ENERGETICS AND NESTING BEHAVIOR OF THE
NORTHERN WHITE-FOOTED MOUSE, PEROMYSCUS
LEUCOPUS NOVEBORACENSIS

A Thesis

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INTRODUCTION

Animals adjust to changing environmental temperatures by some combination of two basic responses, behavioral evasion of unfavorable temperatures and physiological adjustment (Brown, 1968). Metabolic rate and its temperature-adaptive significance in different geographic races of Peromyscus has been reported in the literature (Murie, 1961; Morrison and McNab, 1963; Hayward, 1965a). Hart (1953) found that cold acclimation of white-footed mice did not affect initial average oxygen consumption but prolonged the time that the initial levels could be maintained.

Nest-building constitutes a thermoregulatory activity that is enhanced at low temperatures and reduced at high temperatures and may be responsible for increased tolerance of low temperatures (Sealand, 1952). The relationship of nest insulation to survival of Peromyscus has been demonstrated by Sealand (1952). Sealand also reported that huddling and occupying a nest cavity prolonged the survival time of mice exposed to low temperatures. Kinder (1927) found increased nest-building activity accompanied by increased food intake in the Norway rat (Rattus

norvegicus). Brown (1968) observed that dens of coastal populations of Neotoma cinerea offered less protection than dens of highland populations and were less adequate than those occupied by high desert and subterranean low desert populations of Neotoma albigula. Shredding behavior of white-footed mice was found to increase significantly at low temperatures (Thorne, 1958). Harvest mice (Reithrodontomys megalotis) which constructed nests at 1.0°C were able to lower their metabolic rate by 24% (Pearson, 1960). Several studies have reported that southern species of Peromyscus exhibit a lower level of nest-building activity than northern species (King et al, 1964; Layne, 1969; Wolfe, 1970).

The intent of this investigation was to study the energetics of the northern white-footed mouse, Peromyscus leucopus noveboracensis, at different ambient temperatures and to investigate the insulating effectiveness of nests at moderate and low temperatures. The insulating effectiveness of huddling and occupying a nest cavity were also studied.

LIFE HISTORY

Peromyscus leucopus noveboracensis is found in a wide range of habitat types. They are generally woodland dwellers but have reportedly been trapped in grasslands as well (Hirth, 1959). In northeastern United States, P. leucopus lives in cool, damp boreal forest, often in close association with P. maniculatus (Baker, 1968). They are also reported to inhabit dryer, warmer deciduous forests (Baker, 1968). Blair (1940) found home ranges from 0.3 to 1.50 acres for Peromyscus with a mean home range of $0.81^{\pm} 0.15$ acres.

Peromyscus are generally active at night and, despite their small size and host of predators, often move about in the open without confining themselves to dense overhead vegetation (Baker, 1968). Their food usually consists of grass, seeds, fruits, and insects (Hamilton, 1941).

Natural nests of P. leucopus are of a globular form, hollow in the center, with the entrance to the nest closed when the nest is in use (Nicholson, 1941). Layne (1969) found natural nests of P. leucopus to be spherical and well-constructed. In winter, floors of nests are built up and are usually roofed over (Nicholson, 1941). White-footed

mice nest in a wide variety of situations that include cavities in logs, stumps, and trees; holes in the ground; crevices in rocks; beneath objects on the ground; human habitations; and old bird and squirrel nests (Hamilton, 1943). Nests are usually constructed from grass, rags, milkwood floss, leaves, feathers, and other materials that may be available (Nicholson, 1941). P. leucopus is solitary in summer, but in winter, several of different ages and sexes may live together (Nicholson, 1941). Mice use arboreal nest sites less frequently in winter than in summer and terrestrial nest sites more frequently in winter than in summer (Nicholson, 1941).

The Peromyscus used in this study were trapped in the Hocking Hills area of southern Ohio. Mice in this area are exposed to wide fluctuations in ambient temperatures with average monthly temperatures varying from 84.0°F in July to 20.2°F in February (U. S. Dept. of Commerce, 1973).

METHODS AND MATERIALS

Experimental Animals:

Twelve northern white-footed mice (Peromyscus leucopus noveboracensis) were trapped in Sherman traps baited with peanut butter during April and May, 1973. The mice were maintained in the laboratory in individual cages at 20° to 25°C on a 12-hour photoperiod (0700-1900 hours) and fed a diet of Purina mouse chow (Ralston Purina Co., St. Louis, Missouri). Animals were maintained in the laboratory for 4 months prior to measurements and appeared to adapt well.

