

# Metabolic rate and environmental productivity: Well-provisioned animals evolved to run and idle fast

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**Even among vertebrate species of the same body mass and higher-level taxonomic group, metabolic rates exhibit substantial differences, for which diverse explanatory factors—such as dietary energy content, latitude, altitude, temperature, and rainfall—have been postulated. A unifying underlying factor could be food availability, in turn controlled by net primary productivity (NPP) of the animal's natural environment. We tested this possibility by studying five North American species of *Peromyscus* mice, all of them similar in diet (generalist omnivores) and in gut morphology but differing by factors of up to 13 in NPP of their habitat of origin. We maintained breeding colonies of all five species in the laboratory under identical conditions and consuming identical diets. Basal metabolic rate (BMR) and daily ad libitum food intake both increased with NPP, which explained 88% and 90% of their variances, respectively. High-metabolism mouse species from high-NPP environments were behaviorally more active than were low-metabolism species from low-NPP environments. Intestinal glucose uptake capacity also increased with NPP (and with BMR and food intake), because species of high-NPP environments had larger small intestines and higher uptake rates. For metabolic rates of our five species, the driving environmental variable is environmental productivity itself (and hence food availability), rather than temporal variability of productivity. Thus, species that have evolved in the presence of abundant food run their metabolism "fast," both while active and while idling, as compared with species of less productive environments, even when all species are given access to unlimited food.**

**M**etabolic rate means the rate at which an animal burns calories to produce energy. Among vertebrate species, there is a  $10^7$ -fold range of metabolic rates. Much research has aimed at understanding the reasons behind this variation. Why are some animals seemingly extravagant, consuming and expending calories rapidly, whereas others are frugal, consuming very little and metering their expenditure accordingly so as to remain in energy balance?

The two factors underlying most of this variation are well known: body mass and higher-level taxonomic affiliation. First, within the same higher-level taxonomic group (e.g., mammals), metabolic rate increases with body mass (the so-called mouse-to-elephant curve) according to approximately the 0.75 power of body mass (1). (Metabolic rate per g of body mass decreases with body mass but by a power smaller than 1.0, so the absolute metabolic rate of a whole animal, the subject of this paper, increases with mass). Second, for species of the same mass there are some differences between higher-level taxonomic groups, notably the *ca.* 8-fold difference between endotherms ("warm-blooded" birds and mammals) and ectotherms ("cold-blooded" reptiles, amphibians, and fish) (2), and also the *ca.* 1.3-fold difference between marsupials and placentals (3) and the *ca.* 2-fold difference between sloths and other placentals (4).

However, even when body mass and higher-level taxonomic affiliation have been taken into account, a *ca.* 6-fold range of variation among species remains to be explained (5). At least five correlates of this unexplained variation have been reported. For

example, desert mammals appear to have metabolic rates unexpectedly low for their mass and taxonomic affiliation (6–9); so do species specializing on diets of low energy density (e.g., insectivores or consumers of high-fiber plant material) (3). Metabolic rates have also been reported to differ between populations or species from habitats differing in latitude, altitude, and temperature (e.g., refs. 6 and 9–13).

Is there any common thread to these five correlates of unexplained variation, or will we be left with just a laundry list of many unrelated correlates? For instance, deserts tend to be characterized by water shortage *and* low primary productivity (hence food shortage) *and* high summer daytime temperatures *and* high intraannual as well as interannual variation in rainfall: does any single one of these factors act as a unifying explanation underlying the low metabolic rates of desert animals as well as of species consuming low-energy diets and species of certain latitudes, altitudes, and temperatures?

A candidate for such a unifying explanation is availability of food or calories, in turn controlled ultimately by net primary productivity [abbreviated NPP: the rate at which plant biomass accumulates (14)]. NPP varies 1300-fold among localities [range 3–4000 g of carbon per  $m^2$  per year (15)] and depends in turn on many factors, such as rainfall, temperature, soil nutrients, light levels,  $CO_2$  levels, and characteristics of the plant species themselves (16, 17). Does metabolic rate increase with food availability or with NPP? If so, then NPP and food availability might integrate all of the factors individually reported to affect metabolic rate and might themselves be the actual controlling variables.

