

**OCCASIONAL PAPERS OF THE MUSEUM OF
ZOOLOGY****UNIVERSITY OF MICHIGAN**

ANN ARBOR, MICHIGAN

**OXYGEN CONSUMPTION AND BODY TEMPERATURE
IN RELATION TO AMBIENT TEMPERATURE
IN THE MEXICAN DEER MICE,
PEROMYSCUS THOMASI AND *P. MEGALOPS***BY GUY G. MUSSER AND VAUGHAN H. SHOEMAKER¹

POPULATIONS of *Peromyscus thomasi* and *P. megalops* occur in cool wet forests in the southern highlands of México (Osgood, 1909; Musser, 1964). Individuals of each species (Plate I) are considerably larger than representatives of other forms of *Peromyscus* for which metabolic and body-temperature data are available. The data on oxygen consumption and body temperature for *thomasi* and *megalops* presented here are interpreted in terms of thermoregulatory capacity and are compared with similar information provided by McNab and Morrison (1963) on *P. crinitus*, *P. eremicus*, *P. californicus*, *P. truei*, and *P. maniculatus*, and by Hayward (1965*b*) on *P. maniculatus* and *P. sitkensis*.

MATERIALS AND METHODS

Examples of the species *Peromyscus thomasi* and *P. megalops* trapped on 13 and 14 June, 1964, near Puerto Chico in the mountains west of Chilpancingo, Guerrero, México, were transported by air from México City to Michigan. Within five days after capture they were housed (singly or in pairs) in wire-mesh cages in a room at the University of Michigan Museum of Zoology where air temperature and relative humidity were regulated at 23° C and 30 per cent, respectively. Photoperiods matched those prevailing for the latitude of Ann Arbor (ca. 42° N). The mice were provided with Purina Mouse Breeder Chow (*ad libitum*), sunflower seeds, fruits, and vegetables. Water was continually available. Cotton batting was supplied for nesting material. During the period of investigation the animals remained in good condition, maintained weight, and some successfully reared young.

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Studies of oxygen consumption and body temperature were conducted between September, 1964, and March, 1965. Only healthy adult animals in full unworn pelage were used. Metabolic data on *thomasi* were obtained from wild-caught individuals, but three laboratory-reared representatives of this form were used in measurements of body temperature. Five wild-caught and one laboratory-reared *megalops* were employed in investigations of both metabolism and body temperature. No differences between wild-caught and laboratory-reared mice were detected in these functions.

MEASUREMENTS OF OXYGEN CONSUMPTION.—Each mouse was placed individually in a new half-gallon paint can where it rested in the dark about one inch from the bottom of the chamber on a platform made of wire mesh. Each chamber was fitted with inlet and outlet pipes for air and an airtight port for a thermocouple. They were placed inside a thermostatically controlled temperature cabinet where the air temperature inside each chamber was monitored via thermocouple leads connected to a suitably calibrated Brown potentiometric recorder. A Beckman paramagnetic oxygen analyzer (Model G 2) used in conjunction with a Brown recording potentiometer provided records of the oxygen consumption of individual mice. The concentration of oxygen in each of four separate air streams (three for air flowing from animal chambers and a fourth to monitor air flowing into the chambers) was recorded at 10-minute intervals. Air flowed from a low pressure line through a tube containing a water absorbant (Drierite) and then through a rotameter for measuring flow rate before entering the animal chamber. The chamber outlet led to another absorbing train containing Drierite and a CO₂ absorbant (Ascarite), then to the oxygen analyzer. The rate of air flow into each chamber was about 600 cm³/min. Tygon tubing was used for all connections in the air line.

The resting metabolism of each mouse was determined at intervals of 5° to 10° C, in the ambient temperature range 5° to 35° C. Some individuals were tested at temperatures beyond these limits. The animals were placed in their chambers between 9:00 and 10:00 A.M. By the time the first resting rates were obtained at about noon, the mice had fasted for at least five hours. After resting rates had been obtained at one ambient temperature, this was changed 5° to 10° C. Rates were thus obtained at two or three ambient temperatures before a run was terminated at about 6:00 P.M.