Oxygen Consumption:

Oxygen consumption was measured in an open-circuit system connected to a Beckman F-3 oxygen analyzer (± 0.06 ccO₂ hr⁻¹) and Heath recorder. The respiration chambers were clear Plexiglass boxes (25 by 20 by 20 cm) fitted with a thermocouple, air intake and an air outlet. An opening (13 by 13 cm) was centered in the top surface and covered by a glass plate (3mm thick). The chambers were submerged in an Aminco temperature-controlled water bath so that the glass window was covered by 1 cm. of water. Temperature in the chambers could be maintained within 0.5°C

of the desired ambient temperature. Oxygen consumption was calculated based on a flow rate of 1000 cc/min and all gas volumes were corrected to STP. Air temperature was recorded with a copper-constantan thermocouple in conjunction with a Leeds-Northrup speedomax potentiometer ($\pm 0.06^{\circ}\text{C}$).

Each measurement of oxygen consumption was obtained on animals that had not eaten for approximately 2 hours. All measurements were made during normal daylight hours. Mice were allowed to adjust to the respiration chambers for at least 30 minutes prior to any measurements. The value used for calculating metabolic rate was that obtained after mice had reached a steady state of oxygen consumption and maintained it for 20 to 30 minutes

Oxygen consumption of a total of 10 mice was measured at 5 degree intervals from 5° to 35°C and at 38°C . Animals were weighed to the nearest 0.01 grams before each measurement. Rectal temperatures were measured to the nearest 0.1°C after oxygen consumption runs using a YSI telethermometer (model #46, Yellow Springs Instrument Co., Inc., Yellow Springs, Ohio) ($\pm 0.15^{\circ}\text{C}$).

Insulating Effectiveness of Nests:

A total of 6 mice were placed in individual respiration chambers fitted with plexiglass brackets to hold water bottles and the chamber openings covered with hardware cloth.

Mice were provided with approximately 100 grams of mouse chow. Each mouse was provided with 13 grams of nesting material consisting of approximately equal volumes of feathers, coarse grass, fine grass, leaves, and pine needles. The chambers were kept at 30°C in a Scherer-Gillett walk-in environmental room (model #810) ($\pm 1.0^{\circ}\text{C}$) and the mice were allowed to build nests until no further construction was observed. Internal and external nest temperatures were measured in the chambers with a iron-constantan thermocouple in conjunction with a Daystrom-Weston potentiometer ($\pm 0.06^{\circ}\text{C}$) for a period of 3 hours after which food and water bottles were removed and oxygen consumption measured as was previously described. Animals were weighed after each run and rectal temperatures were measured.

The same 6 mice were provided with 13 grams of new nesting material and placed in the environmental room at 25°C. The experimental procedures at 30°C were then repeated. Similar experiments were conducted at 5°C using 9, 13, 19, and 25 grams of nesting material. Mice were allowed 2 days rest between each set of measurements.

The effects of huddling were measured at 5°C. Five pairs of mice were placed in individual respiration chambers and oxygen consumption measured as previously described. Each pair of mice was then provided with 13 grams of nesting material and the experimental procedures for a single

mouse with nesting material were repeated.

The insulating effectiveness of a simulated nest cavity without nesting material was measured at 5°C. Six mice were placed in individual respiration chambers and provided with an aluminum can (Area= 12.4 cm²). Oxygen consumption was measured as previously described. The same mice were then provided with 13 grams of nesting material and the experimental procedure previously described was repeated.

RESULTS

Oxygen Consumption:

Oxygen consumption was measured at ambient temperatures from 5°C to 38°C (Fig. 1). The thermal neutral zone extended from 27.5° to 35°C. Oxygen consumption was lowest at 30°C and increased with decreasing ambient temperature from 27.5°C to 5°C. The increase was linear below thermal neutrality and is described by the equation:

$$\text{ccO}_2/\text{gm/hr} = 8.52 - 0.23T_A.$$

Oxygen consumption increased between 35° and 38°C. One mouse ran at 40°C died in the respiration chamber after an exposure period of 40 minutes.

