

MISCELLANEOUS PUBLICATIONS  
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 135

**Adaptation to Environmental Temperature  
in Two Species of Woodrats,  
*Neotoma cinerea* and *N. albigula***

BY  
JAMES H. BROWN

ANN ARBOR  
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN  
FEBRUARY 2, 1968

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## INTRODUCTION

ANIMALS ARE ADAPTED to the temperatures of their environments by some combination of two basic responses, behavioral evasion of some temperature conditions and physiological adjustment to those which are not evaded. Small mammals avoid unfavorable temperatures chiefly by temporarily occupying more equable microenvironments. Physiological responses adjust heat production and heat loss to the environmental heat load. It is only by studying both of these responses that one can evaluate the adaptive significance of either of them and understand how the subtle interaction between them fits each population for survival in its particular environment.

Despite the wealth of recent information on the adaptations of homeotherms to environmental temperature, the majority of this work has been concerned with a taxonomically diverse array of organisms, most of which show highly specialized modifications for inhabiting extreme environments. The less spectacular differences between very closely related populations living in similar or different environments have been largely neglected. This is unfortunate since such studies have great potential, not only for discovering the kinds of adaptations which permit single species to occupy large and climatically diverse ranges, but also for understanding how selective factors in the environment act upon natural populations to produce adaptive phenotypes.

Woodrats of the genus *Neotoma* present excellent material for a comparative study of conspecific or congeneric populations because they are a closely related group with representatives in many major habitats in temperate North America. This study compares three populations of *N. cinerea* (from the Pacific coast of Oregon, the high Rocky Mountains of central Colorado, and the high deserts of eastern Utah) and two populations of *N. albigula* (from the same high deserts of eastern Utah and the low deserts of southwestern Arizona) with respect to microclimatic temperatures during winter and summer, and regulation of body temperature.

## THE FIVE POPULATIONS

*Neotoma cinerea* occurs in the cooler, mountainous regions of western North America (Fig. 1). It ranges from northwestern Canada southward along the Pacific Coast to Oregon and eastward to the Black Hills, South Dakota. To the south it reaches the mountainous regions of southern Nevada, northern Arizona, and northern New Mexico, where it occurs only at higher elevations (above 4000 feet). *N. albigula*, primarily a desert inhabi-

tant (Fig. 1), is sympatric with the lowest populations of *N. cinerea* in southern Utah and Colorado and northern Arizona and New Mexico. From there it ranges southward to central Mexico, eastward to the high plains of eastern Colorado and western Texas, and westward to the valley of the lower Colorado River (Hall and Kelson, 1959).

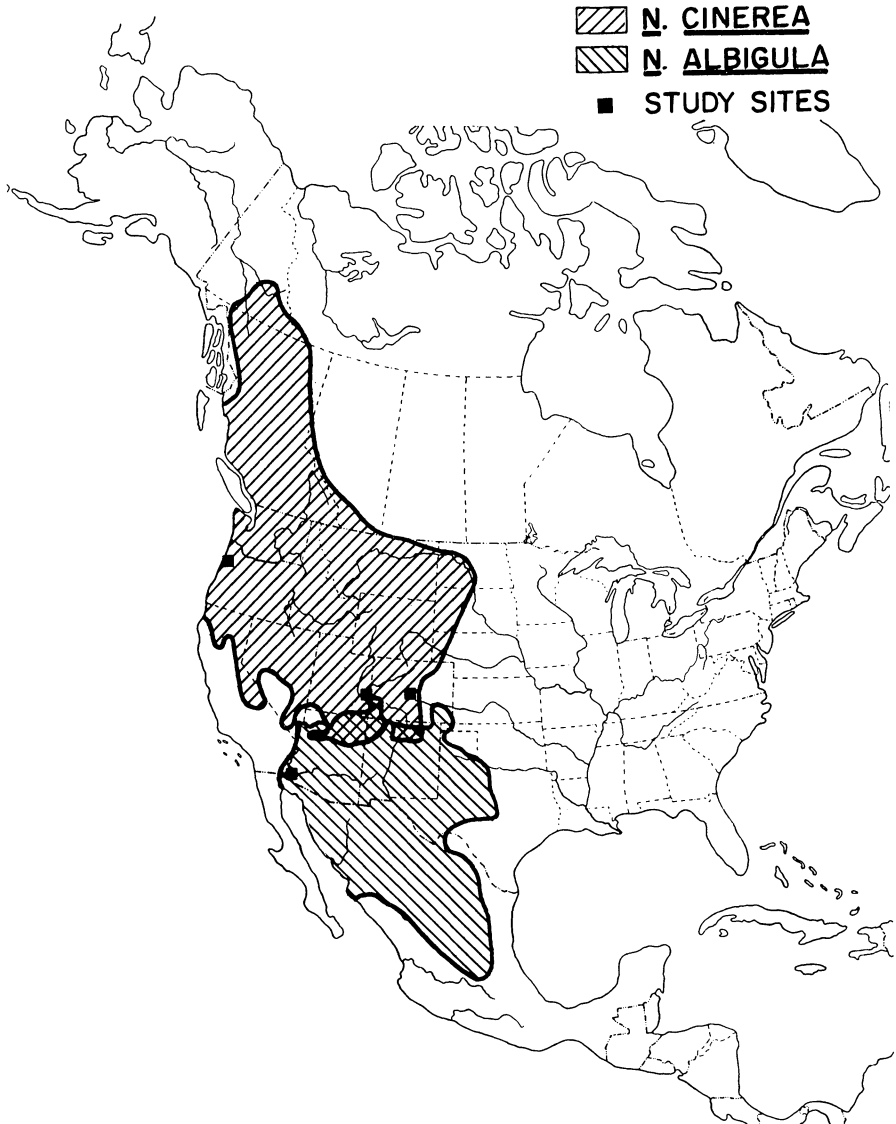


FIG. 1. The relation of the study areas to the geographic distributions of *Neotoma cinerea* and *N. albigula*.



Five populations, representing four localities (Fig. 1), were used for both the laboratory and field aspects of this study. The choice of these localities represents a compromise between attempts to maximize the geographic distances and climatic differences between them and to minimize problems of accessibility. The five populations and the locations of the study sites are as follows:

1. Coastal *N. cinerea* (*N. c. fusca*): elevations of less than 600 feet along the Little Nestucca River in the vicinity of Dolph, Tillamook County, Oregon.
2. Highland *N. cinerea* (*N. c. orolestes*): elevations of 8000 to 10,000 feet in the mountains above Idaho Springs, Clear Creek County, Colorado.
3. High desert *N. cinerea* (*N. c. arizonae*): elevations of 4000 to 5000 feet in Castle Valley and the Colorado River Valley just northeast of Moab, Grand County, Utah.
4. High desert *N. albigula* (*N. a. brevicauda*): elevation of 4800 feet in Castle Valley, Grand County, Utah.
5. Low desert *N. albigula* (*N. a. venusta*): elevation of 250 feet, 14 miles east of Yuma, Yuma County, Arizona.

All available evidence supports the assumption that the populations sampled represent two biological species, each composed of interbreeding populations. Although no complete study of geographic variation is available for either species, the works of Hooper (1940) and Finley (1958) suggest the patterns of intergradation which probably characterize these species. Some local populations may be geographically isolated, particularly in the region of extremely dissected topography of the upper Colorado River drainage system. However, the dramatic altitudinal shifts in climate and vegetation which have occurred in southwestern United States within the last 40,000 years (Wells and Berger, 1967; Wells and Jorgensen, 1964) suggest that any isolates are likely of relatively recent origin. There are no reports of natural or laboratory hybrids between *N. cinerea* and *N. albigula*, and the pronounced differences between these species make the chances of such hybridization very unlikely.

In view of the recent discussion of the role of body size and relative extent of appendages in the climatic adaptation of homeotherms (Scholander, 1955; Mayr, 1956), intraspecific variation in these characters is worth mentioning. In *N. cinerea*, the well-defined variation in body size follows Bergmann's rule. Individuals of northern populations are generally larger than those of southern populations (Hooper, 1940). That body size is correlated with climate rather than latitude per se is supported by the situation in Colorado where the populations inhabiting the higher parts of the Rocky Mountains in the central part of the state are composed of significantly

larger individuals than the populations which inhabit the plateaus and high deserts to the west (Finley, 1958). Individuals of *N. cinerea* from the Pacific Coast have relatively longer tails and hind feet than inland populations (Hooper, 1940), but this is perhaps an adaptation to the arboreal habits of

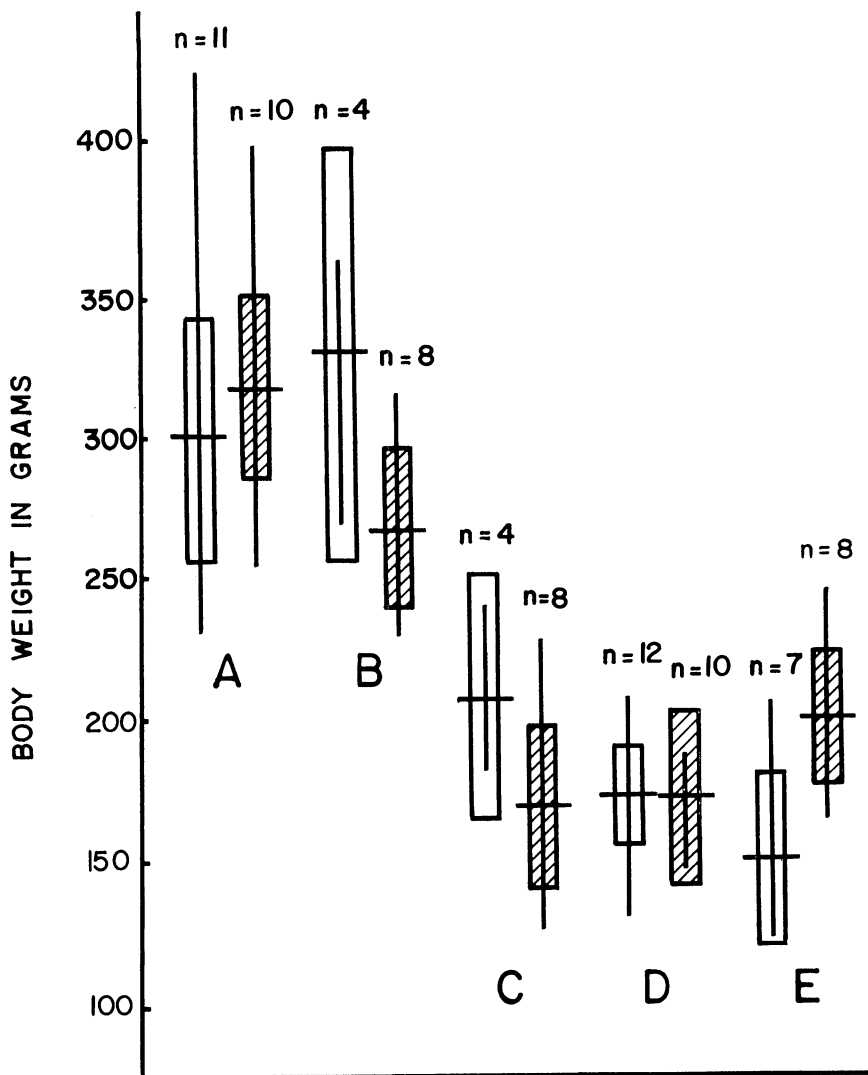


FIG. 2. Body weights of the five populations: A, coastal *N. cinerea*; B, highland *N. cinerea*; C, high desert *N. cinerea*; D, high desert *N. albigula*; E, low desert *N. albigula*. Hatched diagrams indicate laboratory adults; unhatched diagrams, wild adults (see text). Vertical lines represent ranges; horizontal lines, mean values; rectangles, 95 per cent confidence intervals.

the coastal populations in contrast to the more terrestrial or rock climbing habits of the other populations rather than to any climatic factor. Little intraspecific variation exists in body size or relative length of appendages in *N. albigula*. The relatively shorter tail of the northern race *N. a. brevicauda* (Durrant, 1934) constitutes an exception.

Figure 2, showing body weights of samples of the five populations, requires some explanation. The samples designated "wild adults" are composed of animals captured and weighed in the field, identified as adults by pelage, and not subsequently used for any laboratory work. The samples designated "laboratory adults" include all individuals used in the laboratory studies. These animals were captured in the field as adults or subadults, or were born in the laboratory. The weights used here are the last recorded for each individual.

Differences between the mean weights of the wild and laboratory samples of the same populations reflect the age and condition of the animals making up the samples. The lower mean weights for the laboratory adults of the highland and high desert populations of *N. cinerea* may be attributed to the small sample sizes of the wild populations and the greater proportion of younger (and therefore lighter) animals in the laboratory samples. Laboratory adults average heavier than wild adults in the low desert samples of *N. albigula*, and this is probably owing to the better condition of the laboratory animals. Wild adults were almost all excessively lean, whereas the laboratory animals had fat deposits comparable to the wild and laboratory high desert *N. albigula*.

Body weights of the coastal and highland populations of *N. cinerea* are similar and significantly larger than those of the other three populations, which closely resemble each other (Fig. 2). Next to body size and coloration, length of tail is the most conspicuous and significant character in which the five populations differ. The mean ratio of length of tail to length of body is greater for the samples of coastal *N. cinerea* and low desert *N. albigula* (0.87 and 0.88, respectively) than for the other three populations (0.73 to 0.76).

