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A reexamination of the metabolic response of *Peromyscus* to a climatic gradient

Brian K. McNab

Department of Biology, University of Florida

Gainesville, FL 32611, USA

Correspondent: bkm@ufl.edu

There is no conflict of interest

Significance: A clear demonstration of the physiological response of a genus of mammal to a climatic gradient with a potential impact of climate change.

Abstract: An earlier analysis demonstrated that the mass-independent energy expenditure of four species of rodents of the genus *Peromyscus* decreased with increasing aridity along a mesic/xeric climatic gradient. Each species was represented by two populations that were located along the gradient. These data are reexamined with new analytical techniques. A mass analysis accounted for the basal rates of six populations within 10% of the measured rates. The analysis accounted for the rates of all eight populations within 10% when it included the gradient. An apparent limit to this response may restrict the geographic distributions of *Peromyscus* in desert environments, which may have distributional and survival consequences with climate change. One species, *P. californicus* (Gambel, 1848), did not conform to the analysis of the other species. That may reflect the presence of unidentified biological or environmental factors present in this and the other species. A successful analysis of the energy expenditures of species must include their characteristics and those of the environment in which they live because these are the factors that define species and their performance. To determine the effectiveness of an analysis, the estimated expenditures are compared to the measured expenditures, acceptable estimates being within 10% of the measured expenditures.

Key words: basal rate of metabolism, climate change, deer mice, distribution, mesic/xeric gradient, *Peromyscus*, quantitative analyses

Introduction

Appropriate responses of organisms to the requirements and opportunities encountered in an environment are fundamental to their survival. The first attempt to examine the response of mammals to climate was by Bergmann (1847) who argued that they were larger at high latitudes to reduce the surface to volume ratio, thereby reducing heat loss. Allen (1877) suggested that mammals in cold climates reduce heat loss by reducing surface areas. Scholander et al. (1950*a, b, c*) were the first to examine the energy expenditure of birds and mammals for a potential response to climate, in this case the thermal gradient between Panama and Alaska. A correlation between their energy expenditures and climate was not demonstrated. In fact, they concluded that the basal rate is "... phylogenetically non-adaptive to external conditions" (Scholander et al. 1950*c*, p. 265). As it turns out, the response to climate is subtle. Because no species of bird or mammal in arctic Alaska has a close relative in Panama, their differences may have masked any climatic correlation that exists. The first demonstration of a quantitative response of energetics to climate was in a group of closely related rodents distributed along a mesic/xeric gradient (McNab and Morrison 1963).

Original analysis

Five species of deer mice, belonging to the genus *Peromyscus*, were studied. Four, *P. maniculatus* (Wagner, 1845), *P. truei* (Shufeldt, 1885), *P. crinitus* (Merriam, 1891), and *P. californicus*, were represented by two subspecies found at different

locations along the gradient and a fifth, *P. eremicus* (Baird, 1855), had the same subspecies in two different environments (Table 1). I caught individuals from eight of the 10 populations in the field, *P. e. eremicus* was obtained in the field from W. Reeder at Malpais Springs, New Mexico, and *P. crinitus pergracilis* were provided by H. J. Egoscue from a captive colony at the Dugway Proving Grounds, Utah. Energy expenditures were measured as oxygen consumption over a range of ambient temperatures with a Beckman oxygen analyzer (for details see McNab and Morrison 1963).

The scaling of their basal rates encountered a complication. The two populations of *P. californicus* have low mass-independent basal rates compared to the other four species (Fig. 1). Although this species is large for this genus, its low basal rate does not simply reflect scaling. Two of the other species, *P. maniculatus* and *P. truei*, have high basal rates by general mammalian standards at Berkeley, California, where they encounter one of the populations of *P. californicus* (Fig. 2).

The response of *Peromyscus* to climate was originally described with the limited methods available at the time of its discovery and publication. The response to xeric conditions is demonstrated by the decrease in the mass-independent basal rate as a function of an index of aridity (Fig. 1). However, the original demonstration was much more obscure than seen in Figure (1). The index (I) was the mean July temperature at a locale divided by its mean annual rainfall, data for which were obtained from U.S. Dept. Agriculture (1941), U.S. Weather Bureau (1949-1959), and Vaughan (1954). Xeric conditions increase with temperature and a decrease with rainfall. The gradient, as measured by the index, varied from 0.28 to

2.47 (°C/[cm water])). A limitation to this analysis was that there was no means at the time to incorporate the index into a quantitative analysis of the performance of species. Therefore, the analysis was not able to compare estimates of basal rate with measured values to judge the accuracy of the analysis.

