BERGMANN'S RULE AND CLIMATIC ADAPTATION IN WOODRATS (NEOTOMA)

JAMES H. BROWN AND ANTHONY K. LEE

Department of Zoology, University of California, Los Angeles
Department of Zoology, Monash University, Clayton, Victoria, Australia

Received October 16, 1968

Within species and genera of homeotherms the body size of individuals of different populations is often negatively correlated with environmental temperature, and the relative size of appendages is often positively correlated with environmental temperature. Such trends are sufficiently widespread to have been labeled the eceographic rules of Bergmann (body size) and Allen (appendages). More than a decade ago, Scholander (1955, 1956) and Mayr (1956) debated the validity of the inference that these rules reflected physiological adaptations to climate. To that time there had been no study of the thermoregulatory physiology of a large number of conspecific or congeneric populations so that their arguments were theoretical or based on indirect evidence. Subsequently, Hayward (1965a, b) studied the temperature regulation of representatives of several races of Peromyscus, but concluded that the observed size related variation was not adaptive to climate. Other papers have recently discussed eceographic rules (Irving, 1957; Hamilton, 1961; McNab, 1966; Herreid and Kessel, 1967; Kendeigh, 1969), but none provide data on heat exchange of closely related homeotherms of different sizes from different climates.

We now have data on the temperature regulation of representatives of 10 populations of woodrats. These populations vary three-fold in body weight, occur in diverse climates in western North America, and include representatives of four species of the genus Neotoma. Our data permit a direct evaluation of the relationships between metabolism, heat loss, body size, and environmental temperature, and indicate the major avenues of climatic adaptation in this group of rodents.

MATERIALS AND METHODS

Samples of 10 populations of woodrats were obtained from the localities shown in Table 1. The thermoregulatory physiology of eight of these populations has been described by Brown (1968) and Lee (1963). These papers may be consulted for a description of the methods. Subsequently, we have studied a sample of N. lepida from near Indio in southern California, and Bruce A. Wunder has kindly permitted us to use his unpublished data on N. cinerea from the Sierra Nevada of central California. The methods employed in these studies were similar to those described in the earlier papers. The primary data used in the present analysis appear in Table 2.

RESULTS

Environmental Temperature and Body Size.—Woodrats are nocturnal and spend the daylight hours in dens. The nature of these dens varies with species and habitat, but those of the four species studied here all provide microclimatic temperatures which show little daily variation, and are very similar to the mean daily air temperatures outside (Brown, 1968; Brown and Lee, unpublished observations). For this reason, we have used the mean annual temperature at the nearest U.S. Weather Bureau Station (Table 1) as an index to the temperatures to which these woodrat populations are actually exposed.

There is a significant inverse correlation ($P < 0.01$) between the weights of freshly caught adult woodrats and the mean annual temperature where they occur (Fig. 1). This indicates that these populations follow Bergmann's Rule, which states that the larger representatives of closely related homeotherms tend to occur in colder climates.

### Table 1. Populations of woodrats sampled and the nearby U.S. Weather Bureau Station from which climatic data were obtained.