## THE MACROENVIRONMENTS

### THE HABITATS

Within their geographic and altitudinal ranges, *N. cinerea* and *N. albigula* occur in a wide variety of habitats. Their only general requirements seem to be the presence of vegetation suitable as a source of both food and water and the availability of shelters which provide favorable microclimates and protection from predators. The study areas represent some of the more diverse habitats frequented by the two species. These are pictured in Figures 3 and 4 and described briefly below:

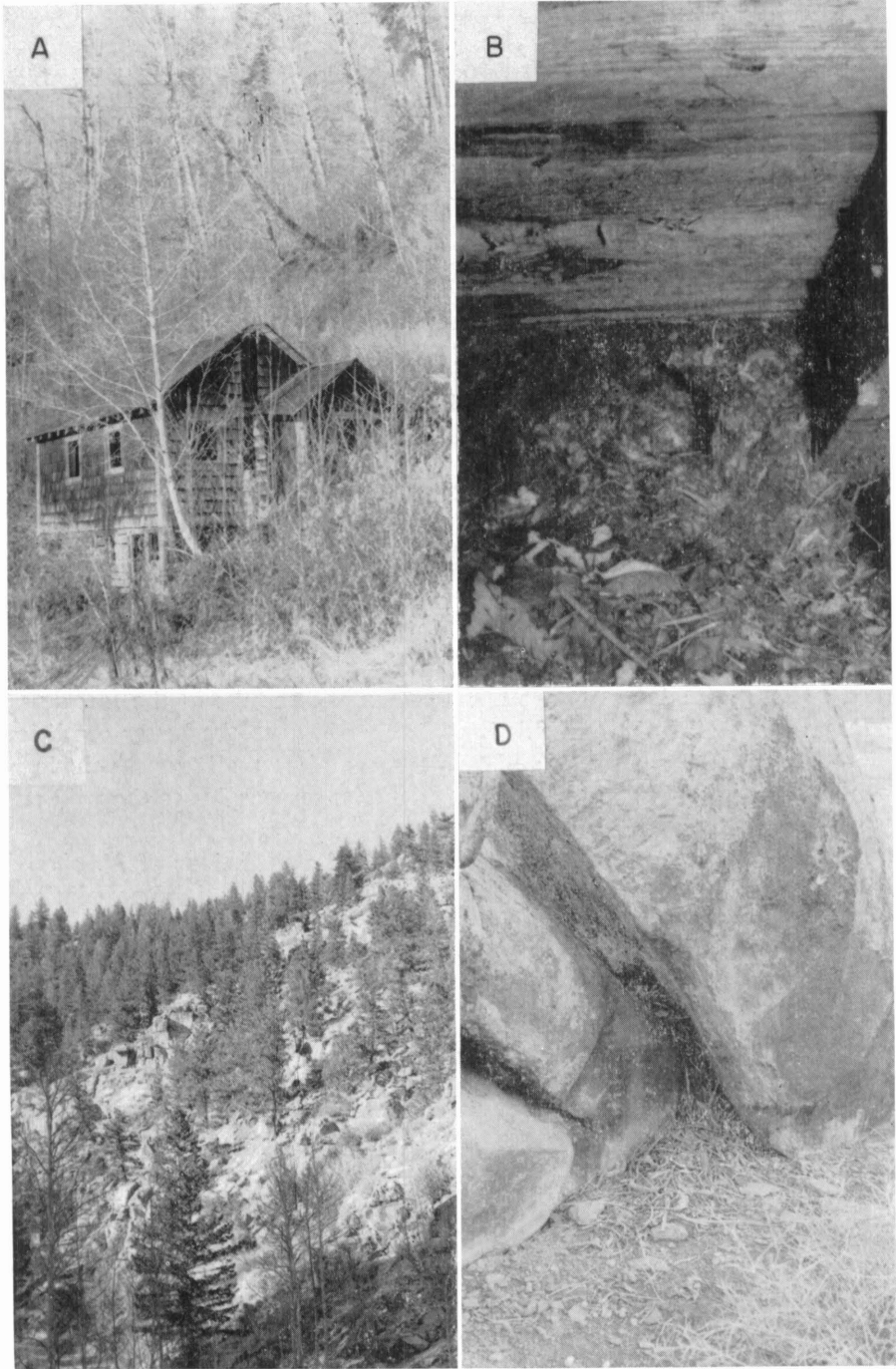


FIG. 3. Habitats and dens of *Neotoma cinerea*. A, habitat of coastal *N. cinerea*, showing an abandoned building used for a den; B, soft, fibrous nest of coastal *N. cinerea*; C, habitat of highland *N. cinerea*; D, den typical of highland and high desert *N. cinerea*.

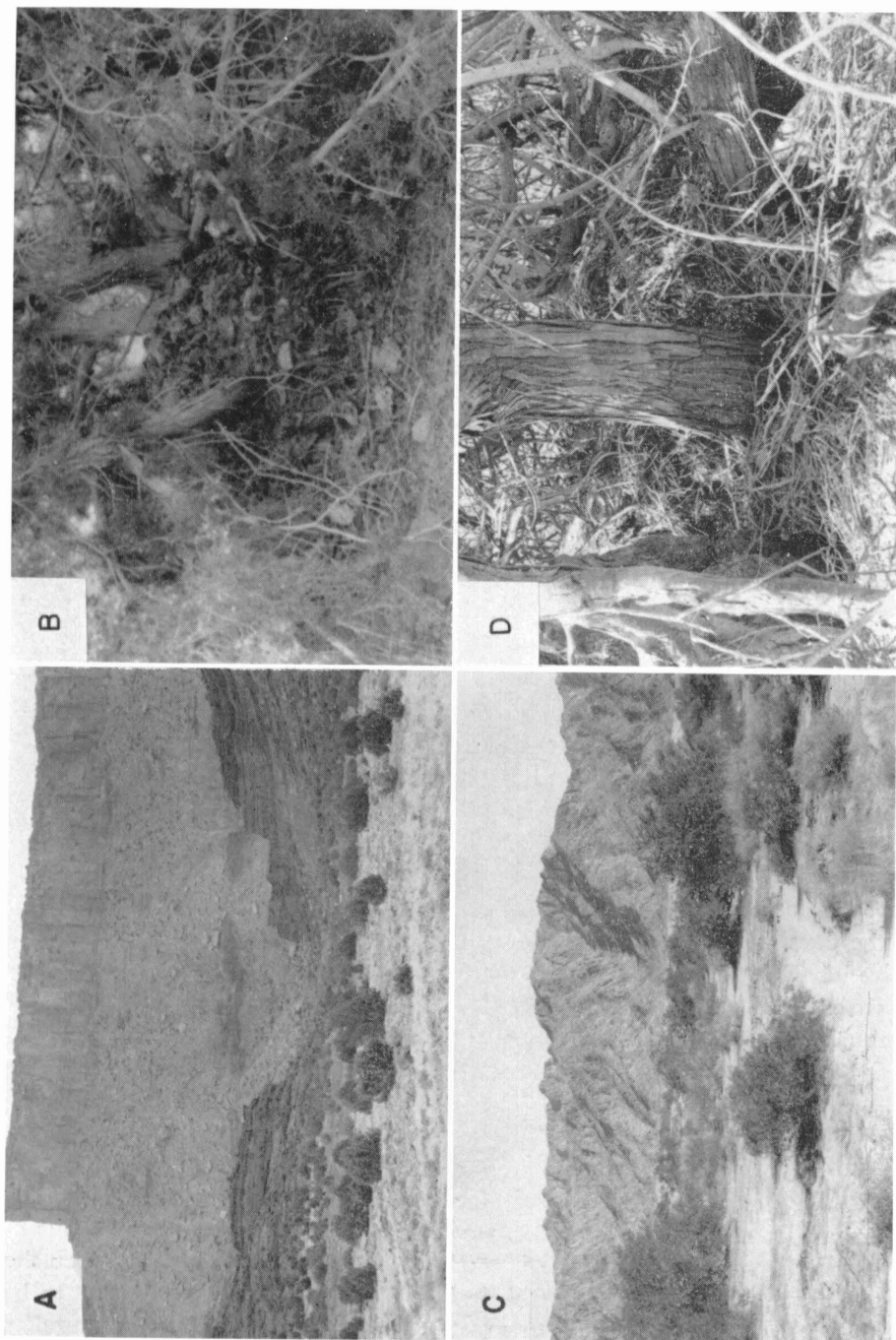


FIG. 4. Habitats of *Neotoma cinerea* and *N. albigula*, and dens of *N. albigula*. A, habitats of high desert *N. cinerea* and *N. albigula* (*N. albigula* occurs on the valley floor in the foreground, and *N. cinerea* occupies the ledgerrock and cliffs in the background); B, den of high desert *N. albigula*; C, habitat of low desert *N. albigula*. D, den of low desert *N. albigula*.

1. Coastal *N. cinerea*: These woodrats inhabit the lush, deciduous-coniferous forests covering the coastal lowlands of northern Oregon. The rats are most abundant around abandoned lumber camps and farms. Here, buildings are used for dens, and the woody and herbaceous second growth, which grows so abundantly in such areas, is the primary source of food. This species is probably more abundant in this area now than before settlement by white men, when it probably relied on hollow trees for den sites. Rock cliffs, the preferred den sites of more inland populations of *N. cinerea*, are uncommon here and those that exist are mostly damp and unsuitable for habitation by woodrats.

2. Highland *N. cinerea*: *N. cinerea* is abundant at elevations between 8000 and 10,000 feet in the central highlands of Colorado wherever cliffs or rock outcrops offer suitable den sites. At the study area on the eastern slope of the Rockies, scattered pines (*Pinus aristata*), Douglas firs (*Pseudotsuga taxifolia*), and aspens (*Populus tremuloides*) comprise the predominant vegetation. Although rock dens are preferred and are occupied almost exclusively when the population is low, these rats also inhabit abandoned dwellings, mills, and mine shafts.

3. High desert *N. cinerea*: In the canyonlands along the Colorado River in southeastern Utah, *N. cinerea* makes its dens in crevices in the vertical sandstone cliffs that dominate the landscape. At the western end of Castle Valley, it also lives under the huge blocks of rock which have weathered off the cliff faces and rolled far out onto the valley floor. Along the cliffs, juniper (*Juniperus utahensis*) and scrub oak (*Quercus gambellii*) (the latter only in more moist, protected situations) are the most conspicuous elements of the vegetation. Sagebrush (*Artemisia tridentata*) is the dominant plant around the dens on the valley floor. The study area, at an elevation between 4000 and 5000 feet, represents the lower altitudinal limit of the range of *N. cinerea* in this area. In the nearby La Salle Mountains this animal occurs at much higher elevations, probably to timberline.

4. High desert *N. albigula*: This woodrat is common in those areas on the floor of Castle Valley where there are scattered junipers and an abundance of prickly pear (*Opuntia sp.*) and grass. Houses of prickly pear pads, sticks, dung, and other debris are constructed at the bases of junipers; dens are also found in crevices in rock faces or under boulders. Where the valley floor meets the encircling sandstone cliffs, *N. albigula* reaches the limits of its range and is locally sympatric with *N. cinerea*. Competition between the two species is possible but unlikely in such situations. Food appears to be abundant. The species tend to select different den sites—*N. cinerea* prefers vertical crevices high in the rimrock, whereas *N. albigula* tends to live under fallen boulders and in horizontal crevices at the bases of the cliffs. Both

species are less likely to compete with each other than with *N. mexicana*, which also occurs in such areas and makes its dens under boulders and in crevices in the rocks.

5. Low desert *N. albigula*: In extreme southwestern Arizona, *N. albigula* is most abundant in the dry washes where vegetation is more abundant and luxuriant than on the surrounding desert floor. Mesquite (*Prosopis juliflora*), palo verde (*Cercidium floridum*), and creosote bush (*Larrea tridentata*) constitute the dominant vegetation in this habitat. The vast majority of dens are constructed at the bases of larger mesquites. These plants provide shade, also thorny sticks for the construction of houses, and juicy leaves and seed pods, the main items in the diet. The sandy soil of the washes permits the construction of rather well-developed subterranean tunnels, a conspicuous feature of the dens of these woodrats.

#### THE MACROCLIMATES

Climatic conditions of the sort measured by U.S. Weather Bureau stations are of interest because they provide a general index to the range of microclimatic conditions available to small mammals in an area. Although insufficient, they are usually the best available indicators of the climatic conditions encountered by small mammals during those periods in which they are active and abroad.

Table 1 presents relevant U.S. Weather Bureau data for a station at approximately the same elevation and within 15 miles of each of the four study sites (U.S. Department of Commerce, 1964). These data describe the major climatic features of each area and will serve as a basis for comparison with the microenvironmental temperatures which will be presented later. The climates of each study area may be summarized briefly as follows:

1. Coastal *N. cinerea*: This population is exposed to the most nearly constant macroclimate owing to the tempering influence of the Pacific Ocean and almost constant cloud cover. Seasonal variation is slight and temperatures above 27° C or below freezing are rare. Rains are frequent and heavy; snow is unusual.

2. Highland *N. cinerea*: In the high Rocky Mountains, daily fluctuations in temperature are great as a result of the high altitude and usually clear weather. Night-time temperatures often fall close to freezing even in midsummer, and in winter they drop well below freezing. Winter snow cover, even at these elevations, is surprisingly light here east of the Continental Divide.

3. High desert *N. cinerea* and *N. albigula*: These populations are exposed to the greatest fluctuations in macroclimatic temperatures. Summer days get very hot but temperatures drop precipitously after dark. Winters

TABLE 1.  
CLIMATES OF THE FOUR STUDY SITES  
(Data from U.S. Weather Bureau)

| Population   | Station                 | Length of<br>record<br>years | Temperature ° C |              | Precipitation<br>Mean Annual<br>mm |
|--|-------------------------|------------------------------|-----------------|--------------|------------------------------------|
|  |                         |                              | Mean<br>Jan.    | Min.<br>July |                                    |
| Coastal <i>N. cinerea</i>                            | Cloverdale, Oregon      | 19                           | 5.7             | 15.8         | 36.7                               |
| Highland <i>N. cinerea</i>                           | Idaho Springs, Colorado | 53                           | -3.0            | 17.0         | 34.4                               |
| High desert <i>N. cinerea</i> and <i>N. albigula</i> | Moab, Utah              | 50                           | -1.9            | 26.2         | 45.0                               |
| Low desert <i>N. albigula</i>                        | Yuma, Arizona           | 14                           | 13.1            | 34.5         | 50.5                               |



are characterized by cool days, and by nights with below-freezing temperatures. Midwinter snow is not unusual, but a deep or lasting snow cover is rare. The annual precipitation averages 224 mm and is quite evenly distributed throughout the year.

4. Low desert *N. albigula*: This population inhabits one of the hottest and driest environments in North America. It is not unusual for summer temperatures to exceed 40° C during the day and remain above 25° C at night. Winters are mild with warm days and cool nights. Frosts are rare. Annual precipitation averages only 56 mm, and less than 5 mm falls during the driest three months, April, May, and June.

### THE MICROENVIRONMENTS

The discovery and utilization of locally favorable conditions or microclimates is one of the important features of the behavior of small mammals. Such behavior permits populations to be successful in habitats where they could not otherwise exist, and it reduces energy requirements and physiological stress in almost all macroenvironments. Woodrats are nocturnal, and their diurnal retreats are either crevices, caves, hollow trees, abandoned buildings, or houses and burrows constructed by the rats themselves. The microhabitats occupied by the five populations of *N. cinerea* and *N. albigula*, and the thermal regimes provided by these retreats, are considered here.

### MATERIALS AND METHODS

Temperatures from the vicinity of woodrat nests were recorded with Yellow Springs Thermistor Telethermometers. The procedure for placing probes depended upon the type of den. For the most accessible and unprotected dens of *N. cinerea*, it was possible to position the probes by hand directly above the nests. Probes were sent deep into rock crevices, using Hayward's (1965b) clip device. The probe was attached to the rump of a rat, which was then released into its den; when it had stopped traveling, the probe was freed from the rat by tugging a light line. Sometimes long, flexible branches were also used to place probes in crevices in rocks. Probes were introduced into houses of *N. albigula* by using Hayward's device or by stabbing a section of aluminum tubing into a chamber within the house, threading a probe through the tubing, then carefully withdrawing the tubing, leaving the probe in position.

Every attempt was made to place probes near nests or in as favorable a situation as was available within each den. Whenever possible, dens were dissected after the completion of the temperature measurements to determine the exact locations of the probes. In some instances, for example, when

nests were deep in crevices in rocks, dissection was impossible. Every effort was made to use occupied dens and those entrances most frequented by their occupants. When a probe was found in a situation which obviously offered less than the maximum protection available in that den, the values obtained from it were discarded.

After the probes were in place, microenvironmental temperatures were recorded at two-hour intervals for 24 hours. Simultaneous records were made of macroclimatic temperatures three feet above the ground in full shade near the den. At least seven acceptable records of microclimatic temperatures were obtained for each population in midsummer and midwinter. Summer measurements were taken between June 22 and July 31, 1966, and the winter records were made between January 7 and February 2, 1967.

### RESULTS

Seven winter and seven summer microenvironmental temperature records for each population are summarized in Table 2. Representative 24-hour records are given in Figures 5 to 7, and photographs of typical den situations are shown in Figures 3 and 4. The microhabitats of each population and the thermal regimes these provided are described below:

1. Coastal *N. cinerea*: Dens of this population were most common in abandoned buildings, one was found under a bridge. The apparent requirements are that they be dry, relatively dark, and inaccessible to predators. Usually the only element of the microenvironment constructed by the rat itself was an open, cupshaped nest composed of dry moss and grass (Fig. 3). Occasionally a pile of sticks and other debris partially shielded the nest, particularly if it was in an exposed situation. This seemed to function in keeping out light and deterring predators.

