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DAILY TORPOR IN THE LABORATORY MOUSE, MUS MUSCULUS VAR. ALBINO¹

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The body temperature (T_{re}) of *Mus musculus* fed ad libitum was labile and varied between 36.0 ± 0.3 and 39.3 ± 0.3 C at ambient temperatures (T_a) ranging from 2.5 to 38.0 C. The thermal neutral oxygen consumption was 1.47 ml $O_2/g \cdot h$, which occurred between the lower critical temperature of 31.0 C and the upper critical temperature of 35.0 C. The thermal conductance decreased from a high of 0.26 ml $O_2/g \cdot h \cdot C$ to a low of 0.15 ml $O_2/g \cdot h \cdot C$ as the T_a decreased from 31.0 to 2.5 C. The conductance increased from the lower to the upper limits of the thermal neutral zone, reaching a maximum of 0.43 ml $O_2/g \cdot h \cdot C$ at a T_a of 35.0 C. The highest conductance was 0.74 ml $O_2/g \cdot h \cdot C$ at a T_a of 38.0 C. The lability of T_{re} increased with a restriction of the daily food ration, averaging 34.5 ± 0.3 C and ranged between 22.0 and 37.0 C at T_a 's of 19-20 C. Five of 14 animals on ad libitum food allotments became torpid within 24 h after food was withheld. Heat production appeared to be suppressed during entry into torpor, which was attributed to a reduction in shivering. The "critical T_{re} " of torpid mice was 16-19 C. Oxygen consumption was directly related to T_{re} at a T_{re} of 31 C and above, but it remained relatively constant at T_{re} 's between 31 and 16 C. The $T_{re} - T_a$ gradient and oxygen consumption of torpid mice increased at T_a 's below 16 C. The length of the torpor period was inversely related to T_a between 23 and 16 C but was frequently interrupted with spontaneous arousals at a T_a below 16 C. During arousal, the oxygen consumption at a particular T_{re} was greater than at the corresponding T_{re} during entry into torpor. Arousal was frequently accompanied by a metabolic peak, followed by a decrease of T_{re} , and a decline in oxygen consumption. The arousal rate ranged between 0.11 C and 0.25 C/min and appeared to be independent of the T_a at which arousal took place. Torpid animals could not right themselves, stand, and shiver until their T_{re} reached 18 C. They could gather and ingest seeds at a T_{re} of 24 C and behaved similarly to normothermic animals when the T_{re} was above 26 C.

INTRODUCTION

Many small mammals allow their body temperature (T_{re}) to approach ambient temperature (T_a) for several hours daily, usually during the early morning hours, often in response to a reduction in the proximate or ultimate availability of food. They keep their T_{re} at or above 15 C (Hudson 1978).

This thermoregulatory pattern is not hibernation in the classical sense of letting the T_{re} approach freezing and remaining there for days or weeks at a time, occurring most often during the winter or autumn, winter, and spring. Daily torpor is not simply a breakdown of thermoregulation due to starvation, for these small mammals maintain control of their T_{re} , as is evidenced by the marked differences in heart rate and respiratory rate between entry and arousal from torpor (Morhardt 1970), indicating suppression during entry and stimulation during arousal. Unlike the classical hibernators, the ability of per-

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fused, isolated hearts from these small mammals to beat and maintain adequate ventricular tension is not very good at temperatures below 15 C (Lyman and Blinks 1959; Hudson 1967; Hudson and Eller 1974). The number of small mammals exhibiting some kind of spontaneous torpor has become so great that it may very well be something which is typical of all small, generalized mammals (Hudson 1973, 1978)—a vestige of their neonatal poikilothermia.