Food availability or NPP would be intuitively plausible as such an integrating variable. Animals living amidst abundant food, in zones of high NPP, may have evolved to "run fast"—i.e., to consume and assimilate calories at a high rate (so-called digestible dry matter intake = DDMI, determined from dry matter intake, DMI), and to burn calories at a high rate (so-called field metabolic rate, FMR). Averaged over times sufficiently long that a nonreproducing animal is in energy balance (i.e., neither gaining or losing mass), daily metabolizable energy consumption (approximated from DDMI) must equal FMR. Animals with access to abundant food, in zones of high NPP, may also have evolved high basal metabolic rates (BMRs)—i.e., energy expenditure when inactive in their thermoneutral zone and not digesting. BMR may be considered to represent the "idling rate" of maintaining metabolic machinery at rest, whereas DDMI or FMR may be considered to represent an animal's total "running costs," time-averaged over periods of activity as well as of rest.

Abbreviations: ANCOVA, analysis of covariance; BMR, basal metabolic rate; CV, coefficient of variation; DEE, daily energy expenditure; DDMI, digestible dry matter intake; DMI, dry matter intake; FMR, field metabolic rate; HIF, heat increment of feeding; NPP, net primary productivity.

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**Table 1. *Peromyscus* species studied and their natural habitats**

Species	Body mass, g	Ancestral site	Habitat type	Productivity, g C per m <sup>2</sup> per y	CV of rainfall
<i>P. eremicus</i>	22.2 ± 2.8	Near Tucson, AZ	Lower Sonoran desert	48	0.27
<i>P. melanophrys</i>	45.0 ± 6.3	Near Zacatecas, Mexico	Yucca/agave desert scrub	67	0.52
<i>P. californicus</i>	43.5 ± 4.5	Santa Monica Mts., CA	Chaparral/coastal sage scrub	340	0.55
<i>P. maniculatus</i>	19.0 ± 1.4	Near Ann Arbor, MI	Deciduous woodland/meadow	600	0.18
<i>P. leucopus</i>	19.1 ± 3.5	Near Linville, NC	Mixed deciduous–coniferous forest	604	0.19

“Ancestral site” is the site at which the wild ancestors of our breeding populations were captured. Body masses are mean ± SD. Productivity values for each habitat were calculated from remote sensing data and ecological information in (see ref. 23). CV, interannual coefficient of variation.

The present paper tests this hypothesized relation between NPP of the environment in which an animal has evolved to live and these two measures of energy flux (BMR and DMI). Our test animals are five species of the genus *Peromyscus* (deer mice and relatives), a ubiquitous genus of North American rodents comprising ca. 65 species that collectively inhabit a wide range of environments, including some of North America’s least productive and most productive environments. Because of the above-cited evidence that species adapted to different diets may differ in metabolic rate, we selected five dietarily similar species, all of which may be characterized as generalist omnivores whose diets in the wild consist mainly of seeds, flowers, fruits, and other energy-dense plant parts, plus arthropods, acorns, and fungi (18–21). Unlike specialized herbivorous rodents, which have relatively large hindguts (fermentative ceca and colons), all five of our species have small hindguts. To further minimize extraneous sources of variation, we maintained captive-bred individuals of all five species under identical conditions in our laboratory on the same diet, in the same laboratory rooms, and in identical cages. Thus, any species differences observed should be genetic differences selected ultimately by the different habitats of origin, rather than nongenetic proximate consequences of different habitats or different rearing or maintenance conditions. For our values of NPP of the habitats of origin, we used modern complex methods of calculation from remote sensing data and other ecological information, instead of the simpler and less accurate methods common in the earlier metabolic literature, in which NPP was estimated from rainfall (or from rainfall and temperature) alone.