Protection from macroenvironmental temperatures seemed to be of little importance in den selection. Temperatures at most nests approximated the daily and seasonal changes in the macroenvironmental temperatures (Fig. 5). During the rare periods of sunshine some attic situations were heated to temperatures considerably above those outside (Table 2).

2. Highland *N. cinerea*: These rats most frequently utilized crevices in cliffs and rock outcrops for dens. Less frequently, usually when populations were high, they also occupied abandoned buildings and mine shafts. Like the coastal *N. cinerea*, they build soft, cup-shaped, fibrous nests in dark, dry places within their dens. Sticks and other debris were usually piled in and around the entrances to the dens, but these were characteristically some distance from the nests and probably had little influence upon the microclimates.

The stability of the microenvironmental temperatures was dependent

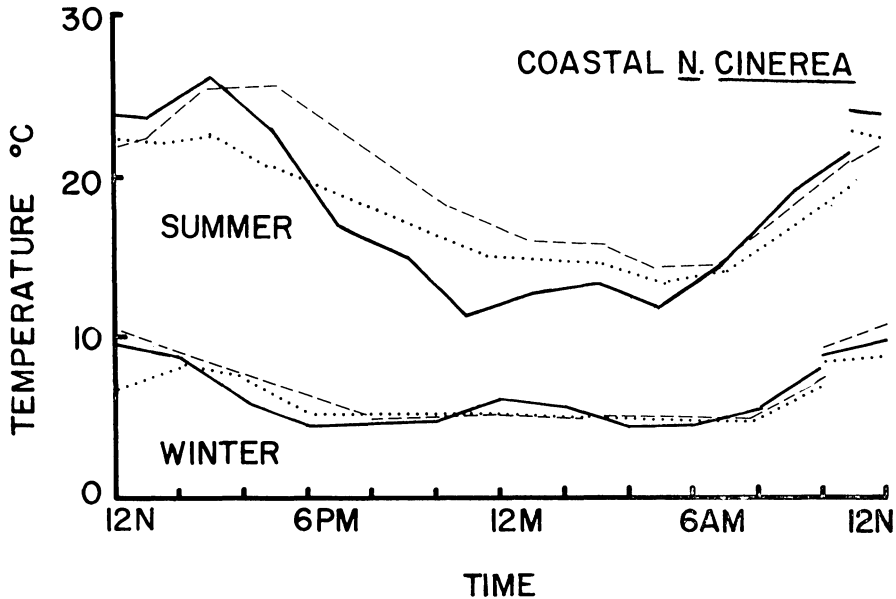


FIG. 5. Microclimatic temperatures of the coastal population of *N. cinerea* during winter and summer. Solid lines represent macroclimatic temperatures; dashed and dotted lines, temperatures in two dens.

upon the type of den (Table 2). Crevices in rocks provided temperatures that fluctuated no more than a few degrees daily and only about 15° C seasonally. Nests in buildings and mine shafts were subjected to more extreme temperatures. On warm summer days, nest temperatures averaged about 13° C; this was slightly lower than the mean macroenvironmental temperatures. In winter the microenvironments offered by rock dens remained near freezing, despite lower average temperatures outside.

3. High desert *N. cinerea*: The representatives of this population occupied dens associated with rocks, either cracks in sandstone cliffs or crevices under boulders. The animals spent the day in fiber nests in the deeper reaches of these places. The thermal characteristics of the sandstone rocks provided interesting summer microclimates of the rats living in and under them. During the long hot summer days, these rocks became heated by the intense solar radiation to the extent that temperatures three or four feet under huge boulders exceeded 30° C (Table 2). During the night and the early part of the next day, as they gradually lost heat, the rocks remained considerably warmer than the surrounding air. The thermal inertia of the large rocks was so great that changes in the microclimatic temperatures of woodrat dens lagged far behind changes in temperature outside (Fig. 6), and a very hot day sometimes produced elevated microenvironmental tempera-

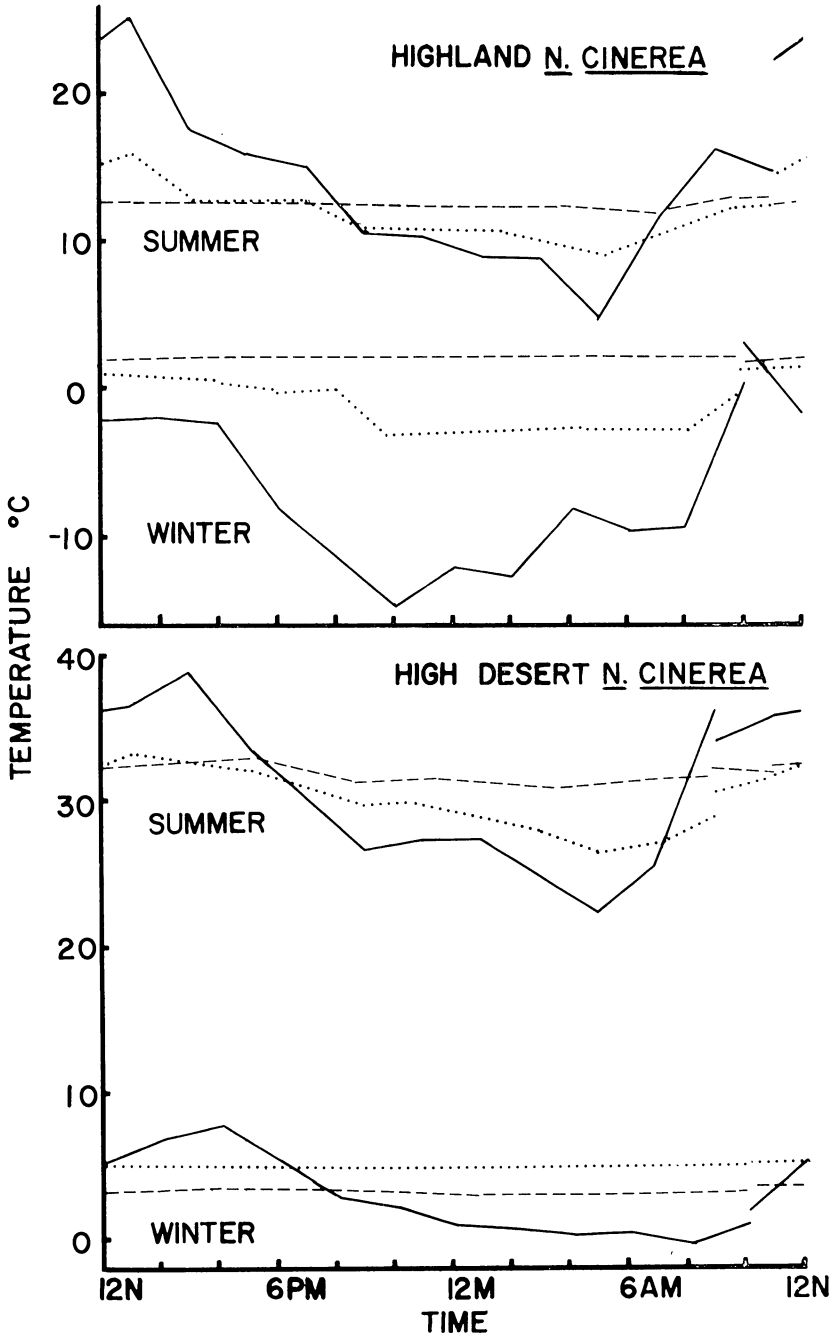


FIG. 6. Microclimatic temperatures of the highland and high desert populations of *N. cinerea* during winter and summer. Solid lines represent macroclimatic temperatures; dashed and dotted lines, temperatures in two dens.

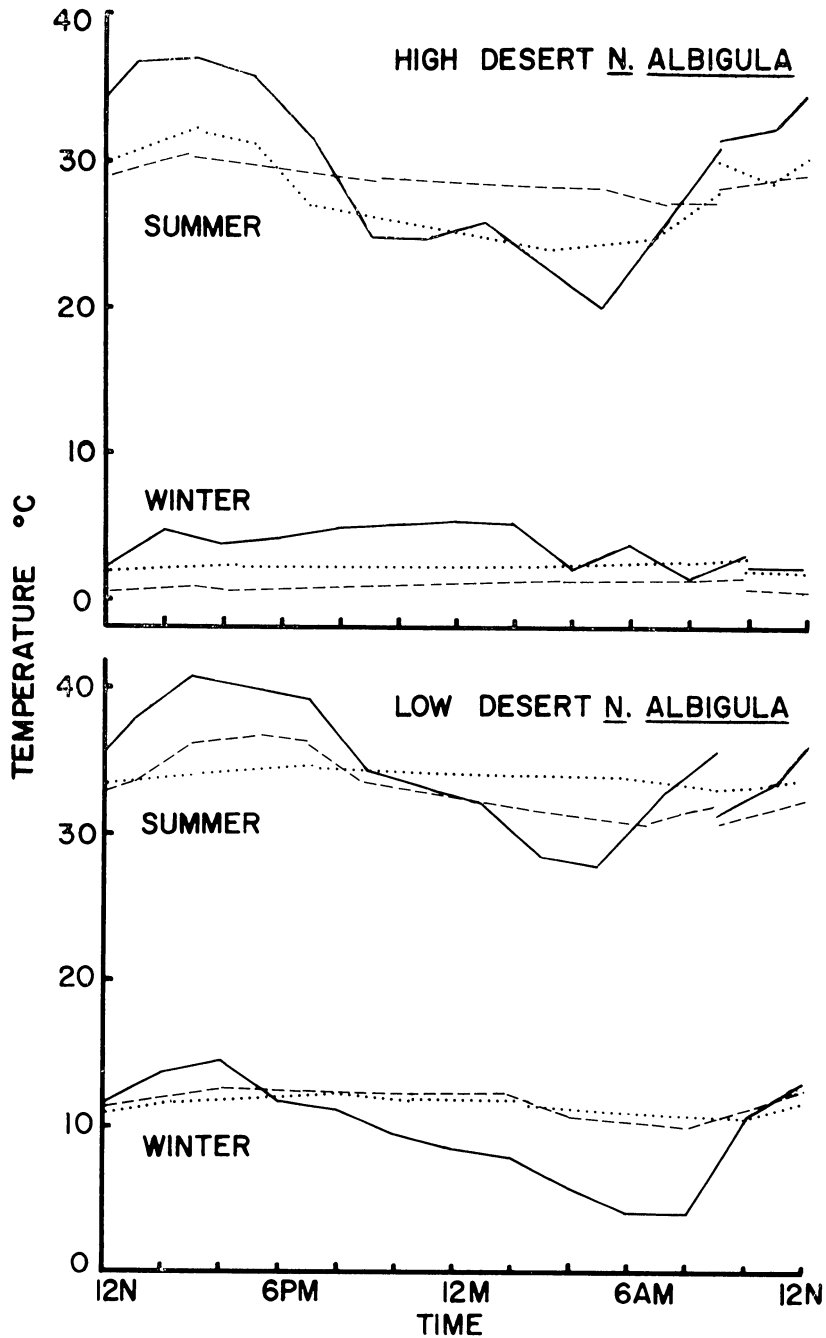


FIG. 7. Microclimatic temperatures of the high desert and low desert populations of *N. albigula* during winter and summer. Solid lines represent macroclimatic temperatures, dashed and dotted lines, temperatures in two dens.

tures that persisted well into the subsequent day and perhaps longer. In midwinter these rats were exposed to microclimatic temperatures just above freezing.

4. High desert *N. albigula*: Although they sometimes lived under boulders or in crevices at the bases of cliffs, these rats usually built houses constructed of prickly pear pads, sticks, dry dung, and other debris, in the deep shade of junipers. These houses were generally 40 to 60 cm high and 90 to 150 cm in diameter. They usually had one or two large chambers above ground and a system of tunnels in the mixture of debris and soil that constituted the base of the house. Sometimes these tunnels extended a few inches below ground level, but they were always shallow. One or more nests were found in either the upper or the lower chambers.

The tunnels at and below ground level provided the most stable microclimates. The temperatures found in such situations were remarkably similar to those observed in the dens of sympatric *N. cinerea* at the same time of year (Table 2). However, the fluctuations of temperature in the microenvironment of *N. albigula* followed the daily macroenvironmental fluctuations more closely than those in dens of *N. cinerea*.

5. Low desert *N. albigula*: These rats constructed their houses almost exclusively in the deep shade of large mesquites. The construction varied, and the size of the stick pile, which constituted the above-ground portion, seemed in a general way to be inversely proportional to the amount of shade. This suggests that the pile may function partially to shade the underlying soil. Although feeding platforms were often located above ground, nests were confined to the subterranean tunnel systems, which were deep and often extensive. Tunnels 10 to 30 cm below ground were characteristic of dens, and much deeper ones were sometimes found.

The deepest of these burrows provided temperatures that fluctuated only a few degrees daily (Table 2). Nevertheless, microclimatic temperatures averaged 33° C and reached as high as 36° C during midsummer. In midwinter the temperatures of the burrows, like those of the macroenvironment, averaged about 15° C lower than in summer.

#### DISCUSSION

A comparison of the microenvironmental temperature regimes of the five populations (Figs. 5 to 7) immediately reveals that the microhabitat of the coastal population of *N. cinerea* is unique in offering almost no protection from daily fluctuations in temperature of the macroenvironment. It is hardly surprising that this population occupies the macroenvironment characterized by the least extreme temperatures and the smallest daily fluctuations.

The other four populations occupy microhabitats that usually provide remarkably stable temperatures in macroenvironments where temperatures fluctuate 15° to 20° C daily. In addition to this stability, the striking similarity between mean microclimatic and mean macroclimatic temperatures for each of these four populations indicates that the den reduces the daily and absolute temperature extremes to which the animals are exposed, but even in their microenvironments the woodrats must face temperatures which fluctuate 15° to 30° C seasonally. It is of interest that such different types of dens, the rock crevices of highland and high desert *N. cinerea*, the large, shaded houses of high desert *N. albigula*, and the subterranean burrows of low desert *N. albigula*, provide similar protection from daily fluctuations in a variety of macroenvironments.

Some records of den temperatures shown in Table 2 are significantly more variable than those of the majority of dens of the population. Some of these records showing the greatest fluctuations may not represent the most favorable microclimates available in these dens. If there were any indication that this was the case, the values for those dens were omitted from the table. The possibility remains that some of these records represent microhabitats that were occupied even though they did not provide equable conditions. It would not be surprising if this happens, particularly when populations are high as they were during the summer of 1966 when many juveniles and subadults were present. If some of these records are indicative of rats occupying marginal microclimates, environmental temperature may exert an important influence upon the dynamics of these populations.

The microclimatic temperatures recorded for the two populations of *N. albigula* are comparable to those obtained by other workers for other populations of this species (Vorhies, 1945; Rainey, 1965) and other species of woodrats that construct houses (Lee, 1963). Temperatures in these woodrat dens are also similar to the burrow temperatures of *Peromyscus maniculatus* which live in similar macrohabitats (Hayward, 1965 *b.*). Most of the microclimates recorded here show greater daily fluctuations than those of the deepest burrowing desert rodents (Vorhies, 1945) or those of *Peromyscus maniculatus* under forest cover or a blanket of snow (Hayward, 1965 *b.*). The heat stored deep in the soil is important during winter in maintaining microenvironmental temperatures near the freezing point for highland *N. cinerea* and *Peromyscus maniculatus* (Hayward, 1965 *b.*), despite lower mean outside temperatures.

