rodentia). *Spec. Publ., Amer. Soc. Mamm.*, 2:1–593.
- KLEIBER, M. 1932. Body size and metabolism. *Hilgardia*, 6:315–353.
- MACMILLEN, R. E. 1965. Aestivation in the cactus mouse, *Peromyscus eremicus*. *Comp. Biochem. Physiol.*, 16:227–248.
- . 1972. Water economy of nocturnal desert rodents. *Symp. Zool. Soc. Lond.*, 31:147–174.
- . 1983a. Water regulation in *Peromyscus*. *J. Mamm.*, 64:38–47.
- . 1983b. Adaptive physiology of heteromyid rodents. *Great Basin Nat. Memoirs*, 7:65–76.
- MACMILLEN, R. E., AND D. E. GRUBBS. 1976. Water metabolism in rodents. Pp. 63–69, in *Progress in animal biometeorology*. Vol. 1, Part 1 (D. H. Johnson, ed.). Swetz and Zeitlinger, Lisse, The Netherlands, 603 pp.
- MACMILLEN, R. E., AND D. S. HINDS. 1983. Water regulatory efficiency in heteromyid rodents: a model and its application. *Ecology*, 64:152–164.
- MACMILLEN, R. E., AND A. K. LEE. 1970. Energy metabolism and pulmonary water loss of Australian hopping mice. *Comp. Biochem. Physiol.*, 35:355–369.
- MAZEN, W. S., AND R. L. RUDD. 1980. Comparative energetics in two sympatric species of *Peromyscus*. *J. Mamm.*, 61:573–574.
- McNAB, B. K. 1966. The metabolism of fossorial rodents: a study in convergence. *Ecology*, 47:712–733.
- . 1968. The influence of fat deposits on the basal rate of metabolism in desert homoiotherms. *Comp. Biochem. Physiol.*, 26:337–343.
- . 1980. Food habits, energetics, and the population biology of mammals. *Amer. Nat.*, 116:106–124.
- . 1983. Energetics, body size, and the limits to endothermy. *J. Zool.*, 199:1–29.
- McNAB, B. K., AND P. MORRISON. 1963. Body temperature and metabolism in subspecies of *Peromyscus* from arid and mesic environments. *Ecol. Monogr.*, 33:63–82.
- MURIE, M. 1961. Metabolic characteristics of mountain, desert and coastal populations of *Peromyscus*. *Ecology*, 42:723–740.
- MUSSER, G. G., AND V. H. SHOEMAKER. 1965. Oxygen consumption and body temperature in relation to ambient temperature in the Mexican deer mice, *Peromyscus thomasi* and *P. megalotis*. *Occas. Papers Mus. Zool., Univ. Mich.*, 643:1–15.
- PEARSON, O. P. 1960. The oxygen consumption and bioenergetics of harvest mice. *Physiol. Zool.*, 33:152–160.
- PETERS, R. H. 1983. *The ecological implications of body size*. Cambridge Univ. Press, Cambridge, 324 pp.
- SCHMIDT-NIELSEN, B., AND K. SCHMIDT-NIELSEN. 1951. A complete account of the water metabolism in kangaroo rats and an experimental verification. *J. Cell. Comp. Physiol.*, 38:165–182.

- SCHOLANDER, P. F., R. HOCK, V. WALTERS, AND L. IRVING. 1950a. Adaptations to cold in arctic and tropical mammals and birds in relation to body temperature, insulation and basal metabolic rate. *Biol. Bull.*, 99:259–271.
- SCHOLANDER, P. F., R. HOCK, V. WALTERS, F. JOHNSON, AND L. IRVING. 1950b. Heat regulation in some arctic and tropical mammals and birds. *Biol. Bull.*, 99:236–258.
- SCHOLANDER, P. F., V. WALTERS, R. HOCK, AND L. IRVING. 1950c. Body insulation of some arctic and tropical mammals and birds. *Biol. Bull.*, 99:225–236.
- THOMPSON, S. D. 1985. Subspecific differences in metabolism, thermoregulation, and torpor in the western harvest mouse *Reithrodontomys megalotis*. *Physiol. Zool.*, 58:430–444.
- U.S. DEPARTMENT OF AGRICULTURE. 1941. *Climate and Man*. U.S. Govt. Printing Office, 1248 pp.
- WHITFORD, W. G., AND M. I. CONLEY. 1971. Oxygen consumption and water metabolism in a carnivorous mouse. *Comp. Biochem. Physiol.*, 40A:797–803.
- WUNDER, B. A. 1975. A model for estimating metabolic rate of active or resting mammals. *J. Theor. Biol.*, 49:345–354.
- . 1985. Energetics and thermoregulation. Pp. 812–844, in *Biology of New World Microtus* (R. H. Tamarin, ed.). *Spec. Publ., Amer. Soc. Mamm.*, 8:1–892.
- WUNDER, B. A., D. S. DOBKIN, AND R. D. GETTINGER. 1977. Shifts of thermogenesis in the prairie vole (*Microtus ochrogaster*), strategies for survival in a seasonal environment. *Oecologia*, 29:11–26.