Body Temperature and Thermal Conductance:

The body temperature of 10 mice between ambient temperatures of 5° and 30°C remained relatively constant (Fig. 2) fluctuating only slightly, whereas, between 30° and 38°C, the body temperature increased significantly ($p \leq .001$). Mean body temperature over a temperature range of 5° and 38°C was $37.16 \pm \text{S.E.M. } 0.75^\circ\text{C}$ but increased from a mean of 36.4°C at 5°C to 38.7°C at 38°C. If Newton's Law of Cooling is assumed, the line fitted to metabolic

Figure 1. The relation of oxygen consumption of the white-footed mouse (Peromyscus leucopus) to ambient temperature. Horizontal lines represent the 95% confidence limits ($t \times$ standard error of the mean), and points represent the mean. The numerals show the number of mice measured at each temperature.

Figure 2. The relation of body temperature to ambient temperature (symbols as in Fig. 1).

rates below thermal neutrality intercepts the T_A at 37.0°C which is close to our findings for body temperature.

Thermal conductance can be calculated by the linear approximation of total heat flow (Kleiber, 1974) which states:

$$MR = C(T_B - T_A) \text{ or}$$

$$C = MR / T_B - T_A,$$

where MR is expressed as oxygen consumption ($\text{ccO}_2/\text{gm/hr}$) and temperature in degrees centigrade. Values for thermal conductance remained relatively constant from 5° to 25°C (Fig. 3) but increased significantly from 25° to 30°C ($p \leq .001$) and again from 30° to 38°C ($p \leq .001$). When ambient temperature equaled or exceeded body temperature, values for thermal conductance were asymptotic. The slope of the line relating oxygen consumption to ambient temperature, as described previously, is equal to the thermal conductance of the animal, $0.23 \text{ ccO}_2/\text{gm/hr}/^{\circ}\text{C}$.

Insulating Effectiveness:

Mean oxygen consumption rates measured on 6 mice at 30°C with a 13 gram nest were $2.10 \pm \text{S.E.M. } 0.07 \text{ ccO}_2/\text{gm/hr}$ as compared to $2.15 \pm \text{S.E.M. } 0.30 \text{ ccO}_2/\text{gm/hr}$ measured without a nest. This decrease was not significant. Thermal conductance and body temperatures were not significantly different. Some mice constructed nests which consisted of

Figure 3. Thermal conductance in relation to ambient temperature (symbols as in Fig. 1).

very shallow depressions, but little or no nest construction was observed after 3 days. As a result, there was no significant difference between internal and external nest temperatures.

At 25°C, the mean oxygen consumption rate was $2.53 \pm$ S.E.M. $0.03 \text{ ccO}_2/\text{gm/hr}$ with a 13 gram nest and $2.88 \pm$ S.E.M. $0.12 \text{ ccO}_2/\text{gm/hr}$ without a nest. This decrease was significant ($p \leq .05$). Thermal conductance decreased significantly ($p \leq .05$) being $0.24 \pm$ S.E.M. $0.01 \text{ ccO}_2/\text{gm/hr}^\circ\text{C}$ without a nest and $0.21 \pm$ S.E.M. $0.01 \text{ ccO}_2/\text{gm/hr}^\circ\text{C}$ with a nest. There was no significant difference in body temperatures. Nests were generally a deep, uncovered bowlshape. Internal and external nest temperatures did not differ significantly.

Mean oxygen consumption rates and thermal conductance (Table 1) for 6 mice at 5°C with 9, 13, 19, and 25 grams of nesting material were significantly lower ($p \leq .001$) than those obtained for the same mice without a nest. Body temperatures were not significantly different. Nests consisted of a thick, bowlshape base and were completely roofed over with a domeshape cover. Construction was usually completed within one day. After 3 days, all 6 mice had constructed nests. Internal nest temperatures were significantly higher ($p \leq .001$) than external nest temperatures (Table 2).

Oxygen consumption and thermal conductance were

measured at 5°C for huddling mice with and without a nest, and for single mice in a simulated nest cavity with and without a nest. In all four cases, body temperature did not differ significantly. A comparison of the values for oxygen consumption and thermal conductance obtained in the various tests is given in Tables 3a and 3b. While in the respiration chamber at 5°C, huddling mice without a nest were observed to curl into a ball on top of each other. When provided with 13 grams of nesting material, huddling mice generally constructed nests within one day. After 3 days all 5 pairs of mice had constructed nests. Nests consisted of a deep bowlshape base with a domeshape cover. Mean internal nest temperature was $17.8 \pm \text{S.E.M. } 0.36^{\circ}\text{C}$ and was significantly higher ($p \leq .001$) than the external temperature ($5.8 \pm \text{S.E.M. } 0.36^{\circ}\text{C}$).