It must be emphasized that the temperatures of the microclimates measured here indicate the conditions available to each population. The specific patterns of behavior by the individual rats determine when and to what extent these conditions are utilized. Woodrats are nocturnal and spend the

TABLE 2  
MICROCLIMATIC TEMPERATURES OF THE FIVE POPULATIONS

| No                                 | Description of microhabitat                                  | Temperature °C |      |      |               |      |       |
|------------------------------------|--|----------------|------|------|---------------|------|-------|
|                                    |  | Microclimatic  |      |      | Macroclimatic |      |       |
|                                    |  | Mean           | Max  | Min. | Mean          | Max  | Min.  |
| <i>Coastal N. cinerea</i> —Summer  |  |                |      |      |               |      |       |
| 1                                  | Nest on a shelf under eaves in a barn                        | 17.7           | 22.7 | 13.1 | 17.6          | 26.0 | 11.2  |
| 2                                  | Nest behind trash pile in abandoned attic                    | 22.3           | 32.4 | 13.8 | 17.6          | 26.0 | 11.2  |
| 3                                  | Nest in open in abandoned attic                              | 19.4           | 25.7 | 13.8 | 17.6          | 26.0 | 11.2  |
| 4                                  | Nest on rafters of abandoned cabin                           | 17.4           | 22.4 | 13.2 | 18.8          | 25.5 | 11.4  |
| 5                                  | Nest on beam on wall of abandoned barn                       | 18.7           | 24.3 | 12.9 | 18.8          | 25.5 | 11.4  |
| 6                                  | Nest on beams of bridge                                      | 18.4           | 20.2 | 16.8 | 17.8          | 23.5 | 14.1  |
| 7                                  | Nest under a board in attic of abandoned cabin               | 18.4           | 22.3 | 16.0 | 17.8          | 23.5 | 14.1  |
| <i>Coastal N. cinerea</i> —Winter  |  |                |      |      |               |      |       |
| 1                                  | Nest under edge of stick pile on floor of abandoned shed     | 7.2            | 9.3  | 6.1  | 6.5           | 9.6  | 4.6   |
| 2                                  | Nest in open in attic of abandoned house                     | 6.3            | 8.5  | 4.8  | 6.3           | 9.6  | 4.9   |
| 3                                  | Nest under eaves of attic of abandoned house                 | 6.6            | 9.1  | 4.8  | 6.3           | 9.6  | 4.9   |
| 4                                  | Nest on high shelf in room of abandoned lumber camp          | 6.5            | 10.2 | 4.9  | 6.3           | 9.6  | 4.9   |
| 5                                  | Nest under eaves in attic of abandoned house                 | 6.5            | 10.2 | 5.0  | 6.3           | 9.6  | 4.9   |
| 6                                  | Nest on beam in basement of abandoned house                  | 7.0            | 10.3 | 5.4  | 7.5           | 14.5 | 5.0   |
| 7                                  | Nest on rafters of abandoned cabin                           | 6.5            | 10.2 | 4.9  | 7.5           | 14.5 | 5.0   |
| <i>Highland N. cinerea</i> —Summer |  |                |      |      |               |      |       |
| 1                                  | Nest within inside partition in abandoned building           | 12.7           | 17.8 | 7.6  | 14.7          | 26.2 | 6.0   |
| 2                                  | Nest within outer wall of abandoned building                 | 13.1           | 24.1 | 5.6  | 14.7          | 26.2 | 6.0   |
| 3                                  | 135 cm back in crevice in rock outcrop                       | 13.8           | 14.9 | 12.2 | 14.7          | 26.2 | 6.0   |
| 4                                  | 43 cm back in crevice in rock outcrop                        | 12.4           | 13.0 | 12.0 | 14.0          | 25.0 | 5.2   |
| 5                                  | 43 cm back in crevice in rock outcrop                        | 13.0           | 13.2 | 12.7 | 14.0          | 25.0 | 5.2   |
| 6                                  | Nest 91 cm back in abandoned mine shaft                      | 11.9           | 16.0 | 9.1  | 14.0          | 25.0 | 5.2   |
| 7                                  | Nest 740 cm back in covered entrance to abandoned mine shaft | 13.7           | 16.0 | 11.0 | 14.8          | 23.2 | 8.0   |
| <i>Highland N. cinerea</i> —Winter |  |                |      |      |               |      |       |
| 1                                  | 104 cm back in vertical crevice in cliff                     | 0.3            | 3.8  | -1.9 | -6.6          | 2.9  | -14.7 |
| 2                                  | 135 cm back in vertical crevice in cliff                     | 2.0            | 2.2  | 1.7  | -6.6          | 2.9  | -14.7 |
| 3                                  | 104 cm back under fallen block of rock                       | 1.0            | 3.0  | -0.2 | -6.6          | 2.9  | -14.7 |
| 4                                  | 74 cm back in vertical crevice between two rocks             | -1.3           | 1.2  | -3.2 | -6.6          | 2.9  | -14.7 |



TABLE 2 (Cont.)

| No                                     | Description of microhabitat  | Temperature °C |       |       |               |      |      |
|--|--|----------------|-------|-------|---------------|------|------|
|  |  | Macroclimatic  |       |       | Microclimatic |      |      |
|  |  | Mean           | Max   | Min.  | Mean          | Max  | Min. |
| 5                                      | 91 cm back in crevice in tall pillar of rock                             | -2.0           | -1.0  | -3.1  | -4.8          | 4.8  | -9.8 |
| 6                                      | 104 cm back under large boulder  | 2.1            | 2.9   | 1.6   | -4.8          | 4.8  | -9.8 |
| 7                                      | 122 cm back in cleft in vertical cliff                                   | -0.4           | 2.4   | -3.7  | -4.8          | 4.8  | -9.8 |
| High Desert <i>N. cinerea</i> —Summer  |  |                |       |       |               |      |      |
| 1                                      | 91 cm into crevice under large boulder                                   | 30.1           | 33.3  | 26.6  | 30.8          | 38.9 | 22.5 |
| 2                                      | 61 cm into crevice under large boulder                                   | 30.0           | 32.9  | 27.3  | 30.8          | 38.9 | 22.5 |
| 3                                      | 43 cm into crevice under large boulder                                   | 30.0           | 34.2  | 26.3  | 30.8          | 38.9 | 22.5 |
| 4                                      | 43 cm into crevice from large cavity extending 300 cm under huge boulder | 32.0           | 33.0  | 31.2  | 30.8          | 38.9 | 22.5 |
| 5                                      | 122 cm into crevice under large boulder                                  | 27.5           | 28.7  | 26.9  | 33.6          | 43.0 | 21.1 |
| 6                                      | 122 cm into vertical crevice between rocks                               | 29.8           | 32.6  | 28.2  | 33.6          | 43.0 | 21.1 |
| 7                                      | 43 cm into hole in rock outcrop  | 28.8           | 30.7  | 27.4  | 33.6          | 43.8 | 21.1 |
| High Desert <i>N. cinerea</i> —Winter  |  |                |       |       |               |      |      |
| 1                                      | 74 cm back in crevice behind slab of rock                                | 2.6            | 3.6   | 1.6   | 3.0           | 6.9  | -0.7 |
| 2                                      | 91 cm back in vertical crevice in cliff                                  | 2.4            | 2.7   | 2.2   | 3.0           | 6.9  | -0.7 |
| 3                                      | 74 cm back in horizontal crevice in cliff                                | 2.9            | 3.1   | 2.7   | 3.0           | 6.9  | -0.7 |
| 4                                      | 91 cm back in vertical crevice in cliff                                  | 3.3            | 3.5   | 3.1   | 3.0           | 6.9  | -0.7 |
| 5                                      | 104 cm back in vertical crevice in cliff                                 | 5.0            | 5.2   | 4.8   | 2.6           | 7.7  | -0.3 |
| 6                                      | 91 cm into crack behind slab of rock on cliff                            | 4.9            | 5.2   | 4.8   | 2.6           | 7.7  | -0.3 |
| 7                                      | 104 cm in vertical crevice in cliff                                      | 3.2            | 3.3   | 3.1   | 2.6           | 7.7  | -0.3 |
| High Desert <i>N. albigula</i> —Summer |  |                |       |       |               |      |      |
| 1                                      | Partially subterranean cavity in house under juniper                     | 25.4           | 28.0  | 23.3  | 29.3          | 34.9 | 20.9 |
| 2                                      | Subterranean cavity in house under juniper                               | 27.8           | 33.2  | 21.3  | 29.3          | 34.9 | 20.9 |
| 3                                      | At ground level under large juniper                                      | 28.4           | 35.3  | 20.9  | 29.3          | 34.9 | 20.9 |
| 4                                      | Partially subterranean cavity in house under juniper                     | 26.5           | 29.4  | 24.3  | 29.3          | 34.9 | 20.9 |
| 5                                      | Ground level in house under juniper                                      | 28.0           | 32.2  | 24.2  | 29.4          | 37.2 | 20.3 |
| 6                                      | Ground level in house next to large rocks                                | 28.9           | 30.9  | 27.5  | 29.4          | 37.2 | 20.3 |
| 7                                      | Subterranean cavity in house under juniper                               | 28.1*          | 30.1* | 26.3* | 29.4          | 37.2 | 20.3 |
| High Desert <i>N. albigula</i> —Winter |  |                |       |       |               |      |      |
| 1                                      | Subterranean cavity in house under juniper                               | 3.3            | 4.5   | 1.8   | 3.8           | 5.5  | 1.7  |
| 2                                      | Partially subterranean cavity among rocks in house under juniper         | 2.9            | 4.5   | 1.4   | 3.9           | 5.6  | 1.3  |
| 3                                      | Crevice far under large boulder  | 3.2            | 4.3   | 2.5   | 3.9           | 5.6  | 1.3  |
| 4                                      | Ground level in house under juniper                                      | 2.1            | 3.5   | 1.5   | 3.9           | 5.6  | 1.3  |

TABLE 2 (Cont.)

| No                                    | Description of microhabitat   | Temperature °C |      |      |               |      |      |
|---------------------------------------|---|----------------|------|------|---------------|------|------|
|                                       |   | Macroclimatic  |      |      | Microclimatic |      |      |
|                                       |   | Mean           | Max  | Min. | Mean          | Max  | Min. |
| 5                                     | Subterranean tunnel in house under juniper  | 2.4            | 3.0  | 2.0  | 3.9           | 5.6  | 1.3  |
| 6                                     | Partially subterranean cavity in house under juniper                              | 1.4            | 1.8  | 1.1  | 3.9           | 5.6  | 1.3  |
| 7                                     | Subterranean tunnel in small house under dead juniper                             | 1.2            | 1.7  | 0.7  | 3.9           | 5.6  | 1.3  |
| Low Desert <i>N. albigula</i> —Summer |   |                |      |      |               |      |      |
| 1                                     | In cavity 10 cm below ground in medium-sized house at base of mesquite            | 33.5           | 36.3 | 32.2 | 34.6          | 41.0 | 28.1 |
| 2                                     | In tunnel 10 cm below ground in large house at base of mesquite                   | 34.0           | 34.8 | 33.2 | 34.6          | 41.0 | 28.1 |
| 3                                     | In tunnel 2.5 cm below ground in large house between two mesquites                | 33.4           | 37.2 | 31.2 | 34.6          | 41.0 | 28.1 |
| 4                                     | In tunnel 15 cm below ground in small house at base of mesquite                   | 34.0           | 38.7 | 31.2 | 34.4          | 41.5 | 27.8 |
| 5                                     | Deep in tunnel below ground in medium-sized house at base of mesquite             | 33.7           | 34.9 | 32.8 | 34.4          | 41.5 | 27.8 |
| 6                                     | In tunnel 30 cm below ground in large house at base of mesquite                   | 32.9           | 34.4 | 31.9 | 34.4          | 41.5 | 27.8 |
| 7                                     | In tunnel 25 cm below ground in medium-sized house at base of mesquite            | 34.1           | 37.4 | 32.4 | 34.4          | 41.5 | 27.8 |
| Low Desert <i>N. albigula</i> —Winter |   |                |      |      |               |      |      |
| 1                                     | In cavity deep below ground in small house under bushes at base of mesquite       | 15.2           | 15.6 | 14.9 | 10.0          | 14.2 | 5.0  |
| 2                                     | In tunnel 30 cm below ground in medium-sized house at base of mesquite            | 11.5           | 12.1 | 10.7 | 9.7           | 14.3 | 4.1  |
| 3                                     | In tunnel 30 cm below ground in medium-sized house under dense brush              | 12.5           | 13.7 | 11.0 | 9.7           | 14.3 | 4.1  |
| 4                                     | In tunnel 15 cm below ground in large house in flood debris between two mesquites | 11.7           | 12.5 | 10.1 | 9.7           | 14.3 | 4.1  |
| 5                                     | In tunnel 15 cm below ground in medium-sized house under mesquite                 | 11.0           | 13.3 | 9.0  | 9.7           | 14.3 | 4.1  |
| 6                                     | In tunnel 61 cm below ground in medium-sized house at base of mesquite            | 13.9           | 14.8 | 12.4 | 10.0          | 14.2 | 5.0  |
| 7                                     | In tunnel 20 cm below ground in small house at base of mesquite                   | 13.5           | 14.3 | 12.0 | 10.0          | 14.2 | 5.0  |

\* Based on 7 readings.

daylight hours in their dens, thereby avoiding extreme heat outside. Movement within dens in response to changing temperatures probably occurs, and it is likely that the coastal *N. cinerea* abandon their attic dens on those rare occasions when the temperature becomes stressfully high. At night woodrats leave their dens and expose themselves to lower temperatures of the macro-environment. The exact conditions and duration of exposure depend upon the patterning of nocturnal activity, an important variable which has not been measured.

### TEMPERATURE REGULATION

Microhabitat selection permits woodrats to avoid the extreme temperatures of the macroenvironment, but even in their dens the animals are exposed to different thermal regimes. Adaptation to these temperatures should involve modifications of the thermoregulatory process. In woodrats, where active evaporative cooling is of minimal importance (Lee, 1963), homeothermy is maintained by coordinated adjustments of insulation and metabolic heat production. Therefore, the relationships between metabolism and ambient temperature in the different populations should elucidate the main patterns of physiological adaptation.

### MATERIALS AND METHODS

**CARE AND ACCLIMATION OF THE ANIMALS.**—The animals used in these laboratory studies were either trapped in the field during the summers of 1965 and 1966 or born in the laboratory to females pregnant when captured. The rats were individually housed in wire cages and given a diet of Purina Mouse Breeder Chow and fresh apples and vegetables. The temperature in the vivarium was maintained between 19° and 22° C, and relative humidity remained about 27 per cent.

Wild-caught animals were acclimated to the laboratory for 60 days before being used in experiments; laboratory-reared young were permitted to attain adult weight. Only healthy animals in fresh adult pelage were used. These experiments were conducted during the winter months (October to May).

**OXYGEN CONSUMPTION.**—Metabolic responses to ambient temperature were measured by monitoring oxygen consumption with a Beckman G-2 Paramagnetic Oxygen Analyzer and a recording potentiometer. With this system the metabolic rates of three animals could be measured concurrently; the oxygen consumption of each animal was recorded at 12-minute intervals. The rats were contained in chambers constructed by fitting one-gallon metal paint cans with wire mesh platforms and air ports. Dry air flowed through these chambers at rates of about 600 cm<sup>3</sup>/min. Carbon dioxide and water

vapor were absorbed from the air leaving the chambers before it entered the analyzer. A constant temperature cabinet maintained the temperatures in the chambers within 1° C.