## Materials and Methods

**Animals.** Sixty-four *Peromyscus* mice of five species (10–15 individuals each of *P. californicus*, *P. eremicus*, *P. leucopus*, *P. maniculatus*, and *P. melanophrys*) were bred from ancestral stocks previously captured at five North American locations characterized by very different rainfalls and productivities (Table 1). Parent mice were obtained from the *Peromyscus* Genetic Stock Center (Univ. of South Carolina, Columbia), where the stocks had been held for 10–40 generations in captivity. We bred and maintained our mice in the Univ. of California, Los Angeles (UCLA), Health Science Vivarium, in a single room at 27°C, on a 16-h/8-h light/dark cycle. All mice were provided with *ad libitum* quantities of water and of the same diet [a commercial purified rodent diet based on maltose and casein and manufactured by Dyets (Pittsburgh)]. To further minimize sources of variation, we made measurements only on adult males between 8 and 15 months old, maintaining constant body mass. When mice were not being used for experimental measurements, we housed them in same-sex pairs in large plastic rodent cages (40 × 25 × 20 cm) that allowed room for running and jumping. During experimental measurements of food intake and digestibility we housed single mice in cages appropriate to their body size: 25 × 15 × 12 cm for the smaller *P. eremicus*, *P. leucopus*, and *P. maniculatus*, 40 × 25 × 20 cm for the larger *P. californicus* and *P. melanophrys*. Metabolic rate was measured on individual mice

placed in round plastic chambers 20 cm in diameter and 10 cm high. All cages contained environmental enrichment in the form of cotton nesting material and PVC (polyvinyl chloride) pipes for hiding places. Mice were kept on aspen shaving bedding except during digestibility trials, when they were placed on wire grids to enable collection of feces. All techniques were approved by the UCLA Animal Research Committee and met federal standards for animal care and welfare.

**Measurements. Metabolic rate.** We assessed BMR as oxygen consumption rate ( $V_{O_2}$  in units of ml·min<sup>-1</sup>), measured by open-flow respirometry with an Ametek oxygen analyzer model S-3A.  $V_{O_2}$  was measured between 1200 and 1800 hours, the animals’ quiescent phase, when these mice (which are active and feed at night) had completed digestion. A mouse was placed inside a lighted 3-liter Plexiglas chamber to which it had been previously acclimated. The chamber was held at 27°C, within the thermoneutral zone of these mice and the same as the temperature at which the animals were housed. Air samples were monitored continuously (Sable Systems, Las Vegas, NV) in 40-min blocks, using outside air as the reference. For each individual mouse we selected the minimum 10-min  $V_{O_2}$  out of a 30-min measurement period during which mice were visibly at rest, averaged the values for four such periods per day, and made and averaged such measurements on three separate days, then we averaged the results over 10–15 individuals to obtain the mean BMR for that species.

**Feeding and digestion.** We used the same 64 individual mice for which  $V_{O_2}$  was measured. A mouse was transferred to a cage with a wire grid bottom to permit collection of feces, and with *ad libitum* availability of food and water. After the mouse had adapted to the cage for 3 d, food offered, food remaining, and feces produced were weighed daily for 10 d and were dried in an oven at 60°C to obtain dry mass. Food consumed (DMI) was calculated as food offered minus food remaining, corrected for water content. Apparent dry-matter digestive efficiency (%) was calculated as food consumed minus feces produced, divided by food consumed. This measurement allowed calculation of digestible dry-matter intake, or DDMI [= DMI (g) × digestive efficiency (%)], which we consider functionally equivalent to calories assimilated. Body mass was recorded to the nearest 0.1 g daily during food intake measurements, and also before each measurement of  $V_{O_2}$ .

**Intestinal nutrient transport rates.** We used the everted sleeve technique *in vitro* to measure maximal carrier-dependent D-glucose uptake rates across the small intestinal brush-border membrane (22). Briefly, we anaesthetized a mouse with an intraperitoneal injection of pentobarbital and excised the intact small intestine, which was then flushed with mammalian Ringer’s solution, everted onto a glass rod, and incubated for 2 min in a Ringer’s solution containing 50 mM D-glucose (the transported isomer) labeled with <sup>14</sup>C, plus a trace amount of <sup>3</sup>H-labeled L-glucose (the nontransported isomer) to correct for adherent fluid and passive glucose transport (see ref. 22 for explanation). We measured uptake rate (units of mmol·min<sup>-1</sup>

per mg of intestinal wet mass) in three consecutive regions (proximal, mid, and distal) of the small intestine, multiplied each regional rate by the region's wet mass, and summed these products over the three regions to obtain the uptake capacity of the whole length of the small intestine (units of  $\text{mmol}\cdot\text{day}^{-1}$ ).