Minimal metabolic rates were readily selected from the potentiometer record because the oxygen concentration in the air from each animal chamber (which reflected the oxygen consumption of the mouse) was

recorded every 10 minutes. When the lowest level of oxygen consumption observed for a mouse at a given temperature was maintained within 5 per cent for two or more successive 10-minute intervals and was approximated within this limit on four or more occasions, these values were averaged and designated as the resting rate. Mice were kept at each temperature for at least two hours; sometimes up to four hours were required to obtain consistent resting values. On one occasion three mice were run at the same temperature for eight hours and minimal metabolic rates recorded in the first two hours did not differ from those observed subsequently. Values for oxygen consumption were calculated from flow rates and oxygen concentrations using the appropriate formula given by Depocas and Hart (1957) and converted to conditions of standard temperature and pressure. The weight of each mouse, taken at the beginning of a run, was used in the calculation of weight-specific rates.

MEASUREMENTS OF BODY TEMPERATURE.—Temperatures of mice were measured to the nearest 0.1° C using a fine copper-constantan thermocouple. To obtain deep body (core) temperatures, the thermocouple was inserted through the anus and advanced into the colon for a distance of 5 cm from the anal opening. Thus, the thermocouple rested near the center of the body just behind the liver as diagramed by Morrison and Ryser (1959). Temperatures were obtained from mice that had been resting singly in the metabolism chambers for two or more hours at ambient temperatures ranging from -5° to 40° C. The thermocouple was inserted immediately following removal of a mouse from its chamber, and a stable temperature reading was recorded within 30 seconds.

In one series of determinations, colonic temperatures were taken at successive one-cm stages as the thermocouple was inserted. A stable reading was obtained within 5 to 10 seconds at a given depth, and temperatures at five depths were obtained within a minute after the animal chamber was opened. The mice, handled only by their tails, struggled very little during insertion of the thermocouple.

RESULTS

OXYGEN CONSUMPTION.—The relationships between resting metabolic rate and ambient temperature for *P. thomasi* and *P. megalops* (Figs. 1 and 2) provide a basis for evaluation and comparison of basal metabolic rates and thermal conductances of these species. Basal metabolic rates (BMR) were determined by averaging the rates of oxygen con-

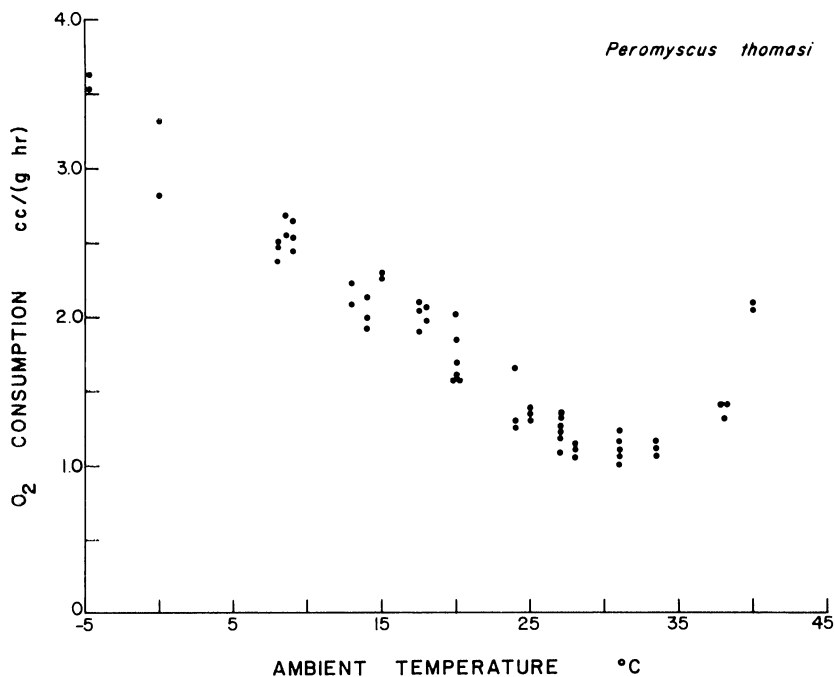


FIG. 1. Resting rate of oxygen consumption of nine *Peromyscus thomasi* in relation to ambient temperature.

sumption of individual mice resting at ambient temperatures ranging from 30.5° to 33.5° C. In the few instances in which two resting rates were available for a single individual within this temperature range, the mean value for that individual was used in the computation of the overall average. The mean BMR for eight *thomasi* was 1.12 cc O₂/(g hr), with a range from 1.01 to 1.24 cc O₂/(g hr), whereas the BMR for five *megalops* averaged 1.37 cc O₂/(g hr) and ranged from 1.19 to 1.46 cc O₂/(g hr). Mean weight of the *thomasi* was 110.8 g (range 93–132 g); *megalops* averaged 66.2 g (range 46–74 g). No apparent differences existed between metabolic rates in resting males and non-pregnant females within our samples of either *thomasi* or *megalops*. Hayward (1965b) reports similar results for his samples of *Peromyscus*. Metabolic rates of *thomasi* and *megalops* resting at temperatures below 25° C were higher than basal rates and appeared linearly and inversely related to ambient temperature. A least-squares regression line was fitted to these data for each species. For data of *thomasi* this line is described by the equation $\text{cc O}_2/(\text{g hr}) = 3.16 - 0.072t$ (where t is the ambient tempera-