Experiments were conducted between 8:00 A.M. and 6:00 P.M. when the rats were normally inactive. Oxygen consumption was recorded for at least three hours at a given ambient temperature. An hour was allowed before and between these test periods to permit the animals to adjust to the new conditions. The pair of values representing the 12-minute period of minimal metabolism for each individual during a test were averaged. From this mean and the flow rate, oxygen consumption (expressed as volume of dry gas at standard temperature and pressure) was calculated using the appropriate formula of Depocas and Hart (1957). Rats were weighed at the beginning and end of each day and the mean weight was used to calculate weight-specific metabolic rates. Animals were tested at temperature intervals of about 5° C between -10° C and their respective upper lethal temperatures. These intervals were somewhat larger at the lower ambient temperatures and somewhat smaller near the upper lethal temperatures. The minimal value for each individual at each temperature tested was plotted to construct a metabolism-temperature curve for each population.

It was impossible to insure that rats were postabsorptive during the metabolic measurements. Depriving them of food for a 5- to 10-hour period before experiments resulted in increased activity, often followed by fatal hypothermia at the lower ambient temperatures. Animals were given no food during tests, and metabolic rates early in the day did not differ from those obtained at the same temperature four to seven hours later. This suggests that specific dynamic action is not an important variable in these studies, probably in part because of the high carbohydrate content of the food.

To evaluate the insulation provided by the moss and grass nests of the coastal *N. cinerea*, the oxygen consumption of three individuals, each in its nest, was measured at two ambient temperatures. For this purpose several nests were collected in the field and the rats were permitted to construct new nests of this material in large glass metabolic chambers.

**BODY TEMPERATURE AND LETHAL AMBIENT TEMPERATURE.**—A Hotpack Environmental Chamber was used to study the relationship between body temperature and ambient temperature and to determine lethal ambient temperatures. Rats were placed in the chamber in 5 × 5 × 12-inch wire cages. Test periods of four hours were chosen to correspond to the length of exposure to a single temperature in the metabolic experiments. Temperature was controlled within 0.5° C and, at all temperatures above 20° C, relative humidity was 50 ± 2 per cent.

Body temperature was measured immediately upon removal of an animal from the chamber. Measurements were made with a Yellow Springs Thermistor Telethermometer by inserting a small probe 4.5 cm into the rectum. The peripheral-core body temperature gradient for the two populations of *N. albigula* was obtained by recording the temperature as the probe was inserted into the rectum in successive 1.0-cm increments.

Upper lethal ambient temperatures were determined by noting the number of individuals that died or suffered permanent heat damage as a result of the four-hour test. The temperatures of successive exposures (at least 24 hours apart) were increased by intervals of 2° C.

STATISTICAL ANALYSIS.—Wilcoxon's two-sample test, modified to deal with unequal-sized samples (Steel and Torrie, 1960), was employed for statistical analysis of the physiological data. This nonparametric test was used to evaluate the differences between the populations in lethal ambient temperatures, peripheral body temperatures (*N. albigula* only), oxygen consumption at approximately 6° C, and insulation indices at about 36° C (desert populations only) and 6° C.

#### RESULTS

OXYGEN CONSUMPTION.—The relationships between metabolism and ambient temperature for all five populations are curvilinear (Figs. 8 to 12).

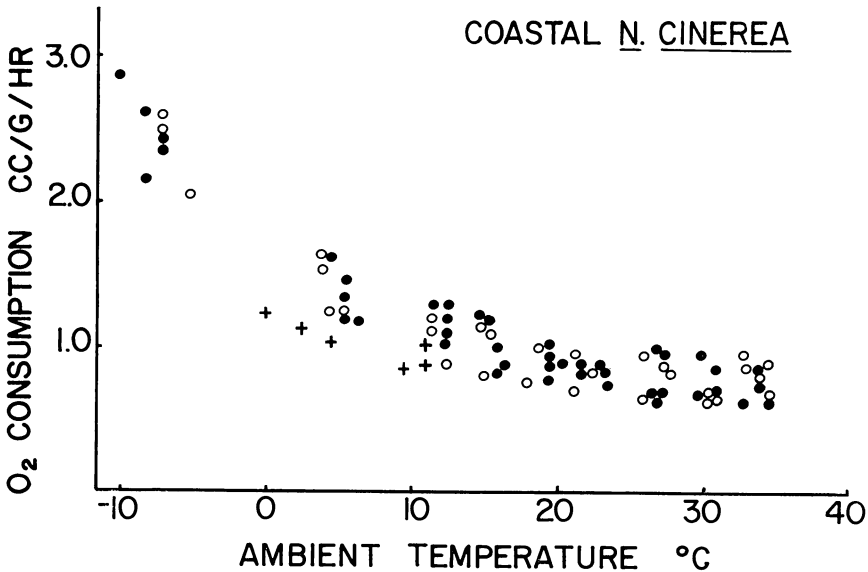


FIG. 8. The relation between oxygen consumption and ambient temperature in coastal *N. cinerea*. Shaded circles represent wild caught individuals; unshaded circles, laboratory-reared individuals; crosses, animals in nests.

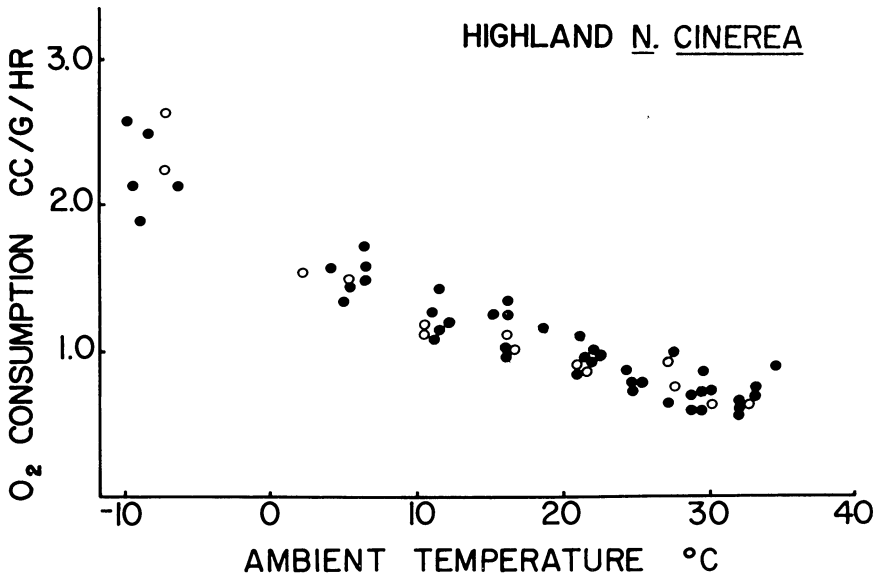


FIG. 9. The relation between oxygen consumption and ambient temperature in highland *N. cinerea*. Shaded circles represent wild caught individuals; unshaded circles, laboratory-reared individuals.

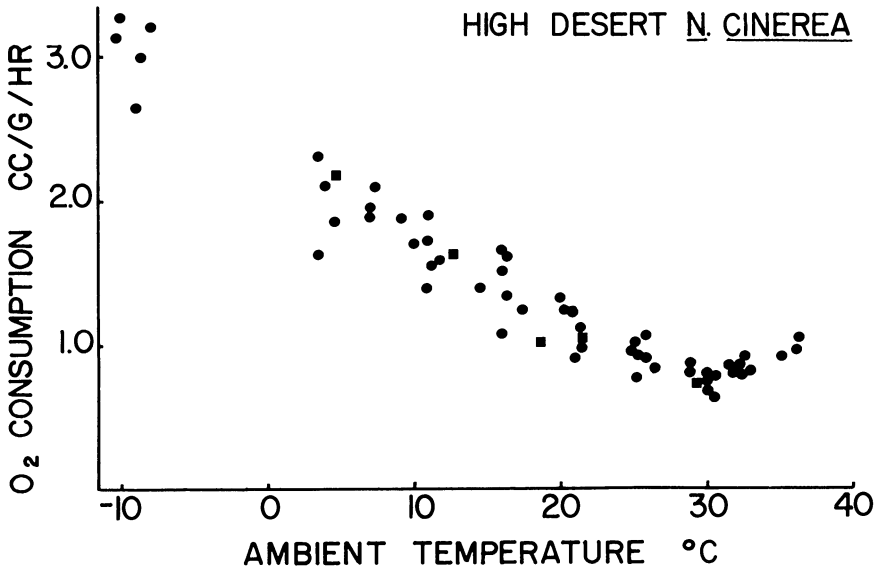


FIG. 10 The relation between oxygen consumption and ambient temperature in high desert *N. cinerea* (shaded circles). Squares indicate a single individual taken in similar habitat and at a similar elevation in Montrose County, Colorado, less than 25 miles from the study site.

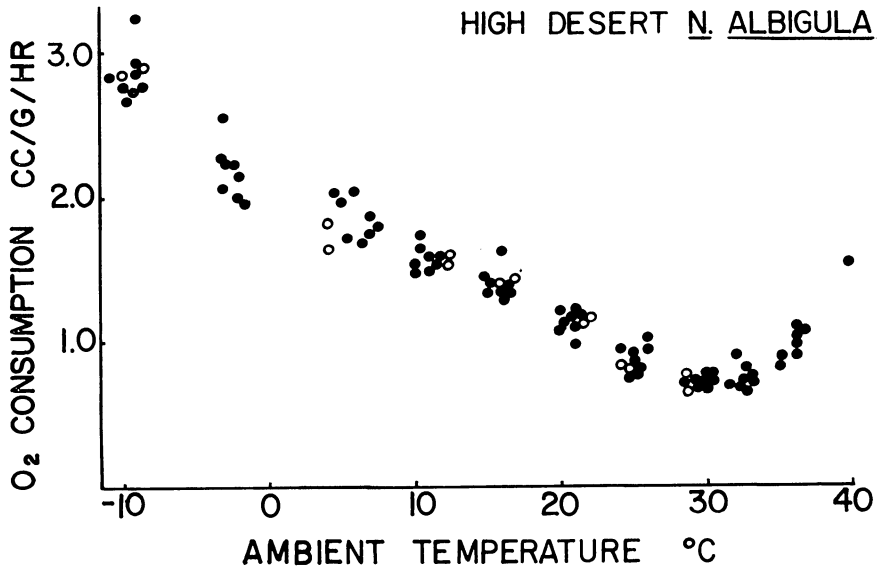


FIG. 11. The relation between oxygen consumption and ambient temperature in high desert *N. albigula*. Shaded circles represent wild caught individuals; unshaded circles, laboratory-reared individuals.

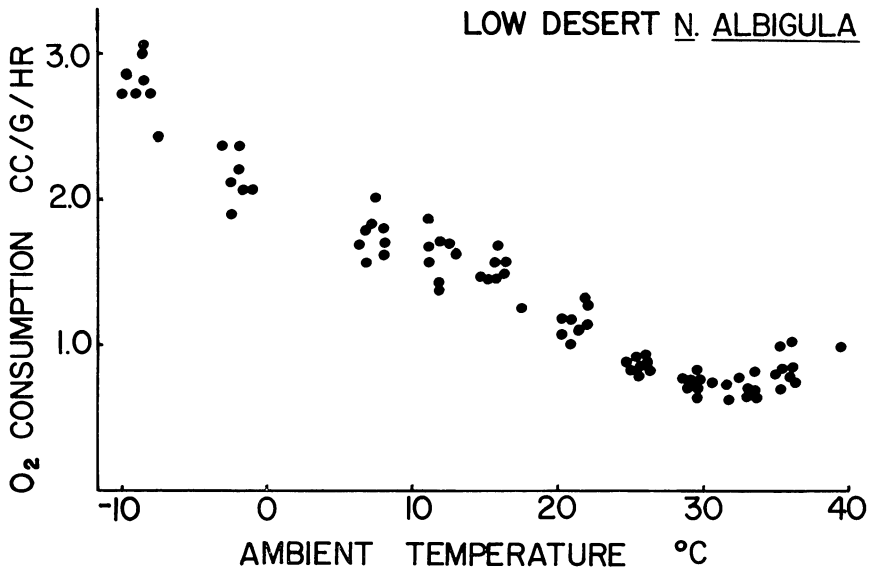


FIG. 12. The relation between oxygen consumption and ambient temperature in low desert *N. albigula*.





desert *N. albigula*, and low desert *N. albigula* populations do not differ significantly.

Animals born and reared in the laboratory were available for three populations, coastal *N. cinerea*, highland *N. cinerea* and high desert *N. albigula*. In all instances the responses of these animals could not be distinguished from those of wild-caught, laboratory-acclimated animals (Figs. 8, 9, and 11). It should be noted that two of the four adults of coastal *N. cinerea* designated as laboratory-reared were actually taken in the field within a week after birth, while still blind and naked.

**BODY TEMPERATURE AND LETHAL AMBIENT TEMPERATURE.**—All individuals of all populations maintained constant and similar body temperatures after four-hour exposures to ambient temperatures between  $-10^{\circ}$  and  $30^{\circ}$  C (Figs. 14 and 15). Individuals of all populations responded to ambient temperatures above  $32^{\circ}$  C with elevated body temperatures.

When handling low desert *N. albigula* after exposures to  $0^{\circ}$  or  $10^{\circ}$  C, it was noticed that the feet and tails of these rats were remarkably cold to the touch. This was not apparent in the high desert representatives of this species. A comparison of peripheral-core body temperature gradients in the two populations at  $0^{\circ}$  C revealed significantly ( $P < 0.01$ ) greater peripheral cooling in the low desert population (Fig. 16).

The effects of high ambient temperatures become apparent when the body temperatures at these temperatures (Figs. 14 and 15) are compared with the lethal ambient temperatures (Figs. 17). Coastal and highland *N. cinerea* are capable of tolerating only limited hyperthermia. At ambient temperatures of  $34^{\circ}$  to  $36^{\circ}$  C, several individuals of these populations suffered explosive rises in body temperature and died during the four-hour exposures. No representatives of these populations survived four hours at  $38^{\circ}$  C. In contrast, the two populations of *N. albigula* readily tolerated hyperthermia resulting from ambient temperatures of  $34^{\circ}$  to  $38^{\circ}$  C. Significant mortality occurred only at  $40^{\circ}$  C, and one-third of the low desert population tested survived at this temperature for four hours. The high desert *N. cinerea* were intermediate between the *N. albigula* and the other *N. cinerea* populations in their tolerance of high ambient temperatures.