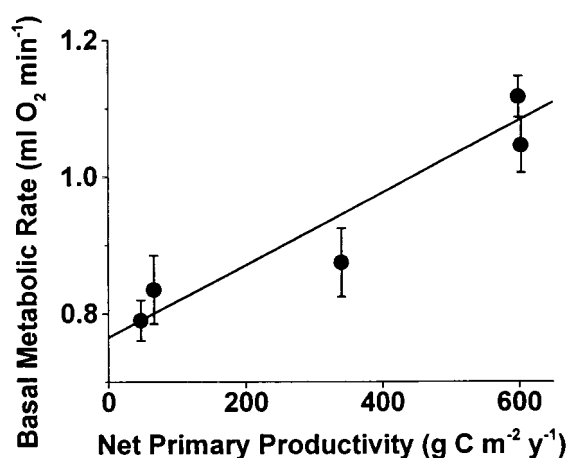
**Environmental Productivity.** Values for terrestrial NPP were calculated for 32 months (1997–2000) by a model (modified CASA: Carnegie–Ames–Stanford Approach) that integrates absorbed photosynthetically active radiation (APAR) from satellite-based remote sensing measurements, with values for efficiency of conversion of radiation to biomass based on physiological and ecological information such as water availability and suitability of temperature for plant growth (17, 23). From maps and collectors' field records, we determined as closely as possible the coordinates of the site where the founders of each laboratory breeding population of the five mouse species had been captured, then we determined the average annual NPP for a square 18 km on a side and centered on this location (Table 1).

**Statistical Analysis.** Our species differed over a factorial range of 2.4 in body mass, but differences in body mass are by themselves a major cause of differences in metabolic rate. To correct the measurements of metabolic rate to effectively the same body mass for all five species, we analyzed metabolic rate measurements by analysis of covariance (ANCOVA) with body mass as the covariate (JMP statistical software, SAS Institute, Greenville, SC). Alternatively, we also analyzed metabolic rate measurements by scaling them according to the accepted allometric coefficient for *Peromyscus* (0.73; ref. 12), but that analysis yielded results statistically equivalent to the ANCOVA and so will not be reported separately.

As emphasized by many authors (e.g., refs. 24–26), phylogeny is a potentially confounding factor in any analysis in which one compares species differing with respect to some factor to detect a putative relation between that factor and the measured quantity. For instance, in our comparison of metabolic rates of five *Peromyscus* species from environments of differing NPP, our measured metabolic rates might be similar or different among species not because of similarities or differences among environments in NPP (the variable of interest to us) but because of the constraints imposed by phylogeny. Each of the five species is more or less closely related to the other four species phylogenetically, and differences in metabolic rate might merely reflect differences in phylogenetic inheritance of shared ancestral metabolic rates. We factored out such effects of phylogeny by the method of phylogenetically independent contrast analysis, determined by using the program COMPARE 4.4 (ref. 27; <http://compare.bio.indiana.edu>), which uses Martins' (28) adaptation of Felsenstein's (26) method of analysis. Our phylogeny for these five species was developed from published information on *Peromyscus* systematics (29), with all branch lengths set arbitrarily to 1.0. It turned out that the statistical strength of all five of our principal results (the relations between BMR and NPP, DMI and NPP, DMI and BMR, DDMI and NPP, and DDMI and BMR) remained unchanged after factoring out effects of phylogeny, so we shall not discuss the contrast analysis further. That is, these relationships are not merely a legacy of phylogeny.