When provided with a nest cavity without a nest, mice were observed to curl into a ball inside the cavity while in the respiration chambers at 5°C. When the mice were given 13 grams of nesting material, nests were usually constructed in the nest cavity within one day. After 3 days, all 6 mice had constructed nests. Nests conformed to the shape of the nest cavity with the mouse completely surrounded by nesting material. Mean internal nest temperature was $19.0 \pm \text{S.E.M. } 0.44^{\circ}\text{C}$ and was significantly higher ($p \leq .001$) than the external nest temperature ($5.1 \pm \text{S.E.M. } 0.30^{\circ}\text{C}$).

Table 1. Mean oxygen consumption and thermal conductance for 6 mice at 5°C.

Nest Weight	Oxygen Consumption (ccO ₂ /gm/hr) (± S.E.M.)	Thermal Conductance (ccO ₂ /gm/hr/°C) (± S.E.M.)
Without nest	7.45 ± 0.13	0.25 ± 0.02
9 grams	4.88 ± 0.13	0.16 ± 0.02
13 grams	4.44 ± 0.22	0.14 ± 0.01
19 grams	4.37 ± 0.19	0.15 ± 0.02
25 grams	4.24 ± 0.14	0.13 ± 0.02

Table 2. Mean internal and external nest temperatures for 6 mice at 5°C with 9, 13, 19, and 25 grams of nesting material

Nest Weight	Internal Temperature (°C ± S.E.M.)	External Temperature (°C ± S.E.M.)
<hr/>		
9 grams	12.5 ± 0.36	4.6 ± 0.30
13 grams	14.5 ± 0.34	4.5 ± 0.37
19 grams	14.8 ± 0.44	4.9 ± 0.27
25 grams	14.9 ± 0.41	4.8 ± 0.30

Table 3a. Comparison of oxygen consumption rates at 5°C
with significance levels.

Test	ccO ₂ /gm/hr (±S.E.N.)	p ₂			
		Huddling without nest	Huddling with nest	Nest Cavity without nest	Nest Cavity with nest
Without nest	7.45±0.13	.001 (-)	.001 (-)	.001 (-)	.001 (-)
9 grams	4.88±0.13	(o)	.01 (-)	(o)	.05 (-)
13 grams	4.44±0.22	.01 (+)	.05 (-)	.02 (+)	(o)
19 grams	4.37±0.19	.01 (+)	.05 (-)	.02 (+)	(o)
25 grams	4.24±0.13	.01 (+)	(o)	.02 (+)	(o)
Huddling without nest	5.43±0.28		.001 (-)	(o)	.02 (-)
Huddling with nest	3.69±0.17	.001 (+)		.001 (+)	(o)
Nest Cavity without nest	5.50±0.22	(o)	.001 (-)		.01 (-)
Nest Cavity with nest	4.08±0.22	.02 (+)	(o)	.01 (+)	

(+) significantly higher
 (-) significantly lower
 (o) no significant difference

Table 3b. Comparison of thermal conductance at 5°C
with significance levels.

Test	ccO ₂ /gm/hr/°C (±S.E.M.)	p _L			
		Huddling without nest	Huddling with nest	Nest Cavity without nest	Nest Cavity with nest
Without nest	0.25±0.02	.001 (-)	.001 (-)	.001 (-)	.001 (-)
9 grams	0.16±0.02	(o)	.001 (-)	(o)	.02 (-)
13 grams	0.14±0.01	.01 (+)	.02 (-)	.02 (+)	(o)
19 grams	0.15±0.02	.01 (+)	.05 (-)	.02 (+)	(o)
25 grams	0.13±0.02	.01 (+)	(o)	.02 (+)	(o)
Huddling without nest	0.17±0.02		.001 (-)	(o)	.02 (-)
Huddling with nest	0.12±0.01	.001 (+)		.001 (+)	(o)
Nest Cavity without nest	0.17±0.01	(o)	.001 (-)		.02 (-)
Nest Cavity with nest	0.12±0.02	.01 (+)	(o)	.02 (+)	