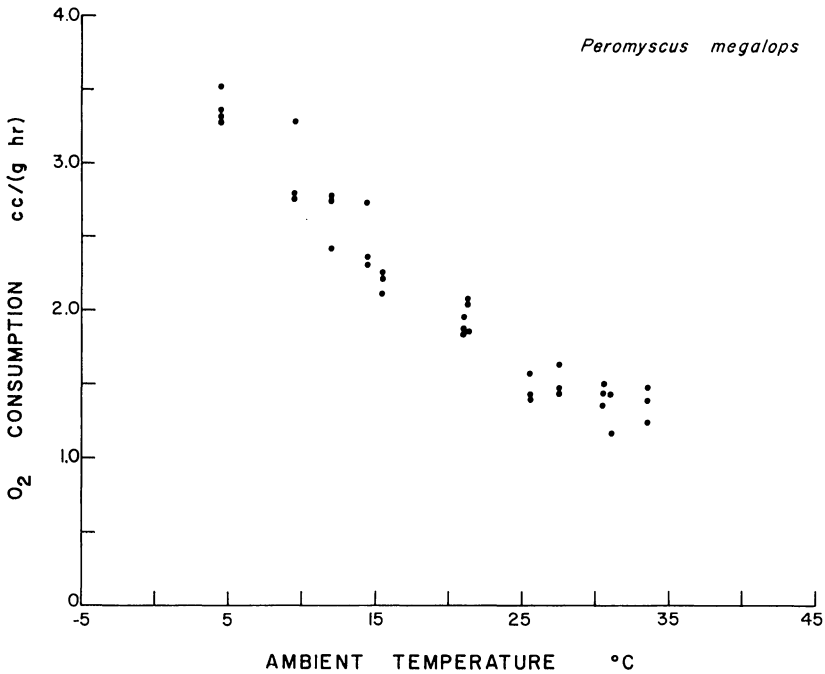


FIG. 2. Resting rate of oxygen consumption of six *Peromyscus megalops* in relation to ambient temperature.

ture in degrees centigrade) and extrapolates to 43.9° C at zero metabolism. The corresponding equation for data from *megalops* is $\text{cc O}_2/(\text{g hr}) = 3.72 - 0.087t$; the line it describes extrapolates to 42.8° C at zero metabolism. Lower critical temperatures, calculated as the temperature at which the regression line intersects the mean basal metabolic rate, were 28.3° C for *thomasi* and 27.1° C in *megalops*. No effort was made to determine upper critical temperatures, but metabolic rates for *thomasi* at ambient temperatures of 38° and 40° C were distinctly higher than the mean basal level. We do not have metabolic data for *megalops* at ambient temperatures above 34° C.

BODY TEMPERATURES.—Core body temperatures of *P. thomasi* and *P. megalops* did not vary significantly over the range of ambient temperatures investigated below 32° C (Fig. 3). Mean core temperatures in this range were 37.8° C for *thomasi* and 38.0° C for *megalops*. No difference in core temperatures was apparent between sexes. Mice of both species became hyperthermic as ambient temperatures approached and exceeded their normal body temperatures. Exposure to these high am-

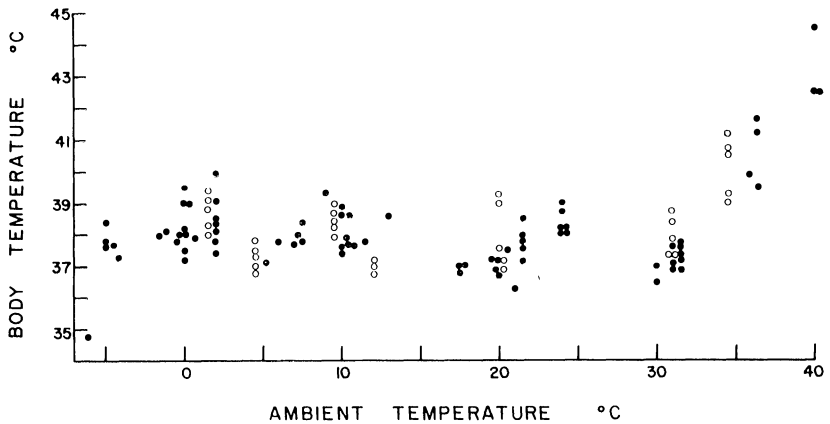


FIG. 3. Core (colonic) body temperatures of nine *Peromyscus thomasi* (filled circles) and six *P. megalops* (unfilled circles) at various ambient temperatures.