## Results

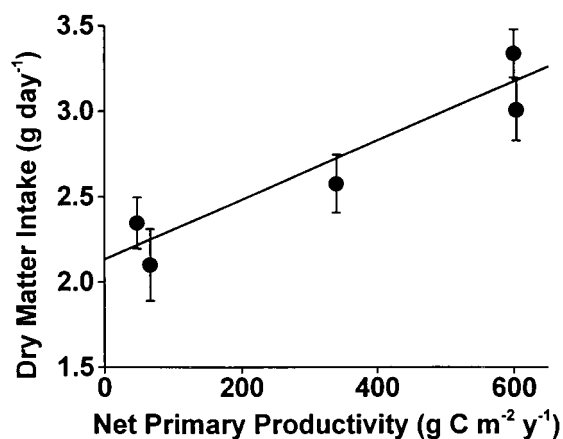
**BMR.** After we had adjusted for species differences in body mass by means of ANCOVA, a 1.4-fold range of BMRs among the five species remained. Mass-adjusted BMR was closely correlated with NPP, the productivity of each species' habitat of origin (Fig. 1,  $P = 0.02$ ,  $R^2 = 0.88$ ): that is, NPP accounted for 88% of the variation in BMR.



**Fig. 1.** BMR, measured as oxygen consumption (body-mass-adjusted  $V_{O_2}$  in units of  $\text{ml of O}_2 \text{ min}^{-1}$ ), of five species of *Peromyscus* mice, as a function of habitat NPP (units of  $\text{g of carbon m}^{-2} \text{ y}^{-1}$ ). Points are least-squares species means  $\pm$  SEM, adjusted by ANCOVA with body mass as covariate for species differences in body mass.  $P = 0.02$ ,  $R^2 = 0.88$ ; 10–15 mice per species were studied. Note that BMR increases with NPP.

**Daily Food Intake (DMI).** Water-corrected food intake (DMI) was even more closely correlated with NPP than was BMR ( $P = 0.01$ ,  $R^2 = 0.90$ ) (Fig. 2). Because BMR and DMI were both closely correlated with NPP, they were also closely correlated with each other ( $P = 0.02$ ,  $R^2 = 0.88$ ). Apparent dry-matter digestive efficiency equaled  $89\% \pm 2\%$  and did not vary significantly among the five species. (That is, 89% of the ingested dry matter was actually absorbed by mice, and only 11% passed out undigested in the feces). Hence not only daily food intake, but also digestible dry matter intake (DDMI), was closely correlated with NPP ( $P = 0.03$ ,  $R^2 = 0.82$ ) and with BMR ( $P = 0.02$ ,  $R^2 = 0.86$ ).

**Activity.** In the steady state, for an animal in mass balance as were our mice at the time of study, daily food intake must equal daily energy expenditure when both are expressed in the same units (e.g., calories). What could account for the observed differences



**Fig. 2.** As Fig. 1, but ordinate is body-mass-adjusted ad libitum daily food intake (grams of dry matter) of five species of *Peromyscus* mice, as a function of habitat NPP. Note that food intake increases with NPP of the ancestral habitat of origin ( $P = 0.03$ ,  $R^2 = 0.82$ ), even though all mice had been bred for many generations in the laboratory and were being maintained on identical diets.



in daily food intake or energy expenditure among our five mouse species?

Total daily energy expenditure (DEE) of our caged animals (which is analogous to FMR of a free-living animal) may be partitioned into three components: energy expenditure while resting and not digesting (BMR); the energetic costs of digestion (termed heat increment of feeding, HIF); and the energetic costs of activity. For our mouse species, measured BMR values were 53–68% of total energy input as estimated from food intake times the caloric content of food, when all values are expressed as metabolizable energy. We did not determine HIF for our mice, but measurements for other rodent species eating just enough to maintain body mass yield values equivalent to about 12% of DEE (30, 31). The remainder of DEE, constituting about 20–35% of it [ $100\% - (53-68\%) - 12\%$ ], must be the cost of activity. (Of course, for a wild animal running around outdoors and not living in a small cage, DEE and activity would be much higher, and BMR would be a much lower percentage and activity a much higher percentage of DEE).

We found BMR and total energy expenditure (equal to total energy intake, measured as food intake) to differ in virtually the same rank order among our species. Because our five species have similar natural diets and similar gut anatomies, it seems unlikely that the percentage contribution of HIF to total energy expenditure varies greatly among the species. Instead, one would expect most of the species differences in DEE unaccounted for by differences in BMR to arise from species differences in activity.