It has been variously argued that hibernation is a primitive feature, an advanced feature, or an advanced feature superimposed on animals which are morphologically primitive (Lyman 1958; Cade 1964). The recent observation of *Mus musculus* torpid in their field nests alongside their potential predator, the marsupial mouse, *Sminthopsis crassicaudata*, with T_{re} 's of 18.2–19.6 C at a T_a of 12.0 C or 19.2–21.5 C at a T_a of 11.0 C (Morton 1978) supports the earlier observations of Fertig and Edmonds (1969) that house mice can become torpid. Cade (1964) thought that murid rodents were probably too advanced for hibernation, unlike their phylogenetic progenitors, the cricetids (Simpson 1945), which include several well-known hibernators such as hamsters. All these observations suggested to us the possibility that perhaps the ordinary laboratory mouse, particularly since its heart was more similar to hibernators than nonhibernators (Hudson 1967), might be capable of daily torpor. Also, Fertig and Edmonds (1969) report that "laboratory workers have often observed that when mice are subjected to cold and are inadequately fed, they may lapse into a state of torpor." We found that 54 out of 62 animals became torpid when exposed to food restriction and/or low T_a 's (< 20 C) and now report the physiological features of this torpor in some detail.

MATERIAL AND METHODS

One hundred and eleven *Mus musculus* var. albino (hereafter referred to as white mice) used in this study were from two different sources: HA (ICR) from Blue Spruce Farms, Altamont, New York, and random-bred mice from Agway, Ithaca, New York. The thermoregulatory patterns of all strains were similar. The mice were individually housed in plastic cages kept in a windowless room. Wood shavings served as litter, and animals were given water ad libitum. Some were fed Charles River Mouse Formula 1000 and millet ad libitum, while others were given rations of 1–3 g millet per day, depending upon the T_a to which the mice were exposed. The animal room photoperiod was 12:12. The room temperature throughout the course of the year varied between 20 and 24 C.

Body temperature was measured in one of three ways: (1) a Yellow Springs small animal probe thermistor inserted approximately 2 cm into the rectum; (2) a 30-gauge copper-constantan thermocouple implanted into the abdomen just posterior to the kidneys and led under the skin to exit from the head, where it was attached to a mercury inertialess connecting swivel, which in turn was connected with a Leeds and Northrup Speedomax G stripchart thermocouple recorder; or (3) with telemetry. Model X mini-mitters were potted in a 50:50 paraffin-beeswax coating and surgically inserted into the abdominal cavity of anesthetized animals. The static created by the temperature-sensitive intermittent oscillation of the telemetry circuit could be identified as a "click" on a small AM radio. The transmitters (as well as thermocouples and thermistors) were calibrated at a variety of known T_a 's against a Bureau of Standards calibrated thermometer. "Click rate" could

be converted into T_{re} (for convenience, all three methods will be referred to as revealing the T_{re}). If the radio speaker was directly bypassed and the radio output connected with an impedance pneumograph connected with the pre-amplifier of a physiograph (Narco Biosystems), the click became a displacement of the recording stylus, making it possible to record for extended periods of time and directly count clicks as lines. The mini-mitter was periodically compared with the temperature readings of a calibrated thermistor inserted into the rectum. From these comparisons, the maximum drift rate over a 30-day period was determined to be 1 C.

For all T_{re} and oxygen consumption measurements, animals were housed in 1-gal paint cans which had wood shavings on the floor and an inverted graduated cylinder to which a glass tube with a J shape, sealed at one end, was cemented into the side of the can so that water was available ad libitum at all times. There was a flared opening located subterminally in the $\frac{1}{2}$ -inch glass J to facilitate drinking without spillage. When oxygen consumption was to be measured, a lid with three ports—one for a thermocouple to measure T_a inside the chamber, one for introduction of dry air at the rate of 300–500 cc/min measured with a factory-calibrated Brooks Rotameter, and one to carry air away from the chamber—was used to seal the chamber. The exhalant air was dried so as to remove all water before directing a fraction (between 100 and 200 ml) of the stream to a G-2 Beckman Paramagnetic Oxygen Analyzer. Whenever standard metabolism was measured, ascarite was added to the desiccating tube to absorb the carbon dioxide. The equation from Depocas and Hart (1957) for downstream calculations was used to determine oxygen consumption. If patterns of torpor, rather than absolute

values of oxygen consumption, were to be observed, no ascarite was placed in the desiccating tube, since over long periods of time at low flow rates the ascarite tended to form a hardened plug which blocked (or reduced) air flow. The gallon can, whether used for measuring oxygen consumption or T_{re} , was placed in a constant-temperature box (Forma) and the T_a controlled to within 0.25 C of a selected temperature.