bient temperatures was limited to two hours, and we are not certain that the observed body temperatures reflect a thermal steady state or that mice could survive for a longer period at these ambient temperatures. Three individuals (two 138-g *thomasi* and one 84-g *megalops*) failed to survive for two hours at 35°–36° C. Another *thomasi* (109 g) became heated to 44.5° C after two hours at 40° C and died shortly after its removal from the chamber. Individuals that survived periods of hyperthermia showed no subsequent ill effects.

Whereas core temperatures did not decline as ambient temperature was reduced below 32° C, superficial temperatures decreased markedly. Mean differences between core temperatures (5 cm) and those at 1, 2, and 3 cm are plotted against ambient temperature in Figure 4. The greatest change in the thermal gradient between the core and peripheral areas occurred between 20° and 30° C. Colonic temperatures registered at a depth of 4 cm in the samples of both species always averaged about 0.1° C less than those at 5 cm, and the gradient became progressively steeper and more dependent on ambient temperature at shallower depths.

DISCUSSION

Since representatives of *Peromyscus thomasi* and *P. megalops* are among the largest deer mice, comparison of their metabolic rates with those of their congeners (Fig. 5) is of some interest.

The basal rates for *thomasi* and *megalops* fall within the range predicted by the equation of Brody (1945), kcal/day = 70.5 kg^{0.7}, and that

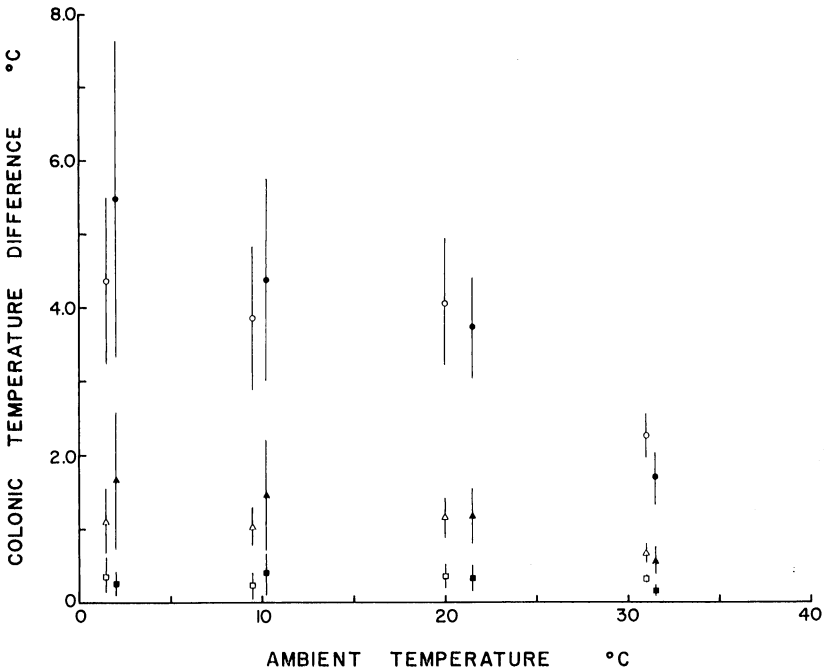


FIG. 4. Differences between deep (5 cm) colonic temperature and temperatures at depths of 1 cm (circles), 2 cm (triangles) and 3 cm (squares) in relation to ambient temperature. Filled symbols represent means for six *Peromyscus thomasi* and unfilled symbols indicate means for five *P. megalops*; vertical lines are ± 2 S.E.