This expectation accords well with our qualitative observations of activity in the course of handling and caring for the mice. The two species with the highest DEE and BMR (*P. leucopus* and *P. maniculatus*) were jumpy, bit frequently and forcefully, escaped readily from their cages, and required a net for recapture in the vivarium. The two species with the lowest DEE and BMR (*P. eremicus* and *P. melanophrys*) were placid and calm in the hand. *P. californicus* was intermediate in both DEE and BMR and in its activity. Our observations accord with those of previous researchers, who noted that *P. maniculatus* (our species with the highest DEE and BMR) tends to be “more restless” (32) and “nervous” (10) than other *Peromyscus* species. This is not a surprising observation, because food requirements of “nervous” or “high-strung” domestic animals as well tend to exceed those of their more placid cage-mates or stall-mates.

**Intestinal Glucose Uptake Capacity.** One would expect an animal eating more food to have greater intestinal capacity for absorbing food nutrients. Hence we measured intestinal brush-border D-glucose uptake capacity as the integrated product of small intestinal mass times glucose uptake rate per unit mass of intestinal tissue, integrated over the length of the small intestine. Species differences in intestinal mass, uptake rate, and uptake capacity all fell in approximately the same sequence as species differences in NPP, BMR, and DDMI. The strongest relations were between small intestinal mass ( $P = 0.03$ ,  $R^2 = 0.75$ ) or uptake capacity ( $P = 0.03$ ,  $R^2 = 0.76$ ) and BMR. That is, species with higher food intake and basal metabolisms tend to have larger small intestines and higher glucose uptake rates.

## Discussion

We shall now discuss five topics: the relation between our study and previously published studies; the measures of metabolic rate that are related to environmental productivity; the question whether productivity itself, or perhaps instead its temporal variability, is the driving variable; evidence for a role of factors other than productivity; and the question whether productivity or food could provide a unifying explanation for variation in metabolic rate independent of body mass and higher-level taxonomic affiliation.

**Comparison with Previous Studies.** Two previous laboratory studies (8, 10) of *Peromyscus* populations from different habitats found a trend for metabolic rate to be lower for mice from arid environments than for mice from mesic environments. A literature review (6) of basal metabolic rates of 497 mammal species, assigned to six terrestrial zoogeographic zones defined mainly by latitude and rainfall, similarly found mammals of xeric environments to have significantly lower BMRs than mammals of mesic environments. Our study agrees with these conclusions but makes the argument more compelling in two respects.

First, we related metabolic rates to a continuously varying habitat measure (NPP) rather than to a coarser assignment of habitats to one of several categories. Our conclusion is that the relevant feature of our habitats associated with low metabolic rate is low productivity.

Second, instead of compiling from the literature metabolic measurements obtained in different studies by different methods, we measured all of the data ourselves by identical methods, using animals born in our laboratory and maintained under identical conditions, including identical diets. Thus, extraneous sources of variation (including nongenetic effects of differing environments and diets in studies of wild-caught animals) were minimized. This minimization of extraneous variation may have contributed to the very high correlation of metabolic rate with environmental productivity that we obtained: NPP explained 82–90% of the variance in metabolic rate after removing effects of body mass. During the 10–40 generations that our mouse stocks had been bred in captivity at the *Peromyscus* Genetic Stock Center, selection for adaptation to their original natural environments was undoubtedly relaxed. First-generation offspring of wild-caught individuals would presumably have yielded even higher correlations of metabolic rate with environmental productivity.

**Measures of Metabolic Rate.** We found three measures of metabolic rate to be correlated quantitatively (BMR, DMI, and DDMI), and one to be correlated anecdotally (behavioral activity), with NPP. Interspecies comparisons of FMR (approximately equal to DDMI in the steady state) and BMR have shown a correlation of these two measures with each other in rodents (33). That is, animals with access to abundant food have evolved to “run fast” (high FMR and DDMI) and also to “idle fast” (high BMR). The link between BMR and FMR arises because BMR is in effect the maintenance cost of the biological machinery (muscles, heart, intestine, liver, kidneys, etc.) that enables animals to sustain high metabolic rates while active.