Revised analysis

The distinctive energy expenditure of *P. californicus* needs to be examined. If its two populations are included with the other four species and their eight populations, no statistically significant relationship exists between basal rate and the index ($P = 0.908$). This is demonstrated by the dashed curve in Figure (1). An “objective” conclusion, therefore, might be that no relationship exists between these variables, but that ignores the obvious relationship in the four other species. Why does this incongruity occur? To answer this question, *P. californicus* is examined separately, whereas the four species are analyzed as a unit.

The impact of body mass in the presence of the gradient is complicated (Fig. 2). In the four species, body mass only accounts for 85.4% of the variation in the BMR ($P = 0.0012$), using equation (1) as the standard. The low r^2 reflects a limited range in mass (2:1), whereas the range in the gradient is large (9:1):

$$\text{BMR (mLO}_2\text{/h)} = 1.44 \text{ mass}^{1.04}. \quad (1)$$

This analysis estimated the variation of basal rate of three of the eight populations within 5% of the measured rates and in six within 10%. The large power of mass results from combining small desert species with large mesic and desert-mountain species (Fig. 2). That is, the interaction of body mass and the gradient determines

the power of mass. This interaction cautions against assuming that a fixed power for mass exists.

From an all-mammal mass scaling curve (McNab 2008), the Berkeley populations of *P. maniculatus* and *P. truei* have basal rates that are ca. 40% greater than expected and the desert mountain populations are 16% greater (Table 1, Fig. 2). The four desert populations fall on the scaling curve, which indicates that the expenditures of the desert populations are not low, but lower than the expenditures of the mesic and desert mountain populations, which raises the question why the mesic populations are so high. The depression of basal rate in the two populations of *P. californicus* is less marked when compared to the standard scaling curve, but they are still low, 85 and 86% of the value expected from mass (Table 1).

In addition to the mesic/xeric gradient, some of the residual variation around the scaling curve could be related to altitude. These populations are found at altitudes from 150 to 2100 m (Table 1). However, when altitude is included with body mass, altitude does not have a significant impact on BMR ($P = 0.646$).

An equation that includes body mass and the mesic/xeric gradient theoretically would demonstrate the influence of the gradient. The gradient can be included in an analysis either through localities that fall along the gradient or directly through the index. For example, if an equation incorporates the numerical values for body mass and basal rate, ANCOVA assigns a mean rate to each location. The localities (L), the indices for which are in Table (1), are mesic (Berkeley, California), the semi-mesic (San Gabriel Mountains near Los Angeles), desert mountains (Spring and Charleston Mountains near Las Vegas, Nevada), and lowland

deserts (Malpais Spring, New Mexico, Dugway, Utah, and Las Vegas, Nevada). These localities were incorporated into the analysis by ANCOVA via JMP, when localities ($P = 0.0014$) were combined with mass ($P = 0.0002$):

$$\text{BMR (mLO}_2\text{/h)} = 2.67 (L) \text{ mass}^{0.816}, (2)$$

which accounts for 99.4% of the variation in basal rate. Basal rate is not different among the lowland desert populations ($P = 0.497$), but it is between them and desert-mountain populations ($P = 0.031$), between the Berkeley populations and the desert populations ($P = 0.0006$), and between the desert-mountain and the Berkeley populations ($P = 0.041$).

The mean mass-independent basal rate coefficient correlates with a locality (L) equal to 1.00 in desert populations, 1.12 in desert mountain populations, and 1.34 in the Berkeley populations, each of which is a statistically significant correlate with basal rate. That is, species at Berkeley, other than *P. californicus*, have mass-independent basal rates that average 34% greater than those living in deserts and 20% greater than in the desert mountain populations, while the desert mountain populations have rates that are only 12% greater than those in the desert. Equation (2) estimates the basal rates of seven populations within 5% of the measurements and all eight within 10% (Table 2). The estimates from equation (2) are almost identical to the measured rates, the residual variation seen in Figure (2) has disappeared (Fig. 3).