of Kleiber (1961), $\text{kcal/day} = 70 \text{ kg}^{0.75}$. Hayward (1965*b*) measured oxygen consumption in *P. sitkensis* and five races of *P. maniculatus*, and found BMR varied with body weight according to Brody's approximation. On the other hand, McNab and Morrison (1963) found a less consistent relation between body weight and BMR in the forms of *Peromyscus* they investigated. For several races from "xeric" habitats they report mean basal rates falling well below levels predicted by the general equations of Brody and Kleiber. Similar observations have been made on some heteromyid, sciurid, and murid rodents from arid regions (Dawson, 1955; Bartholomew and MacMillan, 1961; Carpenter, 1963; Lee, 1963; Hudson, 1964). With the exceptions of desert populations, interspecific variations in BMR within *Peromyscus* appear to follow the relation to body weight characteristic of mammals generally. However, Hayward (1965*a, b*) found that the relation of BMR to body weight may differ considerably from the general pattern when adult individuals of the same form are compared. Further, he suggests that a

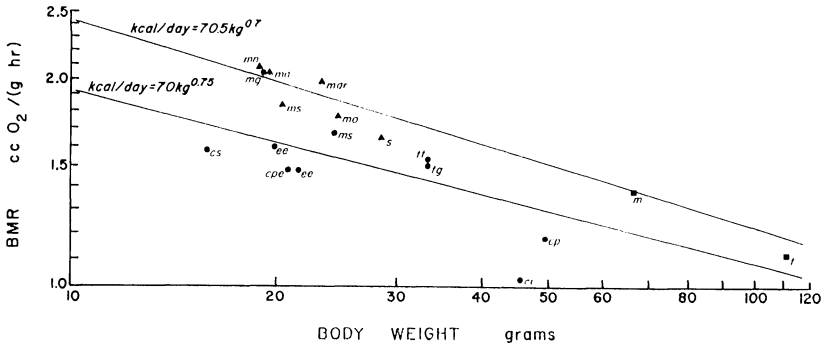


FIG. 5. Relation between mean basal metabolic rate and mean body weight in several species of *Peromyscus*; circles, data from McNab and Morrison, 1963: *P. eremicus eremicus* (*ee*), *P. californicus insignis* (*ci*), *P. californicus parasiticus* (*cp*), *P. crinitus stephensi* (*cs*), *P. crinitus pergracilis* (*cpe*), *P. maniculatus gambeli* (*mg*), *P. maniculatus sonoriensis* (*ms*), *P. truei truei* (*tt*), *P. truei gilberti* (*tg*). Triangles, data from Hayward, 1965b: *P. maniculatus nebrascensis* (*mn*), *P. m. austerus* (*ma*), *P. m. sonoriensis* (*ms*), *P. m. artemisiae* (*mar*), *P. m. oreas* (*mo*), *P. sitkensis* (*s*). Squares: *P. thomasi* (*t*), *P. megalops* (*m*). Coordinates are logarithmic.

BMR lower than predicted from the standard curve may be partly a result of high fat levels and that proposed adaptive differences in BMR be checked for correlation with body composition.

Minimal thermal conductance is often calculated as the slope of the regression of metabolic rate on ambient temperature below the lower critical temperature. Valid results are obtained by this procedure only when these data extrapolate to body temperature at zero metabolism in accordance with predictions of the Newtonian model (Scholander *et al.*, 1950). Metabolic rates of *thomasi* and *megalops* extrapolate to zero metabolism at ambient temperatures (T_A) well above body temperature (T_B). Thus, characterization of minimal conductance values for these species is complicated by the fact that conductance (O_2 consumption/ $T_B - T_A$) continues to decrease with ambient temperature below the thermoneutral zone. For example, conductance of *thomasi* falls from 0.106 cc O_2 /(g hr °C) at 25° C to 0.088 cc O_2 /(g hr °C) at 5° C. Similar calculations for *megalops* yield values of 0.119 and 0.099 cc O_2 /(g hr °C) at 25° and 5° C, respectively. Similar changes in conductance in several other *Peromyscus* are indicated by data of McNab and Morrison (1963). They found regressions of metabolic rate on ambient temperature below thermoneutrality to extrapolate to zero metabolism at temperatures above mean body temperature in some of the forms they studied. Data on *P. maniculatus* and *P. sitkensis* (Hayward, 1965b), on the other

hand, do not indicate change in conductance below the thermoneutral zone. To compare thermal conductance of the various forms of *Peromyscus* for which metabolic data are available, conductance values were calculated using mean resting rates of oxygen consumption at the lower critical temperature of each species. These conductance values are plotted as a function of mean body weight in Figure 6. In general, weight-specific conductance of deer mice is inversely related to body weight as would be expected (see Lasiewski, 1963). Values shown in