<table>
<thead>
<tr>
<th>Population</th>
<th>Collecting locality</th>
<th>Elevation m</th>
<th>U.S. Weather Bureau Station</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coastal <em>N. cinerea</em></td>
<td>Little Nestucca River, Tillamook Co., Oregon</td>
<td>200</td>
<td>Cloverdale</td>
</tr>
<tr>
<td>Highland (Colorado) <em>N. cinerea</em></td>
<td>near Idaho Springs, Cedar Creek Co., Colorado</td>
<td>2700</td>
<td>Idaho Springs</td>
</tr>
<tr>
<td>Highland (California) <em>N. cinerea</em></td>
<td>near Sequoia National Park, Tulare Co., California</td>
<td>1800</td>
<td>Giant Forest</td>
</tr>
<tr>
<td>High desert <em>N. cinerea</em></td>
<td>Castle Valley, Grand Co., Utah</td>
<td>1450</td>
<td>Moab</td>
</tr>
<tr>
<td>High desert <em>N. albicula</em></td>
<td>Castle Valley, Grand Co., Utah</td>
<td>1450</td>
<td>Moab</td>
</tr>
<tr>
<td>Low desert <em>N. albicula</em></td>
<td>near Yuma, Yuma Co., Arizona</td>
<td>100</td>
<td>Yuma</td>
</tr>
<tr>
<td>Coastal <em>N. lepida</em></td>
<td>near Pomona, Los Angeles Co., California</td>
<td>350</td>
<td>Pomona College</td>
</tr>
<tr>
<td>Intermediate desert <em>N. lepida</em></td>
<td>Antelope Valley, Los Angeles Co., California</td>
<td>1000</td>
<td>Palmdale</td>
</tr>
<tr>
<td>Low desert <em>N. lepida</em></td>
<td>near Indio, Riverside Co., California</td>
<td>sea level</td>
<td>Indio</td>
</tr>
<tr>
<td>Coastal <em>N. fuscipes</em></td>
<td>near Westwood, Los Angeles Co., California</td>
<td>200</td>
<td>Santa Monica Airport</td>
</tr>
</tbody>
</table>

### Table 2. Data on environmental temperatures, body weights, and temperature regulation of woodrats. Figures in parentheses indicate sample sizes.

<table>
<thead>
<tr>
<th>Population</th>
<th>Mean annual temperature C</th>
<th>Body weight g</th>
<th>Metabolism at 6 C, cc O₂/g/hr</th>
<th>Minimal metabolism cc O₂/g/hr</th>
<th>Body temperature C</th>
<th>Lethal ambient temperature C</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coastal <em>N. cinerea</em></td>
<td>11.1</td>
<td>299.0 (11)</td>
<td>1.40 (9)</td>
<td>0.78 (9)</td>
<td>37.6 (10)</td>
<td>36.3 (7)</td>
</tr>
<tr>
<td>Highland (Colorado) <em>N. cinerea</em></td>
<td>6.3</td>
<td>288.9 (9)</td>
<td>1.51 (8)</td>
<td>0.70 (7)</td>
<td>37.6 (8)</td>
<td>35.6 (5)</td>
</tr>
<tr>
<td>Highland (California) <em>N. cinerea</em></td>
<td>7.0</td>
<td>261.0 (4)</td>
<td>1.25 (3)</td>
<td>0.63 (4)</td>
<td>37.0 (4)</td>
<td>—</td>
</tr>
<tr>
<td>High desert <em>N. cinerea</em></td>
<td>12.8</td>
<td>201.3 (9)</td>
<td>2.00 (8)</td>
<td>0.80 (8)</td>
<td>37.8 (7)</td>
<td>38.7 (6)</td>
</tr>
<tr>
<td>High desert <em>N. albicula</em></td>
<td>12.8</td>
<td>173.0 (12)</td>
<td>1.82 (9)</td>
<td>0.74 (9)</td>
<td>37.3 (10)</td>
<td>39.8 (9)</td>
</tr>
<tr>
<td>Low desert <em>N. albicula</em></td>
<td>22.2</td>
<td>150.6 (7)</td>
<td>1.77 (8)</td>
<td>0.73 (8)</td>
<td>37.7 (8)</td>
<td>40.4 (9)</td>
</tr>
<tr>
<td>Coastal <em>N. lepida</em></td>
<td>16.5</td>
<td>138.5 (24)</td>
<td>1.90 (14)</td>
<td>0.72 (14)</td>
<td>36.7 (7)</td>
<td>—</td>
</tr>
<tr>
<td>Intermediate desert <em>N. lepida</em></td>
<td>16.5</td>
<td>110.3 (22)</td>
<td>2.20 (22)</td>
<td>0.79 (22)</td>
<td>36.8 (11)</td>
<td>—</td>
</tr>
<tr>
<td>Low desert <em>N. lepida</em></td>
<td>22.9</td>
<td>100.4 (7)</td>
<td>2.38 (7)</td>
<td>0.79 (7)</td>
<td>36.9 (7)</td>
<td>41.4 (7)</td>
</tr>
<tr>
<td>Coastal <em>N. fuscipes</em></td>
<td>13.9</td>
<td>186.7 (16)</td>
<td>1.80 (17)</td>
<td>0.79 (10)</td>
<td>36.6 (10)</td>
<td>—</td>
</tr>
</tbody>
</table>
than their smaller relatives. In each species represented by more than a single population, intraspecific variation in body size also tends to follow Bergmann's Rule.