(+) significantly higher
 (-) significantly lower
 (o) no significant difference

DISCUSSION

Oxygen Consumption, Body Temperature and Thermal Conductance:

The mean oxygen consumption rates of the Peromyscus leucopus measured in this study were very similar to those reported by Hart (1953). Pearson (1947) found the basal metabolic rate at 28°C of one 19 gram P. leucopus fasted for 12 hours to be 1.6 ccO₂/gm/hr. We did not obtain any values as low as this. This difference can probably be explained by the small sample size used by Pearson. The thermal neutral zone for mice in this study extended from 27.5° to 35°C which is very similar to the thermal neutral zones reported by Hayward (1965a) for different species of Peromyscus.

Body temperature averaged 37.16°C over a temperature range of 5° to 38°C. This value is in close agreement with the mean body temperature of 37.43°C reported by Morrison and Ryser (1959). Sealander (1953) gave the mean rectal temperature of P. leucopus to be between 37° and 38°C. The mice became slightly hyperthermic at 38°C, with body temperature rising as high as 39.5°C. P. leucopus has an upper lethal body temperature of 42° to 43°C and a

lower lethal of 4.6°C (Sealand, 1953). Morrison and Ryser (1959) report that the body temperature of Peromyscus showed great lability in the face of cold exposure which represented a reduced but regulated level. Lability of body temperature has been demonstrated in the harvest mice at low temperatures (1.0°C) (Pearson, 1960).

Thermal conductance averaged $0.23 \text{ ccO}_2/\text{gm/hr}/^{\circ}\text{C}$ or $1.08 \text{ cal/gm/hr}/^{\circ}\text{C}$. Predicted thermal conductance was calculated from the equation by Herreid and Kessel (1967),

$$\log C = 0.691 - 0.505 \log W$$

and equaled $0.989 \text{ cal/gm/hr}/^{\circ}\text{C}$. Therefore, thermal conductance of P. leucopus is equivalent to other mammals of the same size (24 grams). The curve for thermal conductance (Fig. 3) suggests that the lower critical temperature of thermal neutrality is between 25° and 30°C since thermal conductance is minimal and constant below 25°C and increases at 30°C .

Insulating Effectiveness:

The degree of protection offered by nests must be an important factor influencing the survival of small mammals during periods of cold when they are not actively searching for food (Sealand, 1952). Mice can escape severe cold, at least during their resting period, by going into nests and by huddling together (Scholander et al, 1950a).

Scholander et al, (1950b) state that the major feature in

the adaptation to a cold climate is that of increased insulation, and basal metabolic rate and body temperature are not adaptive to climate. Heat loss in homeotherms is in part a function of insulation which is the significant factor influencing heat dissipation at ambient temperatures below thermal neutrality (Brown, 1968). The major role of the nest is to increase insulation and decrease heat loss. Insulation of mice with and without a nest can be compared by calculating an insulation index $T_B - T_A$ /oxygen consumption, which expresses insulation in terms of the difference between body temperature (T_B) and ambient temperature (T_A) and the metabolism at that ambient temperature (Musser and Shoemaker, 1965; Brown, 1968). Insulation is the reciprocal of thermal conductance (Scholander et al, 1950c). Calculated insulation indices can be found in Table 4. The index is a measure of an animal's capacity to retard the loss of metabolic heat (Brown, 1968).

At 30°C, which is within thermal neutrality, insulation indices were not significantly different. This is expected, since the mice did not build nests at this temperature. At 25°C, mice showed a low level of nest-building activity, but did build deep but uncovered bowlshape nests. The insulation index with a nest was significantly higher ($p \leq .05$) than without a nest, indicating that mice can effectively increase insulation by building nests at moderate

ambient temperatures. A nest's added insulation is most important at low ambient temperatures. Small mammals which have the greatest metabolic response to temperature changes, have only limited possibilities for seasonal insulative changes (Hart, 1956). At 5°C, the mice could significantly increase ($p \leq .001$) their insulation and decrease their heat loss by occupying well-constructed nests. Huddling will also serve to increase insulation. The insulation index for huddling mice without a nest is significantly higher ($p \leq .001$) than for a single mouse without a nest. When huddling of several mice is combined with nesting, the insulation index is significantly higher ($p \leq .05$) than a single mouse in a nest. By occupying a nest cavity, a mouse's insulation is significantly higher ($p \leq .001$) than that of a mouse in the open without a nest. When a nest is built in a nest cavity, the insulation index is significantly higher ($p \leq .05$) than the index of a mouse in an exposed nest.