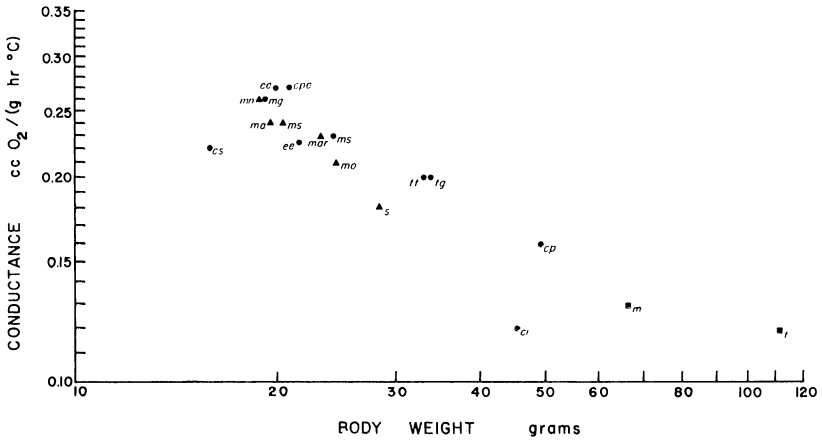


FIG. 6. Weight-specific thermal conductance of *Peromyscus* as a function of mean body weight; symbols and initials as in Fig. 5. Coordinates are logarithmic.

Figure 6 indicate that weight-specific conductance is proportional to body weight $^{-0.5}$, a value previously reported for small temperate mammals by McNab and Morrison (1963). Surface-specific conductance in *Peromyscus* also appears inversely related to body weight since surface area per unit body weight is generally considered to be proportional to body weight $^{-0.3}$ (see McNab and Morrison, 1963).

Lower critical temperatures of *P. thomasi* (28.3° C) and *P. megalops* (27.1° C) are within the same range as those reported for much smaller *Peromyscus* by Hayward (1965b) and McNab and Morrison (1963). Of the 14 forms studied by these investigators, lower critical temperatures of 11 lie within a two-degree span (27°–29° C), and all were between 26° and 30° C. The absence of a strong weight dependence is not surprising. Lower critical temperature (LCT) is related to BMR, conductance at the LCT (C), and body temperature by the equation: $LCT = T_B - (BMR/C)$. Basal metabolic rate and conductance vary similarly with body weight (cf. Figs. 5 and 6).

Mice in the samples of *P. thomasi* and *P. megalops* were able to maintain their core temperatures at a constant level (ca. 38° C) for at least two hours at the lowest ambient temperatures studied—about 0° C in *megalops* and -5° C for *thomasi*. Consequently, these mice are better regulators at low ambient temperatures than are most of those individuals in the samples of *P. crinitus* and *P. eremicus* investigated by McNab and Morrison (1963), and they also do not have the marked individual lability of core body temperature characteristic of *P. leucopus* (Morrison and Ryser, 1959). On the other hand, superficial colonic temperatures tend to decline as ambient temperature decreases (Fig. 4). Moreover, the thermal gradient between the core and superficial areas does not vary linearly with ambient temperature. This gradient increases sharply as the ambient temperature falls from 30° to 20° C and remains relatively constant as ambient temperature is reduced to lower levels. We feel that this observation is significant to the interpretation of the metabolic responses of these animals to ambient temperatures. As mentioned previously, the metabolic data do not conform to predictions of the Newtonian model in that insulation (the reciprocal of conductance) continues to increase as ambient temperature falls below the lower critical level. A value proportional to insulation at a given ambient temperature is readily calculated from metabolic rate and core body temperature. This index of insulation ($(T_B - T_A)/O_2$ consumption) was calculated at temperatures below the thermoneutral zone utilizing the regression of resting metabolic rate on ambient temperature. Mean basal metabolic rates were used to characterize insulation within the zone of thermoneutrality. Results for *thomasi* and *megalops* are shown in Figure 7. Within the thermoneutral zone, insulation of course varies inversely and linearly with temperature. As temperature falls below the lower critical level, insulation continues to rise, but at a progressively diminishing rate. The greatest changes in insulation observed below the lower critical temperature occur within the same range of ambient temperatures in which the greatest increase in the core-subsurface thermal gradient was found (cf. Figs. 4 and 7). Increased insulation may be effected through erection of pelage, postural changes, and lowered peripheral temperatures. Our data are not adequate to permit evaluation of the relative importance of these factors to the observed insulation changes. However, they strongly suggest that decreasing peripheral temperatures contribute to the changes in insulation observed both below and within the zone of thermoneutrality.