Temperature Regulation.—Scholander (1955) reasoned that in theory homeotherms might be expected to physiologically adapt to cold climates in three ways: (1) By decreasing body temperature. (2) By increasing metabolic heat production. (3) By decreasing heat loss. Adaptation might be expected to involve changes in the opposite direction in hot climates. We have evaluated the adaptive significance of each of these mechanisms in woodrats by studying their relationship to mean annual temperature. There was no significant relationship \( r = -0.02, P > 0.05 \) between body temperature and mean annual temperature. If metabolic rate were adaptively related to environmental temperature, one might expect departures from the relationship relating basal metabolic rate \( (M) \) and body weight \( (W) \), \( M = 3.8W^{-0.27} \) in mammals (Morrison, Ryser, and Dawe, 1959). In fact, all of the populations of woodrats examined had lower rates than predicted (Fig. 2), but the deviation from predicted was not significantly correlated with mean annual temperature \( (P > 0.05) \). Thus it appears that neither modifications of body temperature nor metabolic rate have been
major factors in adaptation of woodrats to temperature.

Modifications of the factors influencing rates of heat loss is the remaining possibility for thermal adaptation. It might be expected that populations living in environments where ambient temperatures are consistently far below body temperature would be composed of individuals with characteristics tending to reduce the rate of heat loss, thereby decreasing the metabolic rate required to maintain a constant body temperature. Rates of heat loss, per unit weight, have been compared by calculating the mean thermal conductance (thermal conductance = metabolism/body temperature – ambient temperature) at an ambient temperature of 6 C for the individuals of each population. Thermal conductance, the reciprocal of insulation, is minimal, or nearly so, for representatives of all populations at the temperature measured, for it is well below the lower critical temperatures (20 to 30 C) of these woodrats (Brown, 1968; Lee, 1963). The significant correlation ($P < 0.01$) between thermal conductance and mean annual temperature for the 10 populations (Fig. 3), indicates that the larger animals from colder environments have enhanced capacities for retarding heat loss.

Representatives of populations exposed to environmental temperatures that approach body temperature, particularly the two low desert populations, might be expected to have augmented facilities for heat loss at such ambient temperatures. This has been examined indirectly by comparing the lethal ambient temperatures of individuals of the populations for which data was available. Because the lethal body tem-

**Fig. 2.**—The relationship of the mean minimal metabolism of 10 populations of woodrats, expressed as a percentage of the metabolism predicted from the equation $M = 3.8 W^{-0.27}$, and the mean annual temperature where they occur. Symbols for the populations are identified in Figure 1.
CLIMATIC ADAPTATION IN WOODRATS

Fig. 3.—The relationship between the thermal conductance of 10 populations of woodrats measured at 6°C, and the mean annual temperature where they occur. The least squares regression line, its slope \( b \) and correlation coefficient \( r \) are shown. Symbols are identified in Figure 1.


temperatures (44 to 45°C) and minimal metabolic rates (0.70–0.80 cc O\(_2\)/g/hr) of these populations were essentially identical, the lethal ambient temperature is a good index to heat loss. There is a significant correlation \( (P < 0.05) \) between lethal ambient temperature and mean annual temperature (Fig. 4). Apparently small wood rats from desert habitats dissipate heat more readily at high ambient temperatures than their larger relatives.