Smaller mammals, 2 kg. and below, have much less fur insulation and are capable of only limited seasonal insulative adjustment in comparison with large mammals (Hart, 1956; Hayward, 1965a). Fur and skin insulation, therefore, are not totally effective for regulating heat dissipation. Very small mammals and birds have large surface area-volume ratios and can only carry a limited amount of insulation.

As a consequence, their capacities to produce significant changes in temperature regulation seem to be limited (Brown, 1968). Hayward (1965a, b) suggests that in very small mammals behavioral selection of microclimates may be much more important than physiological adaptations. Building and occupying nests is one possible behavioral selection.

Kinder (1927) found that nest-building by albino rats appeared more promptly at moderate and low temperatures than at high temperatures. This also appears to be true of Peromyscus leucopus. Mice showed little or no nest-building activity at 30°C. At 30°C, mice built deep, bowlshape nests in 3 days. Nest-building activity was most apparent at 5°C, well-constructed nests being completed within 1-2 days. By building a nest at high temperatures, such as 30°C, animals may risk overheating. Soholt (1973) reports that kangaroo rats, Dipodomys merriami, did not build nests at 30°C, which is within thermal neutrality, but did build nests at 15°C.

Estimating from data obtained by Kavanau (1967), a deer mouse, Peromyscus maniculatus, spends at least 56% of each day (13.6 hours) in the nest. This data was obtained at 25°C in the laboratory. We will assume that at 5°C in nature, Peromyscus leucopus will spend at least this much time per day in the nest. If 1 ccO₂ equals 4.7 cal for a

Table 4. Insulation indices of P. leucopus at different ambient temperatures

T_A	Insulation Index $^{\circ}\text{C}/(\text{ccO}_2/\text{gm/hr})$ ($\pm$ S.E.M.)	
	Without Nest	With Nest
30°C	2.94 ± 0.26	3.03 ± 0.26
25°C	4.13 ± 0.11	4.76 ± 0.14
5°C	4.04 ± 0.11	
1) 9 grams		6.32 ± 0.26
2) 13 grams		7.63 ± 0.25
3) 19 grams		7.21 ± 0.37
4) 25 grams		7.69 ± 0.53
5) Huddling	5.83 ± 0.29	8.33 ± 0.36
6) Nest Cavity	5.83 ± 0.25	8.33 ± 0.27

fasted mouse, energy expenditure can be calculated. At 25°C, a mouse expends 7.54 kcal/day or 4.22 kcal in 13.6 hours. The expenditure at 5°C for a single mouse is 20.505 kcal/day or 11.48 kcal per 13.6 hours. Huddling mice without a nest expend 14.92 kcal/day or 7.96 kcal in 13.6 hours. Thus, an estimate of the daily savings in energy expenditure by occupying a nest, a nest cavity, and by huddling can be made (Table 5).

Peromyscus leucopus can decrease its daily energy expenditure as much as 29% by huddling in a nest at 5°C. Nesting in a nest cavity will reduce the expenditure almost as much as huddling in a nest (27%). Building a nest with 9 grams of nesting material, huddling without a nest, and occupying a nest cavity without a nest are least effective in reducing the daily energy expenditure. Even at a moderate temperature (25°C), mice can reduce their daily energy expenditure as much as 10% by occupying an uncovered nest. Brown (1968) reports that Neotoma cinerea at 6°C could save approximately 8 kilo-calories per day by spending 3/4 of its time in a nest.

By building and occupying nests, mice could reduce their minimal heat production (Table 3). The percent decrease in oxygen consumption for the various tests is given in Table 6. Peromyscus leucopus used in this study could decrease its heat production by as much as 12% by

Table 5. Daily savings in energy expenditure by P. leucopus occupying nests at different ambient temperatures

T_A	Kcal/Day Saved	% Savings Daily
25°C	0.737	10
5°C		
1) 9 grams	4.52	19
2) 13 grams	5.13	25
3) 19 grams	5.29	26
4) 25 grams	5.37	26
5) Huddling without nest	3.52	17
6) Huddling with nest	5.98 (2.46)*	29 (17)*
7) Nest Cavity without nest	3.53	17
8) Nest Cavity with nest	5.56 (2.03)**	27 (14)**

* Savings by huddling in a nest compared to huddling without a nest.