In some species of small wild birds maximal insulation is also reached at ambient temperatures well below the lower critical temperature

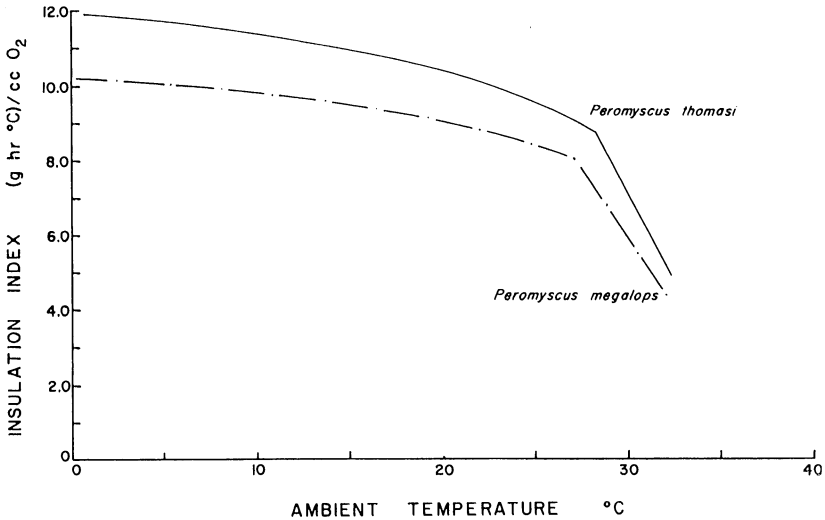


FIG. 7. Index of insulation ($T_B - T_A / O_2$ consumption) in relation to ambient temperature for *Peromyscus thomasi* (solid line) and *P. megalops* (broken line).

(West, 1962). These apparent inconsistencies with predictions of the Newtonian model are not surprising since several simplifying assumptions are implicit therein (see King, 1964).

Representatives of *P. thomasi* and *P. megalops* are good thermo-regulators and have high insulation values compared with those of smaller *Peromyscus*. These characteristics, probably attributable to large size, appear to make these mice well suited to an environment in which low temperatures prevail. Populations of *thomasi* and *megalops* occur sympatrically in southwestern Guerrero at elevations from about 7000 to 9500 feet in deep, cool, wet canyons. This altitudinal range approximates that area mapped as "cloud forest" by Leopold (1950). Towering oaks, a variety of other broadleaf trees, conifers, and a lush understory comprise the forest. Additional topographic and floristic features of the region are described by Goldman (1951) and Davis and Dixon (1959). A description of the habitat where our samples of mice were obtained is presented elsewhere (Musser, 1964). Observations on the macroclimate of these highlands indicate that from June through September dense clouds enshroud the area, soaking rains are a daily event, and low, sometimes near-freezing temperatures prevail. In December a snow cover may be found at elevations around 11,000 feet near Cerro Teotepac, and morning frost is a usual occurrence at lower altitudes (Goldman, 1951). Unfortunately we do not have sufficient data

to characterize completely physical and climatological parameters of the microhabitat in which *thomasi* and *megalops* are found. The information available comes from trapping records. Members of each species have been taken in rock outcrops where traps were placed on moss-covered rock ledges, at or within entrances to deep crevices, in runways along and under moss-covered logs, and under dense shrubbery. *P. thomasi* has been taken predominantly in runway situations. There is no evidence that burrows are excavated by either species; no nests have been located. The deep crevices and other areas providing good cover may have moderate and more stable temperatures than those existing in the macroclimate. Accumulating evidence indicates that some forms of *Peromyscus* and other small non-hibernating mammals avoid the macroclimatic extremes partly through physiological adaptations, but primarily through their behavioral utilization of temperate microclimates (see Lee, 1963; Hayward, 1965c and references cited there). Certainly this aspect of the ecology of *thomasi* and *megalops* requires further study.

SUMMARY

Measurements of oxygen consumption were made on representatives of two species of large deer mice, *Peromyscus thomasi* and *P. megalops*, at various ambient temperatures. Mean basal metabolic rates of these mice fall within the general range predicted by the equations of Brody (1945) and Kleiber (1961) relating basal levels of metabolism to body weight. Both *thomasi* and *megalops* maintained core body temperatures at about 38°C at the lowest temperatures investigated. Metabolic responses to low ambient temperatures indicate that insulation continues to increase with decreasing temperature below the lower critical temperature. These insulative changes were found to parallel changes in the thermal gradient between body core and peripheral levels. Mice of both species become hyperthermic as ambient temperature approaches and exceeds their normal body temperature. Basal metabolic rate, conductance, and body temperature regulation of each species was compared with available data for other forms of *Peromyscus*. Thermoregulatory responses of *thomasi* and *megalops* are discussed in relation to available observations on their habitat.