**Productivity or Variability?** Arid environments tend to be characterized not only by low rainfall and low NPP, but also by high variability of rainfall within and between years (34). One might reason that, all other things being equal, animals from highly variable environments should have evolved lower metabolic rates than animals from less variable environments with similar time-averaged productivity, so as to be able to idle their metabolism at a rate low enough that the environment could constantly support it, even at unproductive times. Several authors have suggested that environmental variability rather than environmental productivity is the primary factor responsible for low metabolic rates of arid-zone species (e.g., refs. 6 and 35).

We tested this idea as follows. Data adequate to calculate the long-term variability of NPP itself were not available, but long-term rainfall records were available, and rainfall patterns are a primary driver of variation in NPP (16, 36). Hence we calculated 30-year coefficients of variation (CV) of annual rainfall (see Table 1) for the capture sites of our five *Peromyscus* populations from data provided by the North Carolina State Climatologist’s office, Michigan State Office of Climatology, and National Oceanic and Atmospheric Administration. In our data

set CV of rainfall did tend to decrease with NPP, but the relation was very loose and not statistically significant ( $P = 0.12$ ,  $R^2 = 0.57$ ). Whereas BMR ( $P = 0.28$ ,  $R^2 = 0.36$ ) and DDMI ( $P = 0.4$ ,  $R^2 = 0.24$ ) both tended to decrease with CV of rainfall, both relations fell far short of statistical significance, and CV of rainfall explained far less of the variation in BMR or DDMI than did NPP ( $R^2 = 0.88$  or  $0.82$ , respectively).

That is, in our limited data set of five species, time-averaged mean productivity rather than its variability is the more important driving variable: possibly because our five species were from habitats encompassing a 13-fold range in NPP. We anticipate that a larger data set might make it possible to demonstrate a separate effect of variability, as well as of NPP itself.

**Other Factors.** The preceding three paragraphs illustrate a qualification worth stressing explicitly. Just because we have succeeded in demonstrating a high correlation between metabolic rate and NPP among five *Peromyscus* species does not prove that NPP is the only important factor underlying all residual variation in metabolic rate (i.e., variation other than that arising from body mass and higher-level taxonomic affiliation). We selected five species especially suitable for testing the postulated importance of NPP: five generalist omnivorous species very similar to each other in their diets and in their gut morphology. Species with different diets and different gut morphologies may yield different results.

For example, we have made preliminary measurements on another *Peromyscus* species, *P. aztecus*, which differs from our other five species in having a very large fermentative cecum, suggesting a dietary strategy of specialized herbivory (37). *P. aztecus* proved to have lethargic behavior and low BMR and DMI, much lower than expected from the NPP of its natural environment (highly productive subtropical cloud forest). These observations of *P. aztecus* are in accord with previous arguments that animals consuming diets of low energy density tend to have low metabolic rates (3, 38).

**A Unifying Theory of Residual Variation?** Whereas *P. aztecus* deviates from predictions based on NPP alone and requires invoking a seemingly separate factor (low-energy diet), both of these factors actually exemplify one common factor: availability of food or of calories. For related species of similar dietary habits but of different habitats, NPP may be a good measure of the differences that they encounter in food availability. But NPP measures the sum of all plant biomass production in a habitat. Species specialized on different diets may encounter different productivities of their particular food classes in the same habitat. For instance, species such as *P. aztecus*, specialized on low-energy diets, experience the world as poorer than do generalist omnivores living in the same habitat.

As we mentioned in the Introduction, some previous studies have noted apparent correlations of metabolic rate with the latitude, altitude, or temperature of an animal's habitat of origin. Productivity and food availability vary in complex ways among habitats differing with respect to each of these three variables. It remains to be seen whether variation in productivity or food availability can account for these apparent correlations of metabolic rate with latitude, altitude, or temperature. Such tests will be best carried out by the two methods used in this paper: calculating NPP for the actual habitat of origin, and measuring metabolic rates of laboratory-maintained stocks of closely related species or populations differing in their habitat of origin but maintained identically in the laboratory. These two conditions did not apply to the previous studies, making it difficult to interpret them. If such future studies yield results similar to those of our study, then three factors may largely account for the enormous range of species variation in metabolic rate: body mass, higher-level taxonomic affiliation, and the conditions of environmental productivity or food availability under which an animal has evolved.

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