**DISCUSSION**

In 10 populations of the genus *Neotoma* from western North America, the size of individuals varies geographically according to Bergmann’s rule. We interpret these interpopulation differences in body size to represent important adaptations to environmental temperature. Larger animals have a selective advantage in the cold climates of northern and alpine habitats because of their ability to conserve metabolic heat. In desert areas smaller animals with greater capacities for dissipation of heat have been favored. Our data provide no indication that the small interpopulation differences in basal metabolic rate and body temperature are adaptations to climate in woodrats.

Body weight varies three-fold and thermal conductance varies nearly two-fold among the populations of *Neotoma* that we have sampled. Within a single species, *N. cinerea*, body size varies at least 50% and follows Bergmann’s rule (this study; Hooper, 1938). The concomitant variation in the rate of heat loss is substantial. These seem to refute Scholander’s (1955) theoretical argument that interpopulation variation in body size according to Bergmann’s rule has a negligible effect on heat ex-
change and cannot be considered an adaptation to climate.

Rates of heat loss are effected by many variables, but in closely related animals of different sizes the following are most likely to be important: (1) Body surface which varies approximately as the two-thirds power of the weight in animals of the same shape (Brody, 1945), or which may be altered by changing shape (e.g., Allen's rule); (2) Insulation, which includes fur, feathers, and peripheral vasoconstriction; (3) Evaporation of water from the integumentary and respiratory surfaces. Our data are not sufficient to enable us to quantify the relative contributions of these three variables to the variation in thermal conductance among woodrats of different sizes. Qualitatively it is obvious that two factors are particularly important. First, the relative body surface of smaller woodrats must be considerably greater than that of the larger ones, since all animals are approximately the same shape and body weight varies by 200%. Secondly, the larger woodrats are better insulated than the smaller ones. The highland and coastal *N. cinerea* have not only longer, denser pelts, but also much more heavily furred tails and feet than the desert-dwelling *N. albicula* and *N. lepida*.

Scholander et al. (1950) have previously shown that insulation is proportional to body size in homeotherms weighing less than a kilogram. Apparently in such small animals, the length and thickness of fur and feathers that can be carried without interfering with such vital functions as
locomotion is highly dependent on body size. Herreid and Kessel (1967) have recently produced equations relating thermal conductance to body weight in small birds and small mammals. The slope of the curve relating conductance and body weight in woodrats (Fig. 5) is almost identical to the slope of Herreid and Kessel's equation relating these parameters in a variety of small mammals, but thermal conductances of woodrats are about 25% lower than predicted by their equation. Perhaps because they are nocturnal, and do not hibernate, all woodrats are well insulated, and the ability of large individuals to carry more insulation interacts positively with their low surface-to-mass ratio to give them a thermoregulatory advantage in the cold climates of northern and alpine habitats.

Only two other studies compare temperature regulation of representatives of a large series of closely related populations of homeotherms. In their studies of deer mice (Peromyscus) neither Hayward (1965a, b) nor McNab and Morrison (1963) implicated body size in climatic adaptation. Hayward observed an inverse correlation between body size and thermal conductance in populations of P. maniculatus, but found no correlation between body size and environmental temperature. He attributed his inability to demonstrate any significant thermoregulatory adaptations to the similarity of the microclimates in the
burrows of all the populations. McNab and Morrison found lower than predicted basal metabolic rates in deer mice from desert habitats. They interpreted these low rates of metabolism to be adaptive to hot, arid environments, where low rates of heat production would lessen the danger of overheating and reduce evaporative water loss. Their reasoning is somewhat tenuous and suffers from the absence of data on the microclimates of their animals. Two additional points should be made about these two papers on Peromyscus. First, both studies were made on populations from localities which collectively experienced a significantly narrower range of macroclimatic temperatures than those of our woodrats. It is the thermoregulatory capacities of woodrats from the extremely hot and cold environments which strengthen our conclusions. Secondly, both papers failed to consider the possible effects of genetic exchange between their populations and others occurring in close proximity, but in different thermal environments. The three populations of N. lepida we chose came from localities within 100 miles of each other. Although one of these localities has a much hotter climate, the three populations contain individuals of similar size and thermoregulatory characteristics. This suggests that significant gene flow between the populations may have counteracted much of the selection for divergence in body size. In the light of these considerations, it must be concluded that the mechanisms of climatic adaptation in Peromyscus remain unresolved. The studies of Hayward (1965a, b), McNab and Morrison (1963), and Musser and Shoemaker (1965) have demonstrated an inverse relationship between body size and thermal conductance within the genus, but the relationships of these parameters to environmental temperature are still uncertain and deserve further study.