A good correlation between apparent quality and density of pelage, and lethal ambient temperature, exists for the coastal and highland populations of *N. cinerea*. Rats with thinner pelts survived at higher temperatures than did those with longer, denser fur. There was a general tendency in all populations for larger individuals to succumb at lower ambient temperatures, but this was marked by numerous exceptions. The ability of individuals of different populations to recover from near lethal body temperatures varied. One low desert *N. albigula*, prematurely removed from a test

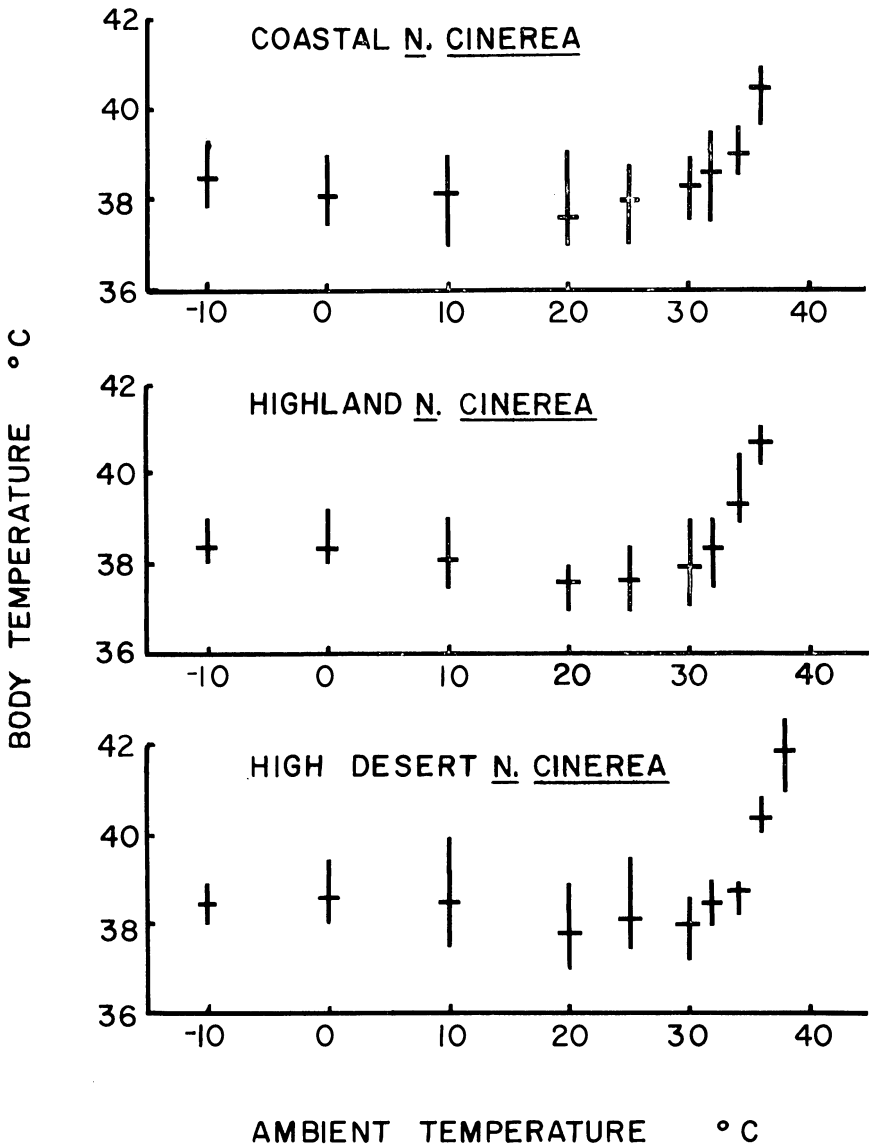


FIG. 14. The relation between body temperature and ambient temperature in the populations of *N. cinerea* after four-hour exposures. Vertical lines represent the ranges; horizontal lines, the mean values.

at 38° C, had a body temperature of 44.0° C, and the posterior half of its body was paralyzed. After 20 minutes at room temperature it had regained some of the use of its hind legs, and 24 hours later it was apparently normal.

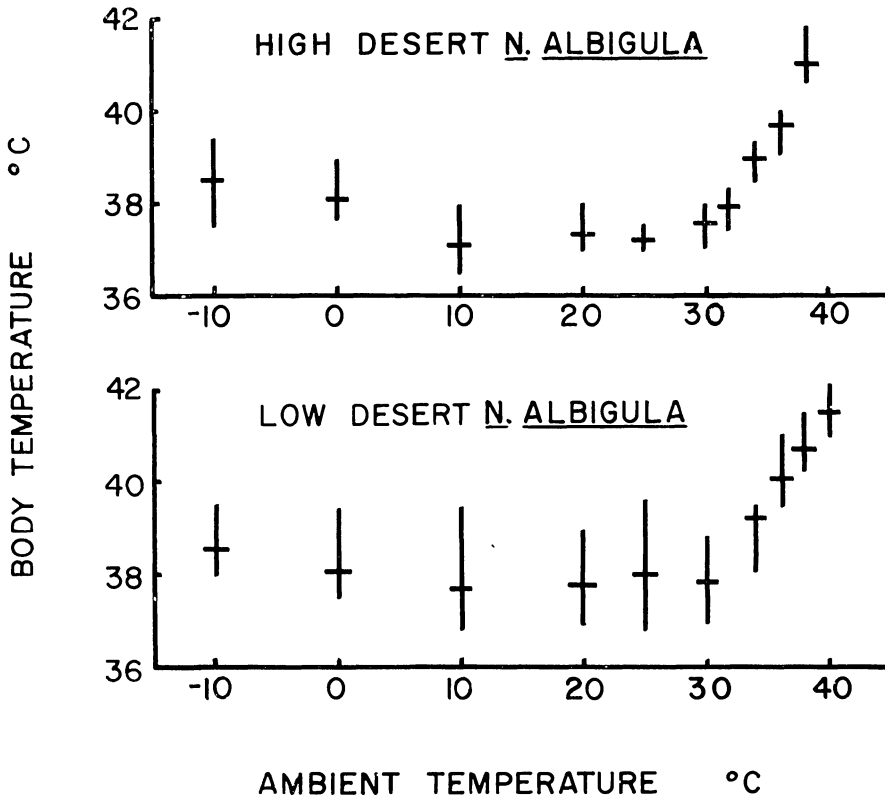


FIG. 15. The relation between body temperature and ambient temperature in the populations of *N. albigula* after four-hour exposures. Vertical lines represent the ranges; horizontal lines the mean values.

One coastal and one highland *N. cinerea* with similar body temperatures (44.0° and 43.5° C, respectively) were in heat comas when removed, and died within a few minutes.

Individuals which died at high ambient temperatures in metabolism chambers are also indicated in Figure 17. It should be noted that sometimes individuals succumbed in metabolism chambers at ambient temperatures slightly lower (0.5° C) than those which they had previously survived in lethality tests. The humidity in the cans was not controlled and the small volume of the can undoubtedly inhibited the postural responses to high temperatures described below. A comparison of survival in metabolism chambers with survival in the lethality tests in the Hotpack indicate that lethal temperatures in the metabolism chambers may be as much as 1.5° lower.

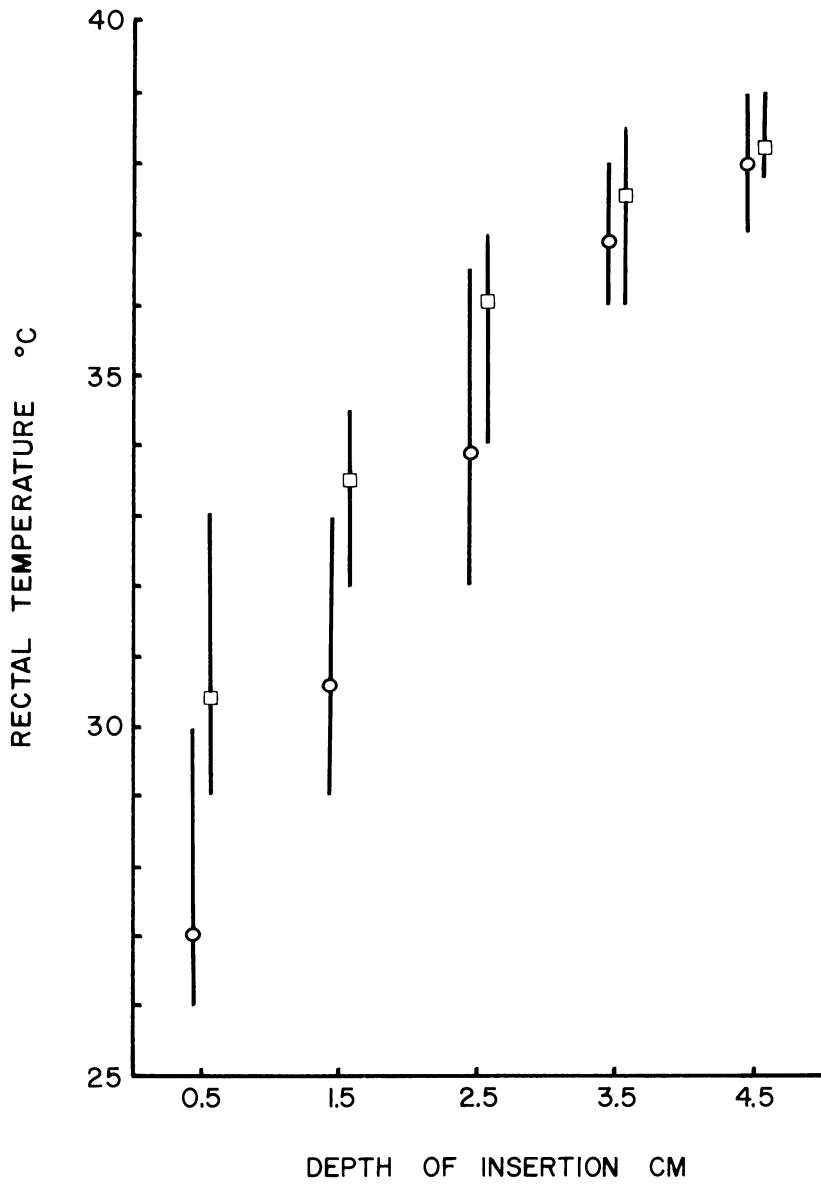


FIG. 16. Core-peripheral body temperature gradients in the high desert (squares) and low desert (circles) populations of *N. albigula*. Vertical lines indicate the ranges; squares and circles, the mean values.

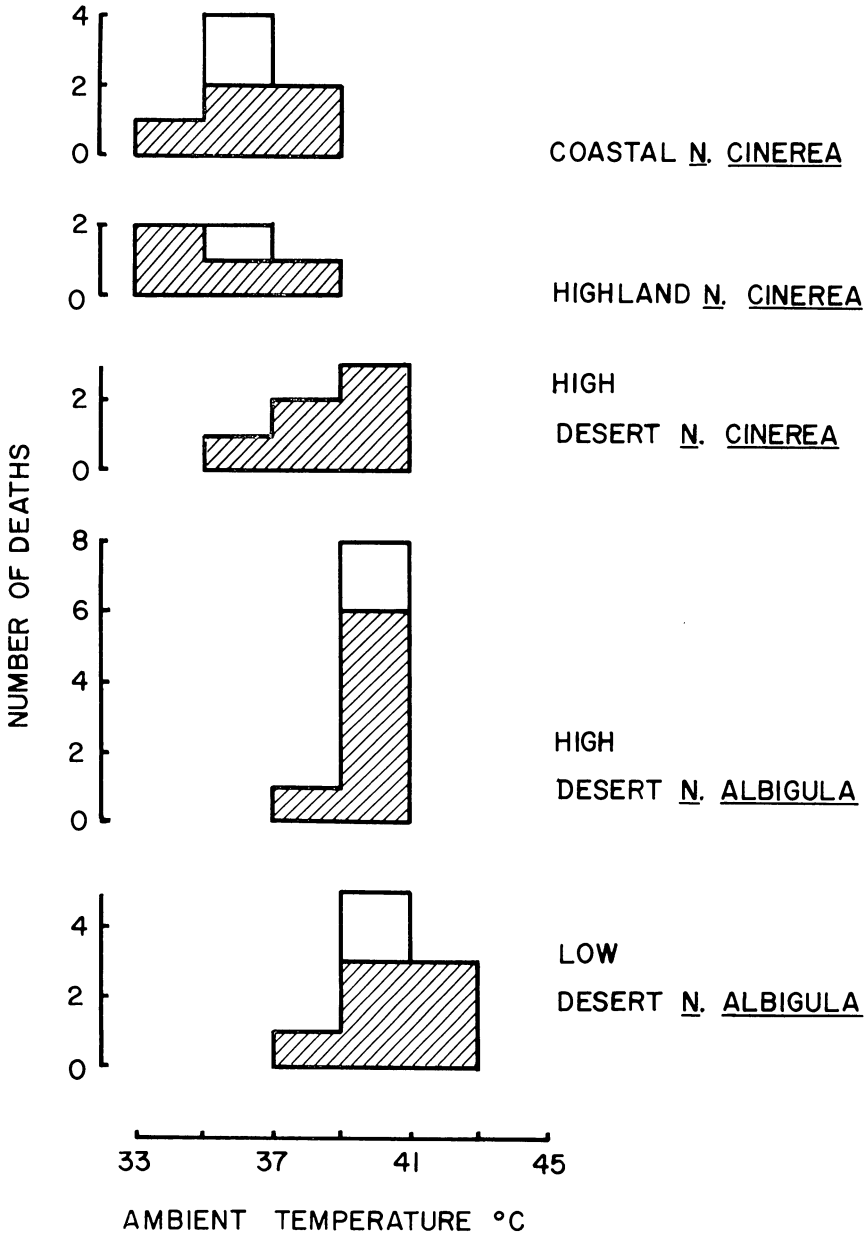


FIG. 17. Lethal ambient temperatures for the five populations, based on four-hour exposures. Hatched areas indicate deaths during tests of body and lethal temperatures, Unhatched areas, deaths during metabolic experiments (see text).

OBSERVED RESPONSES TO TEMPERATURE.—The rats were watched periodically during thermoregulatory tests, and several interesting observations can be described. The influence of ambient temperature on the postures assumed by the woodrats was striking. At temperatures between  $-10^{\circ}$  and  $25^{\circ}$  C the animals tended to remain inactive and often slept. They assumed crouched or tightly balled positions, and shivering was apparent at the lowest temperatures. The low desert *N. albigula* frequently interrupted these periods of immobility with bursts of activity at  $-10^{\circ}$  C. At ambient temperatures above  $30^{\circ}$  C the woodrats assumed extended positions, lying on their bellies and sides with feet and tails extended and much of their bodies in contact with the substrate. Such positions were assumed by *N. cinerea* at  $30^{\circ}$  C, but some high desert *N. albigula* and most of the low desert *N. albigula* failed to assume extended postures until  $32^{\circ}$  C was reached. The animals remained completely inactive except for occasional shifts in position and attempts to escape at temperatures near the lethal ambient temperature.

At ambient temperatures above  $30^{\circ}$  C, peripheral vascularization increased dramatically, particularly in the less heavily furred regions of the body, the ears and feet of *N. cinerea*, and the ears, feet, genital regions, and tails of *N. albigula*. As ambient temperatures approached lethal limits individuals of all populations salivated. The saliva usually wet only the lips and chin. Woodrats were not observed to abandon their extended postures to spread saliva to other parts of the body.

#### DISCUSSION

The basal metabolic rates of all five populations are very similar (Table 3) and resemble those of two populations of *Neotoma lepida* and one population of *N. fuscipes* reported by Lee (1963). Since the mean body weights of these populations differ proportionally more than their basal metabolic rates (BMR's) there are significant departures from the relationship between BMR and body weight ( $M = 17.1 W^{-0.27}$ ) described for mammals by Morrison (1948). Only coastal *N. cinerea* has a BMR near or above the predicted value. Because heteromyid rodents and desert forms of *Peromyscus* typically have lower than predicted basal rates, McNab and Morrison (1963) have suggested that low BMR's are adaptive to desert conditions. The data on *Neotoma* do not support this conclusion. Desert woodrats have lower than predicted BMR's, but so do highland and some coastal populations (Table 3). Deviation from predicted BMR is far better correlated with body size than it is with habitat. This suggests that basal metabolic rate has remained relatively constant during the evolution of woodrats, despite changes in body size and adaptation to various habitats.