Oxygen consumption at thermal neutral T_a 's was measured on animals which had fasted between 5 and 30 h. This period is known to be sufficiently long to insure postabsorptivity, because oxygen consumption of animals fasted less than 1 day and those fasted for more than 24 h were not significantly different: 1.5 ± 0.1 ml O_2 /g·h versus 1.4 ± 0.1 ml O_2 /g·h, respectively. These animals did not become torpid. The photoperiod in the constant temperature box was 12:12 but between 1100 and 2300 (it was assumed some light would be emitted into the oxygen consumption chamber through the plastic cylinder and glass drinking tube), thus placing the animal 4 h out of phase with their customary photoperiod—an unsuccessful effort to have the animals in torpor during the beginning of the working day.

Because the animals entered torpor from their active period, a time when the oxygen consumption markedly oscillated prior to the prolonged depression of oxygen consumption during torpor, it proved necessary to establish criteria for torpor, because it was difficult to differentiate "test drops" from random periods of inactivity. While admittedly arbitrary, torpor is here defined as a state in which the T_{re} , if known, is below 31 C and the oxygen consumption is 25% or more below the level expected for normothermic inactive animals measured during the daytime at the T_a 's in question. The duration of

torpor was that period of time during which metabolism was less than 75% of the expected level. With some animals, the plateau of low oxygen consumption was so marked and lasted sufficiently long that it was easy to recognize, whereas other animals seemed to interrupt their torpor periods easily with marked increases and decreases in metabolism, thought to be the consequence of disturbing ambient noise.

RESULTS

NORMOTHERMIA

Body temperature.—The T_{re} of mice given food and water ad libitum was stable, but increased as the T_a increased from 2.5 to 38.0°C (table 1). Animals without drinking water exposed to T_a 's greater than 35°C had wet muzzles and droats, suggesting they salivated and spread the saliva over themselves. None of the four animals exposed to 34–35°C survived. One of the three mice exposed to 37.0°C died. One of the three mice exposed to T_a 's above 37°C appeared to have bathed itself with water from the drinking tube, since the wood shavings under the drinking tube had dropped 15 ml. One of these three survived a T_{re} of 39.9°C measured after a 1-h exposure to 38.3°C (not graphed) did not cover itself with water; and, even though its T_{re} was only 41.0°C after 1½-h exposure to that

temperature, it was lethargic and subsequently died. Thus, for our experimental conditions, the upper lethal T_a is 38°C. It is, of course, possible that the drinking tubes contributed to a rather high humidity in the chamber, precluding adequate evaporative cooling either by panting or the dissipation of saliva and/or drinking water. A higher air flow might have facilitated greater evaporative cooling.

Oxygen consumption.—A line fitting the oxygen consumption to the T_a 's has been statistically fitted (fig. 1) between 2.5 and 31.0°C. This line intercepts the abscissa at 41.0°C (not shown). The failure of the fitted line to extrapolate to the appropriate T_{re} is probably due to the slight depression of metabolism and T_{re} at low T_a 's which decreases the slope. The equation $MR = C(T_{re} - T_a)$ was used to calculate conductance for all temperatures between 2.5 and 38.0°C. The conductance imperceptibly increased as the T_a went from 2.5 to 31.0°C, rang-

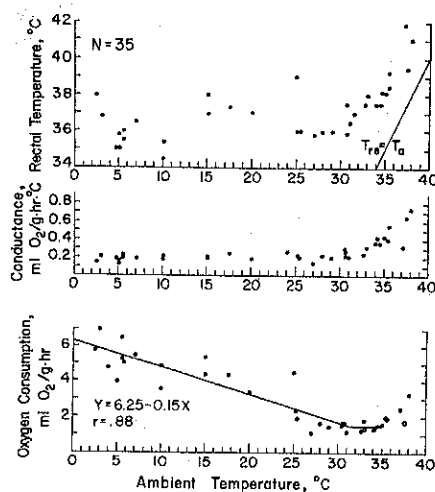


FIG. 1.—The relationship between T_a and T_{re} , conductance, and oxygen consumption. The diagonal line in the lower panel has been fitted by least squares. Open circle represents metabolic value of one animal which covered itself with water from its drinking tube.

ing between 0.15 and 0.26 ml $O_2/g \cdot h \cdot C$. The lower critical temperature of the thermal neutral metabolic zone is estimated to be 31°C. The conductance increased as the T_a within the thermal neutral zone increased from 32.8 to 35.0°C. It is difficult to locate the upper critical temperature with precision, but it probably is 35.0°C, which is the T_a above which animals salivate. The mean oxygen consumption at thermal neutrality (31–35°C) for five animals was 1.47 ml $O_2/g \cdot h$, which is 103% of the level expected for an average body weight of 45.5 g.