** Savings being in a nest cavity with a nest compared to without a nest.

occupying a nest at 25°C; and by as much as 53% by huddling in a nest at 5°C. Pearson (1960) found harvest mice that occupied nests at 1.0°C were able to lower their metabolic rate by 24%; and by 17% at intermediate temperatures. Pearson also found that by huddling without a nest, the rates of metabolism per gram of huddled harvest mice, were 28% less than they would have been for a single one of the mice. This is similar to what was found for P. leucopus, which could decrease its metabolic rate 27% by huddling without a nest. By huddling in a nest, the decrease is doubled (53%). At 6.0°C, Neotoma cinerea could reduce its minimal heat production by 23% by occupying its nest (Brown, 1968). Peromyscus gossypinus and Peromyscus floridanus could decrease their metabolic rate by 22% and 33% respectively when in a nest (Layne, 1969).

Nesting in a simulated nest cavity provided better protection than exposed nests or the simulated nest cavity without a nest. Huddling by several mice in an exposed nest provided better protection than for a single mouse in an exposed nest. Sealander (1952) found that huddling and a nest had a summation effect and prolonged the survival time of 3 species of Peromyscus subjected to low temperature without food or water. We can predict that if the number of huddling mice was increased, and if mice were to huddle in a nest cavity, that their metabolic rate and

Table 6. Percent decrease in oxygen consumption of P. leucopus with a nest at different ambient temperatures

T_A	% Decrease
30°C	2
25°C	12
5°C	
1) 9 grams	34
2) 13 grams	41
3) 19 grams	42
4) 25 grams	43
5) Huddling without nest	27
6) Huddling with nest	53 (33)*
7) Nest Cavity without nest	26
8) Nest Cavity with nest	45 (26)**

* Percent decrease in comparison with huddling without a nest.

** Percent decrease in comparison with a nest cavity without a nest.

daily energy expenditure would be further decreased; and their insulation would be greatly increased.

When the mice were provided with 9, 13, 19, and 25 grams of nesting material, they built nests in all four cases, and used almost all the material provided. We might expect that given additional time and nesting material, that all of the material would have been utilized. However, this additional material would not significantly reduce oxygen consumption and the daily energy expenditure, or significantly increase the insulation. Thirteen grams of nesting material appears to offer the maximum protection from cold temperatures. The insulation index (Table 4) with 13 grams of nesting material was significantly higher ($p \leq .01$) than that of 9 grams. However, 19 and 25 grams of nesting material did not offer significantly more insulation than 13 grams of nesting material. Oxygen consumption (Tables 1 and 6) with 13 grams was 7% lower than 9 grams of nesting material, a significant decrease ($p \leq .05$). The decrease with 19 and 25 grams was only 1% and 2% respectively and was not significantly lower than 13 grams. A similar trend was found in the daily energy expenditure (Table 5). With 13 grams of material, mice could save 0.61 kcal/day more than with 9 grams, a savings of 6% daily. However, the energy savings with 19 and 25 grams of nesting material was 0.26 and 0.35 kcal/day

respectively. This represented a decrease of only 1% daily. The data suggest that an exposed nest weighing approximately 13 grams has maximum effectiveness, and mice would not significantly decrease heat production and energy expenditure or increase insulation by using additional material. Wolfe (1970) reports that Peromyscus leucopus from Illinois, which was provided with 20 grams of nesting material, used only 11.6 grams in nest construction. An hypothesis that if mice were to gather more nesting material than needed, they would only increase their energy expenditure and prolong their exposure to adverse conditions, especially in times when nesting sites and nesting material were scarce. Thus, it would be more advantageous for animals to huddle or build their nests in a nest cavity.

An exposed nest constructed from 9 grams of nesting material offers the least protection from cold temperatures. However, it still served to increase insulation significantly more ($p \leq .001$) than no nest at all and was more effective than huddling without a nest and than a simulated nest cavity without a nest. Nests built from 9 grams of nesting material appeared to be more open than those with 13, 19, or 25 grams, and did not retard the loss of metabolic heat as effectively. However, if this small amount of nesting material is all that is available, a

mouse is still able to decrease his daily energy expenditure by 19% (Table 5), and to decrease his heat production by 34% (Table 6).