The accumulation of data on the thermoregulatory physiology of many closely related populations, such as we have presented for woodrats, is costly and time consuming. For this reason it is inevitable that the adaptive significance of geographic variation in body size of homeotherms will be inferred from theoretical considerations and the results of a few direct studies. The following points are relevant to any consideration of the physiological significance of body size and surface: (1) Only those environments which animals have actually encountered have been involved in the evolution of physiological adaptations. Many birds and mammals alter their thermal environments by behavioral mechanisms, including the assumption of particular postures, selection of microclimates, migration, hibernation, and aestivation. (2) For physiological reasons, some homeotherms more than others are likely to respond to different environmental temperatures with changes in body size. Small mammals and birds are most likely to have modified body size in response to selection by temperature, since in homeotherms weighing less than about one kilogram, insulation as well as surface is a function of body weight. There are also a number of homeotherms which, unlike woodrats, consistently encounter environmental temperatures exceeding body temperature, and maintain homeothermy by evaporating water. So little is known about the interaction of evaporation, insulation, and body surface and their influence on heat exchange, that it is unrealistic to make a general statement about the adaptive significance of body size in these homeotherms at this time. (3) Some populations may have been subjected to selection for changes in body size which are related to environmental temperature, but this has not yet resulted in significant correlations between the two variables. We have already suggested that gene flow between nearby populations subjected to different selective pressures may have prevented or diminished adaptive differentiation. It is also likely that populations which have been recently exposed to new thermal environments, either through climatic change or range expansion, have not had time to
evolve new phenotypes. (4) There are many selective factors other than physiological ones that can influence body size, and the integrated effect of all these factors will determine the direction and rate of evolutionary change. We can expect only those groups of birds and mammals in which environmental temperature has profoundly influenced reproduction and mortality to follow Bergmann's rule for physiological reasons.

**Summary**

We present data on the thermoregulatory capacities of representatives of 10 populations of the genus *Neotoma* from diverse climates in western North America. Body size was inversely correlated with environmental temperature, indicating that the populations follow Bergmann's Rule. In general this was true of intraspecific, as well as intrageneric variation. Among the woodrat populations, thermal conductance and lethal ambient temperature were positively correlated with environmental temperature and inversely correlated with body size. Our data suggest that body size has played an important role in adaptation to environmental temperature because it has influenced rates of heat loss. Larger woodrats have a selective advantage in cold climates apparently because their smaller surface-to-mass ratio and greater insulation permit them to conserve metabolic heat. For the opposite reasons, smaller animals are favored in deserts where heat dissipation is of relatively greater importance.

Our findings appear to refute Scholander's (1955) argument that variations in body size among closely related populations have not resulted from adaptation to environmental temperature. We suggest that a physiological basis for variation in body size following Bergmann's Rule is most likely to be found in those groups of homeotherms which (1) are composed of populations occurring in contrasting thermal environments, and which have had sufficient time and isolation to differenti-

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**Acknowledgments**

This study was supported by a Horace H. Rackham Postdoctoral Fellowship from the University of Michigan (to J.H.B.), grants from Monash University and the Myer Foundation (to A.K.L.), and a grant from the National Science Foundation (GB-5139) administered by G. A. Bartholomew. We thank Drs. G. A. Bartholomew and R. C. Lasiewski for the use of the facilities of their laboratories and for critically reading the manuscript. Dr. C. R. Feldmeth also kindly read the manuscript.

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