The lethal ambient temperatures ( $34^{\circ}$  to  $38^{\circ}$  C), characteristic of coastal

TABLE 3  
 MINIMAL METABOLISM OF POPULATIONS OF *Neotoma*  
 AND THE METABOLISM PREDICTED FROM BODY WEIGHT ( $M = 17.1 W^{-0.27}$ )

| Population                     | Body Weight<br>g | Ambient Temperature<br>°C | Metabolism cc O <sub>2</sub> /g/hr |                   | Source     |
|--------------------------------|------------------|---------------------------|------------------------------------|-------------------|------------|
|                                |                  |                           | Mean Minimal                       | Predicted Minimal |            |
| Coastal <i>N. cinerea</i>      | 320.9            | 26.0–34.5                 | 0.78                               | 0.75              | This study |
| Highland <i>N. cinerea</i>     | 267.7            | 24.0–33.0                 | 0.70                               | 0.79              | This study |
| High Desert <i>N. cinerea</i>  | 168.0            | 29.5–33.0                 | 0.80                               | 0.89              | This study |
| High Desert <i>N. albigula</i> | 172.4            | 28.5–33.0                 | 0.74                               | 0.89              | This study |
| Low Desert <i>N. albigula</i>  | 193.6            | 29.5–34.0                 | 0.73                               | 0.85              | This study |
| Desert <i>N. lepida</i>        | 110.3            | 27.5–33.0                 | 0.79                               | 1.04              | Lee, 1963  |
| Coastal <i>N. lepida</i>       | 138.5            | 28.0–33.0                 | 0.72                               | 0.94              | Lee, 1963  |
| Coastal <i>N. fuscipes</i>     | 186.7            | 24.0–33.0                 | 0.79                               | 0.89              | Lee, 1963  |

and highland *N. cinerea*, are unusually low for small mammals. Such lethal temperatures are apparently typical of a few species, such as the arctic ground squirrel (*Citellus undulatus*) (Sullivan and Mullen, 1954), the pika (*Ochotona princeps*) (Dice, 1927), and several fossorial rodents (McNab, 1966), which, because of their distribution or habits, never encounter high environmental temperatures. The ambient temperatures at which the desert populations of woodrats succumb in four hours (36° to 42° C) resemble closely those for *Neotoma fuscipes* and *N. lepida* from southern California (Lee, 1963), and for other nocturnal desert rodents, including *Dipodomys merriami* (Dawson, 1955; Carpenter, 1966), *Dipodomys agilis* (Carpenter, 1966), and *Microdipodops pallidus* (Bartholomew and MacMillen, 1961).

The relations of oxygen consumption to ambient temperature for high desert *N. cinerea* and the two populations of *N. albigula* (Fig. 13), which are essentially the same, are very similar to those of *N. fuscipes* and *N. lepida* from southern California (Lee, 1963). All these relationships are very different from those of the coastal and highland *N. cinerea*. Of the small mammals studied to date, the responses of these two populations most resemble those of arctic lemmings and weasels (Scholander *et al.*, 1950a). The differences between the three desert populations on the one hand, and the coastal and highland populations on the other, must be largely owing to differences in insulation since the basal metabolic rates of all five populations are similar. Insulation can best be compared by computing an insulation index,  $T_B - T_A / O_2 \text{ consumption}^1$  (Musser and Shoemaker, 1965), which expresses insu-

<sup>1</sup> This index is actually a measure of an animal's capacity to retard the loss of metabolic heat. At ambient temperatures below the "zone of thermoneutrality" insulation is the significant factor influencing heat dissipation. Evaporation accounts for an important fraction of the heat loss at higher temperatures. Lee (1963) found that about 30 per cent of the heat loss by *N. lepida* at 36° C could be attributed to evaporation.

lation in terms of the difference between body temperature ( $T_B$ ) and ambient temperature ( $T_A$ ) and the metabolism at that ambient temperature. An insulation index curve can be calculated directly from the mean metabolism and mean ambient temperature at each temperature interval to show the relationship between insulation and ambient temperature. It does this without making the assumption of constant insulation below the "zone of thermoneutrality" implicit in the Newtonian model advocated by Scholander *et al.* (1950a).

Insulation indices for all five populations (Fig. 18) clearly describe curvilinear functions below the "zone of thermoneutrality." This indicates that insulation is not constant and the predictions of the Newtonian model are not met. Departures from the predictions of the Newtonian model also have been observed in small birds (see West, 1962, for a review) and large mice of the genus *Peromyscus* (Musser and Shoemaker, 1965). The decreases in insulation at the lowest ambient temperatures suggest that these woodrats may increase the vascularization of peripheral tissues and thereby prevent their freezing or suffering cold damage. The weight-specific insulation indices of the coastal and highland *N. cinerea* are significantly ( $P < 0.01$ ) larger than those of the three other populations.

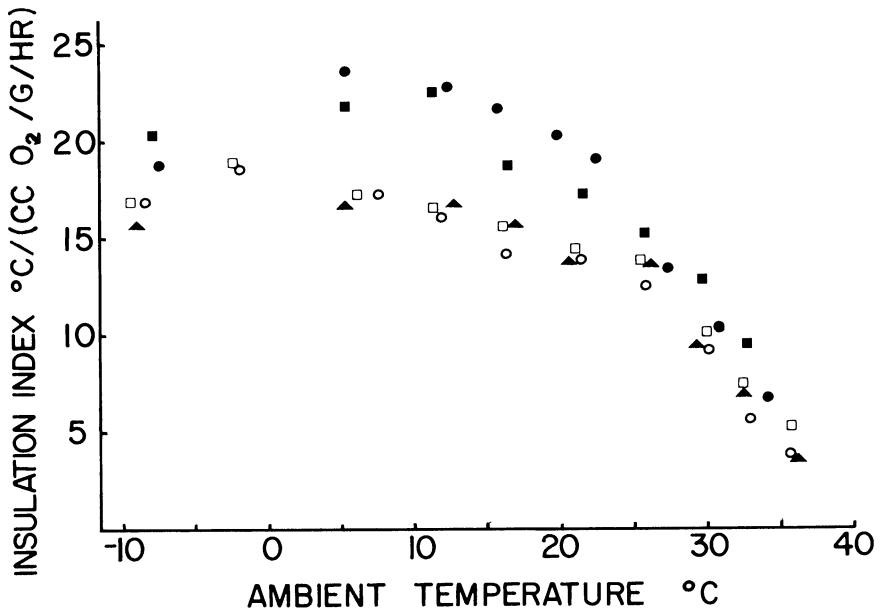


FIG. 18. Weight-specific insulation indices of the five populations (see text). Shaded circles represent coastal *N. cinerea*; shaded squares, highland *N. cinerea*; shaded triangles, high desert *N. cinerea*; unshaded squares, high desert *N. albigula*; unshaded circles, low desert *N. albigula*.



Since heat loss in homeotherms is in part a function of body surface and its insulation, it is desirable to express insulation in terms of surface area when animals of different sizes are being compared. Body surface ( $A$ ) can be estimated from body weight ( $W$ ) by the equation  $A = 10 W^{0.67}$ , and surface-specific insulation indices can be calculated. Table 4 compares surface-specific and weight-specific insulation indices at the same ambient temperatures (approximately  $6^\circ\text{C}$ ). About half of the differences, on a weight-specific basis, between the larger coastal and highland woodrats on the one hand, and the three populations of smaller, desert animals on the other, may be explained in terms of the smaller, surface-to-mass ratio of the coastal and highland *N. cinerea*. The significant differences ( $P < 0.01$ ) of 10 to 15 per cent which remain after correcting for the surface-weight relationship, indicate that per unit of body surface, the coastal and highland populations of *N. cinerea* are better insulated than the desert populations of *N. cinerea* and *N. albigula*.

TABLE 4  
WEIGHT-SPECIFIC AND SURFACE-SPECIFIC  
INSULATION INDICES OF THE FIVE POPULATIONS AT APPROXIMATELY  $6^\circ\text{C}$

| Population                     | Surface-to-mass ratio<br>cm <sup>2</sup> /g | Mean ambient temperature<br>°C | Insulation index*                               |   |
|--------------------------------|---|--------------------------------|---|---|
|                                |   |                                | Weight-specific<br>°C/(cc O <sub>2</sub> /g/hr) | Surface-specific<br>°C/(cc O <sub>2</sub> /cm <sup>2</sup> /hr) |
| Coastal <i>N. cinerea</i>      | 1.44  | 5.1                            | 23.6 (100)                                      | 36.1 (100)  |
| Highland <i>N. cinerea</i>     | 1.54  | 5.2                            | 21.8 ( 92)                                      | 34.8 ( 96)  |
| High Desert <i>N. cinerea</i>  | 1.88  | 5.2                            | 16.7 ( 71)                                      | 30.7 ( 85)  |
| High Desert <i>N. albigula</i> | 1.83  | 5.7                            | 17.3 ( 73)                                      | 31.4 ( 87)  |
| Low Desert <i>N. albigula</i>  | 1.74  | 7.4                            | 17.2 ( 73)                                      | 29.9 ( 83)  |

\* Values in parentheses indicate per cent of insulation index of coastal *N. cinerea*.

The data on body temperature and lethal ambient temperature (Figs. 14, 15 and 17) indicate that coastal and highland *N. cinerea* are inferior to the other populations in dissipating heat at high ambient temperatures. This is corroborated by the insulation indices of these two populations (especially highland *N. cinerea*), which remain higher at higher ambient temperatures. The correlation between apparent quality of pelage and lethal ambient temperature indicates that the inability to reduce pelage insulation greatly is an important factor in the inability of these two populations to tolerate temperatures above  $38^\circ\text{C}$ .

The responses to temperature of the high desert populations of *N. cinerea* and *N. albigula* are nearly identical. The former are more variable in their responses, probably owing to greater variation in body size. In animals from the high desert, *N. cinerea* may be slightly less heat resistant than *N. albigula* (Fig. 17). A comparison of the two populations of *N. albigula*

reveals significant differences. At higher ambient temperatures the high desert population has higher insulation indices ( $P < 0.05$ ) than the low desert one (Fig. 18). This indicates that the former loses heat less effectively and probably accounts for its slightly lower heat resistance (Fig. 17). The low desert population shows significantly greater peripheral cooling at lower ambient temperatures (Fig. 16). Since the heat production (Fig. 13) and the core-ambient temperature gradients of the two populations are almost identical, the differences in the temperatures of peripheral tissues suggest that the pelage insulation of the high desert population is superior.

In all tests the responses of laboratory-born-and-reared animals were identical to those of laboratory-acclimated, wild-caught individuals of the same populations. Therefore, it will be assumed that the differences between the populations of woodrats measured here represent genetic differences between the natural populations.

## GENERAL DISCUSSION

### INTERACTION OF MICROCLIMATE AND TEMPERATURE REGULATION

The descriptions of the winter and summer microclimates have indicated the temperature regimes to which the five populations are exposed in nature. The physiological investigations have revealed the genetic capacities of the populations to tolerate and adjust to ambient temperatures. It should now be possible to determine how these two factors influence the survival of each population in its particular environment.

The coastal population of *N. cinerea* occupies dens which offer essentially no protection from outside temperatures. Environmental temperatures in this area almost never approach lethal levels ( $34^{\circ}$  to  $36^{\circ}$  C). If they should do so, most rats have cooler areas near their dens to which they can retreat. These woodrats are comparatively well insulated, an obvious adaptation to the perpetually cool, damp climate of coastal Oregon. Despite the effectiveness of their insulation, the animals are exposed to temperatures which, even in midsummer, require elevated heat production to maintain body temperature.

That highland *N. cinerea* are also comparatively well insulated is not surprising, since they occupy the coldest environment of the populations studied. Their microclimates are sufficiently cool to require metabolism above basal levels at all seasons of the year. These rats would rarely be exposed to ambient temperatures above  $25^{\circ}$  C; significantly, their capacity for heat dissipation is the poorest of the five populations.

Despite different types of dens, the high desert populations of *N. cinerea* and *N. albigula* are exposed to similar microenvironmental temperatures and

their physiological responses to temperature are nearly identical. On hot summer days the protection offered by the dens of these rats provides the margin of survival in this environment. Tremendous seasonal differences in temperature necessitate the adaptation of these populations to extremes of both hot and cold. In their capacity to lose heat at high ambient temperatures they are superior to the other populations of *N. cinerea* and only slightly inferior to the low desert *N. albigula*. Although these high desert woodrats are not particularly well insulated, they are capable of at least tripling minimal heat production to maintain body temperature at ambient temperatures well below freezing.

The low desert *N. albigula* exist in one of the most severe terrestrial environments. Despite their shaded dens and subterranean burrows, these animals must consistently face summer temperatures only a few degrees below lethal limits. These woodrats are adapted to this thermal regime by having the best capacity for heat dissipation, which is reflected in the highest lethal temperatures. This thermolytic capacity appears to depend on a somewhat inferior pelage insulation and superior vascular mechanisms. They never face extremely low temperatures, and they respond to cold with peripheral cooling and elevated heat production.

Within their dens the woodrats of all populations build soft, fibrous nests providing significant insulation. The effectiveness of this insulation has been measured for the nests of coastal *N. cinerea* (Fig. 8) where it is the only protection from macroenvironmental temperatures. At 6° C an individual can reduce its minimal heat production 23 per cent by occupying its nest. It is estimated that on a typical midwinter day (mean ambient temperature, 6° C) a coastal *N. cinerea* can save about 8 kilocalories per day by spending three-fourths of its time in its nest. The nests of the other populations probably foster similar savings in expenditure of energy during the colder parts of the year. The importance of nests in reducing energy expenditure and increasing survival in winter has been demonstrated in *Glaucomys* (Muul, 1967) and *Peromyscus* (Howard, 1951; Sealander, 1952). Animals of these two genera are also able to reduce individual heat production in winter by huddling in groups of several individuals. This mechanism is unlikely in these woodrats, which apparently are highly territorial and solitary, except during the breeding season.

Most of the physiological and microclimatic characteristics of the populations described here clearly facilitate the survival of the population possessing them and therefore may be considered adaptive. If the microclimatic conditions provided by a den are to be advantageous to its occupant, favorable dens must be obtained before external conditions become stressful. Since woodrats are solitary and opportunities for learning by experience are

limited, den selection or construction, like typical habitat selection (Wecker, 1963), must be largely an inherited characteristic. Den selection in woodrats apparently has had an evolutionary history characterized by the intensification and relaxation of the selection pressure exerted by macroenvironmental temperature. Dens obviously protect their occupants from some predators, rain, snow, and excessive evaporative water loss, in addition to providing fairly equable temperatures. In coastal Oregon protection from macroclimatic temperature probably has been of negligible importance, and other factors have assumed priority in den selection. Macroenvironmental temperature has had much more influence on the other populations. This is particularly true for the desert woodrats which could not exist in their present habitats without the relatively equable summer temperatures provided by their dens.

The three desert populations and perhaps the highland population, do not possess sufficient thermoregulatory mechanisms to tolerate even brief exposures to the extreme macroclimatic temperatures of their environments. However, the physiological adaptations of all the populations are sufficient to cope with the conditions encountered within their dens, and the thermoregulatory capacities are well correlated with the range of temperatures to which the animals are normally exposed. These adaptive modifications of temperature regulation apparently have been achieved by varying pelage insulation, modifying vascular mechanisms of heat exchange, and altering the surface-to-mass ratio through changes in body size.

Although the physiological adaptations described here are sufficient to account for the survival of all the populations, it is likely that in the natural environments some degree of acclimation supplements these genetic capacities. It might be expected that seasonal changes in temperature relations would be especially advantageous. Seasonal changes in the ability to maintain high levels of heat production at low ambient temperatures have been observed in small mammals (Hart and Heroux, 1953 and 1963) and small birds (Hart, 1962). Seasonal changes in insulation have been documented for a variety of northern mammals (Irving *et al.*, 1955; Hart, 1956; Hart *et al.*, 1965) and provisionally for the cardinal (Dawson, 1958). Since woodrats are in worn pelage or moulting in summer (Finley, 1958), their pelage insulation is undoubtedly somewhat reduced during the warmer months. The magnitude of these and other possible phenotypic changes and their importance in the temperature relations of woodrats remain to be determined.