ACKNOWLEDGMENTS

We are grateful for the cooperation of the following persons: D. J. Klingener and I. Muul cared for the mice in transit from México City; W. R. Dawson graciously allowed us to use laboratory facilities under his supervision in the Department and Museum of Zoology; W. H. Burt and T. H. Hubbell of the Museum provided support for Musser's field work in México; J. H. Hughes issued quarantine permits from the U. S. Department of Health, Education and Welfare for transporting rodents across the U. S.-Mexican border; Rodolfo Hernández Corzo, of the Dirección General de Caza, Departamento de Conservación de la Fauna Silvestre, Secretaría de Agricultura y Ganadería, furnished collecting permits. The manuscript was read by Burt, Dawson, and E. T. Hooper; their helpful criticisms are appreciated. The photographs were taken by Joseph Graham and W. H. Burt.

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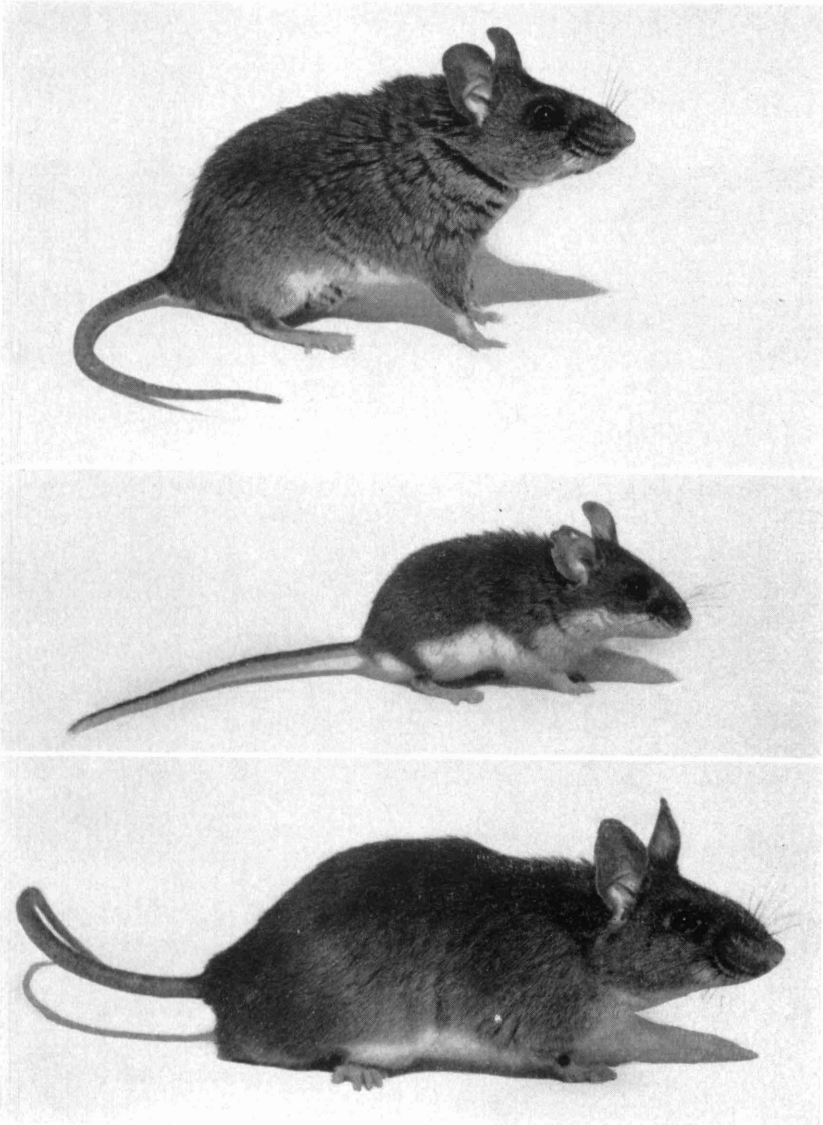


PLATE I

Top, *Peromyscus megalops auritus* (♀, 74 g); middle, *P. maniculatus gracilis* (♂, 22 g); bottom, *P. thomasi thomasi* (♂, 125 g). All adults and about one-half life-size. *P. maniculatus* is included for size comparison.