The mass-independent basal rates, expressed as a percentage of the value expected from a mammalian scaling equation (McNab 2008), correlate as a negative power of the desert index in the four species ($P < 0.0001$; $r^2 = 0.957$) (Fig. 4):

$$\text{BMR (\%)} = 110 (I)^{-0.160}. (3).$$

As with equation (2), this equation accounts for the basal rates of seven populations within the 5% precision category and all eight within the 10% category (Table 3). Therefore, nearly all of the variation in basal rate in the four species is accounted for by the combined effects of body mass and their position along the mesic/xeric gradient in which they live, irrespective whether the gradient is represented by locality or the gradient.

Discussion

Multifactorial analyses of the physiological variation in a group of species and subspecies are effective when the behavioral and ecological factors that distinguish them are included. This analysis has an accuracy that even distinguishes intraspecific populations in their response to the gradient. The only difference in energy expenditure among the intraspecific populations of the four species reflects their response to the aridity gradient. The depression of BMR is relative to the high rates of species in mesic environments (Fig. 2). What determine the performance of species is their characteristics irrespective of their origin.

A reduction in basal rate with an increase in xeric conditions also has been seen in heteromyid rodents (McNab 1979; Hinds and MacMillen 1985), arvicoline rodents (pers. observ.), and larks (Tieleman et al. 2002). Glazier (1985*a, b*) showed that lactation and litter size in *Peromyscus* increased with basal rate, which implies a decrease of reproduction in xeric environments. Using some of the same and other species of *Peromyscus*, including *P. californicus*, Mueller and Diamond (2001)

demonstrated that mass-independent basal rate increased with community primary production, which is compatible with the pattern seen here because community production increases with a decrease of the desert index.

The species and subspecies of *Peromyscus* that tolerate the driest environments appear to approach a maximum adjustment to xeric conditions (Figs. 1 and 4). Such a limit would reduce the ability to respond further to deserts with indexes > 1.5, potentially restricting a rodent's distribution. This implies that an increase in the index in species that had made the greatest adjustment to life in desert are potentially subject to extinction, a concern that relates to climate change.

Many studies have demonstrated that a variety of factors influence basal rate in mammals (McNab 2008, 2015). This applies in equations (2 and 3), which incorporate the mesic/xeric gradient. What then accounts for the low basal rate in *P. californicus*? One possibility is that this species has one or more characters that depresses basal rate. It is semi-arboreal and many arboreal species have low basal rates (McNab 2008). However, *P. truei*, the second largest species, also is semi-arboreal. If arboreality is included in the analysis, it is statistically insignificant ($P = 0.211$) because arboreality is not independent of mass ($P = 0.0005$). On the other hand, maybe what should be explored is the cause(s) for the high basal rates of *P. maniculatus* and *P. truei*. In fact, the high species are higher than *P. californicus* is low (Table 1).

The ability to demonstrate the impact of an environmental gradient requires a comparison of closely related species and populations, thereby reducing the influence of factors that may mask any relationship that is present. This requires

the inclusion in an analysis of the distinctive characteristics of species and those of their environment. Progress can be made to understand the operation of nature by the advancement of observational and experimental techniques, but also through the development of advanced analytical procedures, as hopefully is seen here.

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Figure legends

Fig. 1. Basal rate of metabolism (% expected from mass) (Table 1) in five species of *Peromyscus* as a function of a desert index ($^{\circ}\text{C}/[\text{cm H}_2\text{O}]$). Numbers in parentheses are the number of measurements used to estimate basal rate. The dashed line is a fitted curve when all five species are included in the analysis. The other two curves represent this relationship, one for four species and the other for *P. californicus*.

Fig. 2. $\log_{10}$ basal rate of metabolism (mLO_2/h) of *Peromyscus* as a function of $\log_{10}$ body mass (g) and localities along a mesic/xeric gradient. Populations belonging to the same species are enclosed. Interspecific values in mesic and desert mountains populations are connected. Sample sizes of rate measurements are indicated for each population. The standard scaling curve for mammals is $\text{BMR} (\text{mLO}_2/\text{h}) = 3.50 \text{ mass}^{0.721}$ (McNab 2008).

Fig. 3. Measured basal rate of metabolism as a function of the basal rate of metabolism estimated by the multifactorial equation (2).

Fig. 4. Mass independent basal rate of metabolism (% expected from equation [1]) as a function of the desert index ($^{\circ}\text{C}/[\text{cm water}]$). Populations belonging to the same species are enclosed. The curve fitted for four species is indicated, the equation of which is $\text{BMR} (\%) = 110 (I)^{-0.160}$, where I is the desert index.