The insulation of the nests built by Peromyscus leucopus at 5°C retarded the loss of metabolic heat and effectively raised the temperature of the air immediately surrounding the mice. This is reflected in the substantial difference between internal and external nest temperatures. Internal nest temperatures were significantly higher than the external nest temperatures in all of the tests conducted at 5°C. The metabolic rates measured for mice in exposed nests (9, 13, 19, and 25 grams) approached the level that would be expected at 15°C without a nest, which was approximately the internal temperature of these nests. The metabolic rates measured for huddling mice in a nest and for a single mouse in a nest cavity with a nest approached the level that would be expected at 20°C without a nest. This was approximately the internal nest temperature measured in these tests.

By building and occupying nests, mice were able to create a more optimal microclimate. Behavior responses such as huddling and nest-building may give enough additional protection to offset most of the adverse effects of low air temperature (Sealander, 1953). Nest-building activity will, in part, be limited by the availability of nest sites

and nesting material during periods of cold and adverse environmental conditions. The evolution of nest-building activity, although influenced by gross climatic conditions, has been more closely associated with more proximal ecological factors such as habitat and nest site preferences. These in turn help to determine the specific microclimates under which Peromyscus live (Layne, 1969). One might expect that the limits of thermoregulation would correspond to some extent with the temperature variation in the environment (Morrison and McNab, 1963). Peromyscus can essentially minimize this variation in temperatures by occupying nests and nest cavities, and by huddling. The nest, therefore, represents an important microclimate for Peromyscus. A microclimate in which they can decrease heat production, decrease energy expenditure, and increase insulation, thus minimizing the stress created by cold temperatures and adverse environmental conditions. Selection has apparently acted on the behavior of Peromyscus leucopus enhancing temperature regulation and survival.

SUMMARY

1. Oxygen consumption of 10 Peromyscus leucopus noveboracensis was measured at ambient temperatures from 5° to 38°C.
2. Thermal neutrality extended from 27.5° to 35°C with oxygen consumption lowest at 30°C. The increase below thermal neutrality was linear and is described by the equation:

$$\text{ccO}_2/\text{gm/hr} = 8.52 - 0.23T_A.$$

Oxygen consumption increased from 35° to 38°C.

3. Body temperature increased from 36.4° to 38.7°C over a temperature range of 5° to 38°C with a mean of 37.16°C.
4. Thermal conductance of P. leucopus below thermal neutrality is equivalent to what is predicted for a 24 gram mammal and averaged 0.23 ccO₂/gm/hr/°C.
5. The insulating effectiveness of nests built at 30°C was investigated. Mice exhibited little or no nest-building activity, and, as a result, showed no significant decrease in oxygen consumption, thermal conductance, and daily energy expenditure; and no significant increase in insulation.

6. Mice provided with 13 grams of nesting material built deep, bowlshape nests in 3 days which significantly decreased oxygen consumption, thermal conductance, and daily energy expenditure and significantly increased insulation. Internal and external nest temperatures were not significantly different.
7. The insulating effectiveness of exposed nests constructed from 9, 13, 19, and 25 grams of nesting material was compared at 5°C. In all cases, mice constructed nests in 1-2 days and significantly decreased oxygen consumption, thermal conductance, and daily energy expenditure and significantly increased insulation.
8. A nest constructed from 13 grams of nesting material offered the most protection of the exposed nests. Nine grams offered the least protection.
9. The metabolic rates of mice in exposed nests approached the level expected at 15°C without a nest, which was approximately the internal temperature of these nests.
10. Huddling without a nest at 5°C significantly decreased oxygen consumption, thermal conductance, and daily energy expenditure with significantly increased insulation.
11. Huddling in a nest at 5°C offered the most protection from low temperatures and caused the greatest decrease

- in oxygen consumption, thermal conductance, and daily energy expenditure; and the greatest increase in insulation of all tests conducted.
12. Occupying a nest cavity with and without a nest significantly decreased oxygen consumption, thermal conductance, and daily energy expenditure; and increased insulation. A nest cavity with a nest was more effective than one without a nest.
 13. Metabolic rates measured for huddling mice in a nest and for single mice in a nest cavity with a nest approached the level expected at 20°C without a nest, which was approximately the internal temperature of these nests.
 14. The importance of the nest as a microclimate is discussed.

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