#### PHYLOGENETIC ASPECTS OF TEMPERATURE ADAPTATION

Although comparative studies of closely related populations offer great potential for understanding the evolution of adaptations and the exact

nature of the relationship between organism and environment, there have been few such studies of temperature relations in homeotherms. The most complete of these studies have found either insignificant or only slight adaptive differences between conspecific or congeneric populations. Hayward (1965a) found that insulation and metabolic rate were well correlated with body size in several populations of *Peromyscus maniculatus*, but they showed no relationship to environmental temperature. He concluded (Hayward, 1965b) that the equable microclimates provided by the burrows of these mice were so similar that there had been no selection for physiological adaptations. McNab and Morrison (1963) found greater insulation and lower basal metabolic rates in xerophilous than in mesophilous forms of *Peromyscus* and concluded that these were adaptive to desert conditions. This interpretation, based on tenuous theoretical considerations and not supported by microclimatic measurements, is open to question. Dawson (1954) found temperature adaptations in two species of birds (*Pipilo aberti* and *P. fuscus*) from different environments to consist of behavioral responses supplemented by small differences in physiological capacity.

The comparatively dramatic differences described here between conspecific and congeneric populations of woodrats clearly demonstrate that both behavioral and physiological attributes may be substantially modified in organisms of basically similar morphology, evolutionary history, and genetic background. The success of this study in demonstrating genetic differences in temperature regulation between closely related populations may be attributed to a combination of factors. Woodrats are larger than most of the homeotherms studied in previous comparisons of closely related populations. Very small mammals and birds seem to be limited in their capacities to produce significant changes in temperature regulation. As a direct consequence of their small size, their surface-to-mass ratio is large and the insulation they can carry is limited. Hayward's (1965a, b) work on *Peromyscus maniculatus* suggests that behavioral selection of microclimates may be much more important than physiological adaptations in the thermal relations of very small mammals. Secondly, these populations of *Neotoma*, even in their microenvironments, are exposed to remarkably different thermal regimes which should favor the evolution of adaptive physiological changes. The importance of the thermal environment is demonstrated by the identity of the thermal responses of high desert *N. cinerea* and *N. albigula*. These populations resemble one another more than they do other conspecific populations. Thirdly, the conspecific populations, although apparently connected by interbreeding populations, are isolated from each other by distance and geographic barriers. The gene flow between the populations should therefore be limited, increasing the capacity of each population to respond to selection by genetic divergence.

From an evolutionary standpoint, perhaps the most interesting result of this study is the striking correlation between body size and temperature adaptation in *N. cinerea*. Individuals of the high desert population are smaller, occur in a hotter environment, and have greater heat loss and better tolerance of high ambient temperatures than those of the coast and highlands. The differences in body size between these populations reflect an excellent inverse correlation between body size and ambient temperature within the species as a whole.

The physiological significance of Bergmann's rule, which correlates smaller body size with warmer climates in homeotherms, has been debated by Scholander (1955) and Mayr (1956). The problem has recently been reopened by McNab (1966), but his interpretation of geographic character gradients in pocket gophers (*Geomys*) is inadequately supported by his few, indirect measurements. Scholander (1955) deprecates the importance of intraspecific clinal variation in body size on the grounds that very large changes in body size are required to produce significant changes in surface-to-mass ratio and thermal relations. The data on *N. cinerea* suggest that differences in body size of the magnitude observed in intraspecific clines may be reflected by significant differences in thermal conductance. If this is generally true, at least some examples of Bergmann's rule may reflect important adaptations to environmental temperature.

Scholander (1955) proposes that variation in insulation is of primary importance in the climatic adaptation of homeotherms. The present study shows the adaptive significance of variation in insulation within *N. cinerea*. It also indicates that, at least in this species, insulation is related to body size; the larger animals from the cooler environments apparently have longer, denser pelts (see surface-specific values for insulation in Table 4). This interpretation is supported by data of Scholander *et al.* (1950*b*), showing an excellent correlation between pelage insulation and body weight in arctic mammals weighing less than five kilograms. The significant contribution of peripheral cooling to total insulation in the larger species of *Peromyscus* (Musser and Shoemaker, 1965) suggests that insulation provided by peripheral tissues may also tend to vary with body size. The data on *N. cinerea* suggest that Bergmann's rule may describe an important pattern of temperature adaptation within certain species or genera of small homeotherms, because the advantages of an altered surface-to-mass ratio may be reinforced by changes in insulation that tend to accompany changes in body size.

#### TEMPERATURE AND WOODRAT POPULATIONS

Presumably the temperature adaptations of woodrats evolved as a result of the mortality of individuals with inferior dens and inadequate tempera-

ture regulation. It is probable that such mortality is still occurring and the process of adaptation is continuing. This is particularly true for the populations inhabiting deserts, where even the most favorable dens provide temperatures only a few degrees below lethal levels. The microclimatic data suggest that in summer, when populations are high, individuals (particularly juveniles) may occupy marginal den situations where the daily temperatures approach or reach lethal levels. Dispersing juveniles may suffer significant mortality from occupying inadequate microenvironments and being unable to tolerate the resulting temperatures.

It is also possible that a combination of ambient temperature and lack of suitable microenvironments may directly limit the ranges of woodrats in some regions. Of the two species studied, this is particularly likely in *N. cinerea*, which depends on available rock crevices, caves, and other shelters for dens. Finley (1958) has suggested that the limits of this species on the eastern slope of the Rockies in Colorado may be determined by high ambient temperatures and the absence of large, deep crevices in the rock formations. That highland *N. cinerea* are intolerant of high temperatures (above 36° C) is consistent with this suggestion.

On the eastern face of the Rocky Mountains in Colorado, *N. cinerea* ranges from treeline down to elevations of approximately 6500 feet. This species occurs as low as 4000 feet in the much hotter deserts of western Colorado and eastern Utah. Availability of adequate microhabitats may partially account for these differences in altitudinal and climatic distribution, but steepness of relief may also be involved. The eastern slope is steep and, as a result, populations of *N. cinerea* at lower elevations are not isolated by large distances or geographic barriers from populations in the high mountains. Gene flow from the widespread, cold-adapted, highland populations may prevent establishment of significant adaptations to warmer conditions in the relatively narrow band of populations at the lower limits of the range. In contrast to the steep eastern slope, the terrain slopes rather gradually from the central highlands to the plateaus and deserts to the west. Here the distance and deep river valleys between high mountain and desert populations of *N. cinerea* should restrict genetic exchange and permit adaptive divergence. The significant and presumably genetic differences in body size and insulation between the highland and high desert populations suggest that considerable adaptation to local conditions has occurred.

#### SUMMARY

Adaptations to environmental temperature were studied in five populations of woodrats from contrasting environments. Two main questions were asked. (1) To what extent do woodrats evade the thermal conditions of their

macroenvironments by occupying more equable microhabitats? (2) How are these populations physiologically adjusted to the temperatures to which they are exposed?

The populations studied include three of *Neotoma cinerea* (from coastal Oregon, high elevations in the Rocky Mountains of central Colorado, and high deserts of southeastern Utah) and two of *N. albigula* (from high deserts of southeastern Utah and low deserts of southwestern Arizona).

Winter and summer records of microenvironmental temperatures indicated that protection offered by woodrat dens varies. Dens of coastal *N. cinerea* provide essentially no protection; the microhabitats of the other populations offer considerable protection from the extremes and fluctuations of daily temperature cycles, but even in their dens individuals of these populations are exposed to considerable seasonal temperature variation.

Comparisons of the relation between oxygen consumption and ambient temperature (supplemented by measurements of body temperature and survival at high ambient temperatures) revealed significant and apparently genetic differences between the populations. Basal metabolic rates of all populations are similar (0.70 to 0.80 cc  $O_2$ /g/hr), but both maximal and minimal rates of heat loss are significantly greater for the three desert populations than for the coastal and highland *N. cinerea*, owing to differences in both insulation and surface-to-mass ratio.

The combination of microenvironmental thermal conditions and thermoregulatory capacities are sufficient to explain the survival of each population in its environment, and most of the differences between the populations are certainly adaptive. The dens of the desert populations are particularly important because they protect their inhabitants from the extreme summer temperatures of the macroenvironment, which exceed lethal levels on the hotter days.

Body size in *N. cinerea* is inversely correlated with environmental temperature. This relationship is also associated with differences in temperature regulation, which suggest that Bergmann's rule may describe an important pattern of climatic adaptation.

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## LITERATURE CITED

- BARTHOLOMEW, G. A., AND R. E. MACMILLEN. 1961. Oxygen consumption, aestivation, and hibernation in the kangaroo mouse, *Microdipodops pallidus*. *Physiol. Zoöl.*, 34: 117-183.
- CARPENTER, R. E. 1966. A comparison of thermoregulation and water metabolism in the kangaroo rats *Dipodomys agilis* and *Dipodomys merriami*. *Univ. Calif. Publ. Zoöl.*, 78:1-36.
- DAWSON, W. R. 1954. Temperature regulation and water requirements of the brown and Abert towhees, *Pipilo fuscus* and *Pipilo aberti*. *Univ. Calif. Publ. Zoöl.*, 59:81-124.
- . 1955. The relation of oxygen consumption to temperature in desert rodents. *Jour. Mamm.*, 36:543-553.
- . 1958. Relation of oxygen consumption and evaporative water loss to temperature in the cardinal. *Physiol. Zoöl.*, 31:37-48.
- DEPOCAS, F., AND J. S. HART. 1957. Use of the Pauling oxygen analyzer for measurement of oxygen consumption of animals in open-circuit systems and in short-lag, closed-circuit apparatus. *Jour. Appl. Physiol.*, 10:388-392.
- DICE, L. R. 1927. The Colorado pika in captivity. *Jour. Mamm.*, 8:228-231.
- DURRANT, S. D. 1934. A new wood rat from southeastern Utah. *Jour. Mamm.*, 15:65-67.
- FINLEY, R. B. 1958. The wood rats of Colorado: distribution and ecology. *Univ. Kans. Publ. Mus. Nat. Hist.*, 10:213-552.
- HALL, E. R., AND K. R. KELSON. 1959. The mammals of North America. The Ronald Press Co., N.Y., 1083 pp.
- HART, J. S. 1956. Seasonal changes in insulation of the fur. *Can. Jour. Zool.*, 34:53-57.
- . 1962. Seasonal acclimatization in four species of small wild birds. *Physiol. Zool.*, 35:224-236.
- HART, J. S., AND O. HEROUX. 1953. A comparison of some seasonal and temperature induced changes in *Peromyscus*: Cold resistance, metabolism and pelage insulation. *Can. Jour. Zool.*, 31:528-534.
- . 1963. Seasonal acclimation in wild rats (*Rattus norvegicus*). *Ibid.*, 41:711-716.
- HART, J. S., H. POHL, AND J. S. TENNER. 1965. Seasonal acclimatization in varying hare (*Lepus americanus*). *Can. Jour. Zool.*, 43:731-744.
- HAYWARD, J. S. 1956a. Metabolic rate and its temperature-adaptive significance in six geographic races of *Peromyscus*. *Can. Jour. Zool.*, 43:309-323.
- . 1965b. Microclimate temperature and its adaptive significance in six geographic races of *Peromyscus*. *Ibid.*, 43:341-350.
- HOOPER, E. T. 1940. Geographic variation in bushy-tailed wood rats. *Univ. Calif. Publ. Zool.*, 42:407-424.
- HOWARD, W. S. 1951. Relation between low temperature and available food to survival of small rodents. *Jour. Mamm.*, 32:300-312.
- IRVING, L., H. KROG, AND M. MONSON. 1955. The metabolism of some Alaskan animals in winter and summer. *Physiol. Zool.*, 28:173-185.
- LEE, A. K. 1963. The adaptations to arid environments in wood rats of the genus *Neotoma*. *Univ. Calif. Publ. Zool.*, 64:57-96.

- MAYR, E. 1956. Geographical character gradients and climatic adaptation. *Evolution*, 10:105-108.
- McNAB, B. K. 1966. The metabolism of fossorial rodents; a study of convergence. *Ecology*, 47:712-733.
- McNAB, B. K., AND P. R. MORRISON. 1963. Body temperature and metabolism in subspecies of *Peromyscus* from arid and mesic environments. *Ecol. Monogr.*, 33:63-82.
- MORRISON, P. R. 1948. Oxygen consumption in several mammals under basal conditions. *Jour. Cell and Comp. Physiol.*, 31:281-291.
- MUSSER, G. G., AND V. H. SHOEMAKER. 1965. Oxygen consumption and body temperature in relation to ambient temperature in the deer mice, *Peromyscus thomasi* and *P. megalops*. *Occ. Pap. Mus. Zool. Univ. Mich.*, 643:1-15.
- MUUL, I. 1968. Behavioral and physiological influences on the distribution of the flying squirrel, *Glaucomys volans*. *Misc. Publ. Mus. Zool. Univ. Mich.*, 134:1-66.
- RAINEY, D. G. 1965. Observations on the distribution and ecology of the White-throated Wood Rat in California. *Bull. So. Calif. Acad. Sci.*, 64:27-42.
- SCHOLANDER, P. F. 1955. Evolution of climatic adaptation in homeotherms. *Evolution*, 9:15-26.
- SCHOLANDER, P. F., R. HOCK, V. WALTERS, F. JOHNSON, AND L. IRVING. 1950a. Heat regulation in some arctic and tropical mammals and birds. *Biol. Bull.*, 99:237-258.
- SCHOLANDER, P. F., V. WALTERS, R. HOCK, AND L. IRVING. 1950b. Body insulation of some arctic and tropical mammals and birds. *Biol. Bull.*, 99:225-236.
- SEALANDER, J. A. 1952. The relationship of nest protection and huddling to survival of *Peromyscus* at low temperature. *Ecology*, 33:63-71.
- STEEL, G. D., AND J. H. TORRIE. 1960. Principles and procedures of statistics with special reference to the biological sciences. McGraw-Hill Book Co., N.Y., 481 pp.
- SULLIVAN, B. J., AND J. T. MULLEN. 1954. Effects of environmental temperature on oxygen consumption in arctic and temperate-zone mammals. *Physiol. Zool.*, 27:21-28.
- U.S. Department of Commerce. 1964. Climatography of the United States No. 86: decennial census of United States Climate. U.S. Government Printing Office, Washington.
- VORHIES, C. T. 1945. Water requirements of desert animals in the Southwest. *Univ. Ariz. Col. Agric., Tech. Bull.* 107:487-525.
- WECKER, S. C. 1963. The role of early experience in habitat selection by the prairie deer mouse, *Peromyscus maniculatus bairdii*. *Ecol. Monogr.*, 33:307-325.
- WELLS, P. V., AND R. BERGER. 1967. Late Pleistocene history of coniferous woodland in the Mojave Desert. *Science*, 155:1640-1647.
- WELLS, P. V., AND C. D. JORGENSEN. 1964. Pleistocene wood rat middens and climatic change in the Mojave Desert: a record of juniper woodlands. *Science*, 143:1171-1174.
- WEST, G. C. 1962. Responses and adaptations of wild birds to environmental temperature. *In: Comparative Physiology of Temperature Regulation* (J. P. Hannon and E. Viereck editors), Arctic Aeromedical Laboratory, Ft. Wainwright, Alaska, Pp. 291-333.

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