Fig. 1

Fig. 2

Fig. 3

Fig. 4

Table 1. Energetics of *Peromyscus*

Populations	Mass (g)	BMR ¹ (%)	Location	Desert index	Conditions
<i>P. eremicus eremicus</i>	21.5	99	Las Vegas, Nevada	2.47	desert, 800 m
<i>P. eremicus eremicus</i>	19.9	105	Malpais Spring, New Mexico	1.12	volcanic desert, 2100 m
<i>P. californicus insignis</i>	45.5	85	San Gabriel Mtn, California	0.39	coastal mountains, 1200 m
<i>P. californicus parasiticus</i>	49.6	86	Berkeley, California	0.28	coastal mesic, 150 m
<i>P. crinitus stephansi</i>	15.9	98	Las Vegas, Nevada	2.47	desert, 800 m
<i>P. crinitus pergracilis</i> ²	20.9	99	Dugway, Utah	1.74	desert, 1500 m
<i>P. maniculatus gambeli</i>	19.1	133	Berkeley, California	0.28	coastal mesic, 150 m
<i>P. maniculatus sonoriensis</i>	24.2	116	Spring/Charleston Mtn, Nevada	0.78	desert mountains, 2000 m
<i>P. truei truei</i>	33.2	116	Spring/Charleston Mtn, Nevada	0.78	desert mountains, 2000 m
<i>P. truei gilberti</i>	33.3	143	Berkeley, California	0.28	coastal mesic, 150 m

¹ Estimated by an all-mammal equation (McNab 2008): $BMR (mLO_2/h) = 3.50 \text{ mass}^{0.721}$.

² Captive population

Table 2. Energetics of *Peromyscus* estimated by mass and locality

Observed species	Measurement	Estimated basal rate ¹			
	Basal rate (mLO ₂ /h)	Mass ²	M/C ³	Locality ⁴	M/C ³
<i>P. eremicus eremicus</i> (Nevada)	31.8	35.0	0.91*	32.6	0.97*
<i>P. eremicus eremicus</i> (New Mexico)	31.8	32.3	0.98*	30.6	1.04*
<i>P. crinitus stephansi</i> (Nevada)	25.1	25.6	0.98*	25.5	0.93*
<i>P. crinitus pergracilis</i> (Utah)	30.9	34.0	0.91*	31.9	0.97*
<i>P. maniculatus gambel</i> (Berkeley)	39.0	30.9	1.26	39.7	0.98*
<i>P. maniculatus sonoriensis</i> (desert mtns)	40.4	39.6	1.02*	40.3	1.00*
<i>P. truei truei</i> (desert mtns)	50.8	55.0	0.92*	52.1	0.97*
<i>P. truei gilberti</i> (Berkeley)	62.6	55.2	1.13	62.5	1.00*
	Σ 5%		3		7
	Σ 10%		6		8

¹ *Estimated basal rate within 10% of the measured basal rate.

² Estimated by equation (1)

³ Measured basal rate/calculated basal rate

⁴ Estimated by equation (2)

Table 3. Energetics of *Peromyscus* estimated by the desert index

Observed species	Measured	Estimated basal rate ¹	
	Basal rate (%) ²	Desert index ³	M/C ⁴
<i>P. eremicus eremicus</i> (Nevada)	99	95	1.04*
<i>P. eremicus eremicus</i> (New Mexico)	105	108	0.97*
<i>P. crinitus stephansi</i> (Nevada)	98	95	1.03*
<i>P. crinitus pergracilis</i> (Utah)	99	91	0.99*
<i>P. maniculatus gambeli</i> (Berkeley)	133	135	0.99*
<i>P. maniculatus sonoriensis</i> (desert mtns)	116	114	1.02*
<i>P. truei truei</i> (desert mtns)	116	114	1.02*
<i>P. truei gilberti</i> (Berkeley)	143	135	1.06*
	Σ 5%		7
	Σ 10%		8

¹ * Estimated basal rate within 10% of the measured basal rate.

² Estimated by an all-mammal equation (McNab 2008): $M \text{ (mLO}_2\text{/h)} = 3.50 m^{0.721}$

³ Estimated basal rate from equation (3).

⁴ Measured basal rate/estimated basal rate.