TORPOR

Induction.—There was only one case of spontaneous torpor observed in animals fed ad libitum, and this was an animal which was kept in an open can

placed in the incubator in a quiet room at a T_a of 20.0°C. On the first day, the T_{re} was 30.5°C at 1500 and 36.5°C at 1900. The second day, the T_{re} was 27.0°C at 1300 and 38.0°C at 1510. The body weight, W_b , declined 2.7 g and 1.4 g the first and second day, respectively. No further episodes of spontaneous torpor were observed.

Many mice readily became torpid within 24 h after food was withheld even though they were fed ad libitum prior to their placement in the metabolism chamber (fig. 2). The average time for five mice to become torpid after food was withheld was 18 h and ranged from 5 to 46 h. Seven mice measured for periods of 35–94 h with a daily ration of 2.0 g millet did not become torpid.

The duration of time between food

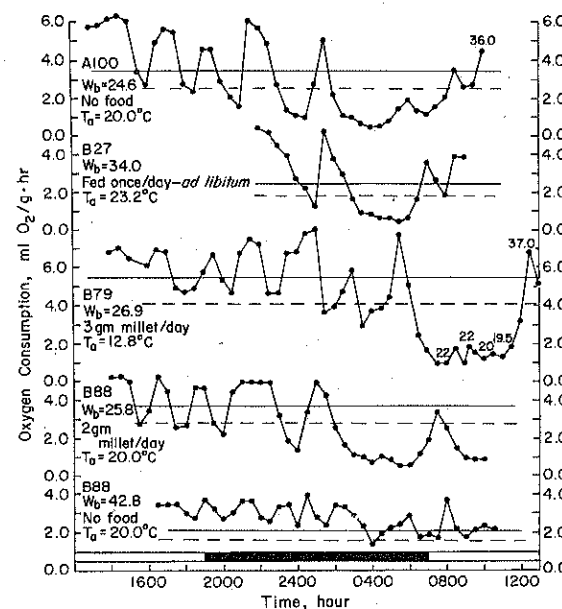


FIG. 2.—Representative records of the oxygen consumption of four *Mus musculus* exhibiting varying periods of torpor. W_b is body weight in grams. The T_{re} for animal B79 was telemetered. All other T_{re} 's were measured with a calibrated thermistor. The upper solid horizontal line in each recording is the resting metabolic level of that individual measured during the day, while the dashed line represents a 25% reduction for that particular T_a . The solid rectangle at the bottom of the figure represents the dark period in the animal room, whereas the dark period during the measurements was between 2300 and 1100.

TABLE 1

EFFECT OF AMBIENT TEMPERATURE ON RECTAL TEMPERATURE OF "MUS MUSCULUS" VAR. ALBINO

T_a (°C)	No. of ANIMALS	T_{re} (°C)	
		Mean ^a	SE _m ^b
5-10.9.....	16	36.0	±.3
10-29.9.....	23	36.7	±.2
30-34.9.....	18	37.4	±.2
35-38.0.....	13	39.3	±.3

Every \bar{X} T_{re} significantly different from each other.
SE_m = standard error of the mean.

restriction and torpor bore no obvious relationship to body weight. Torpor could be induced in some individuals more readily than in others. For example, one of the individuals graphed in figure 2 (B88), a 43-g female, became torpid within 11 h after food was withheld; yet torpor was not detected in a 19.5-g female (not graphed) after several days with a food ration of 2 g millet/day. If torpor did occur in the 19.5-g female, it must have taken place at night.

The average weight loss of five mice before their first bout of torpor was 1.8 ± 0.8 g, which is equal to a daily weight loss of 1.5 g per day. After their first bout of torpor, the daily weight loss dropped to 0.7 g per day, whereas three mice which showed no metabolic reduction lost an average of 1.8 g per day.

The duration of torpor seems to increase as the total body weight decreases. For example, the first episode of torpor was barely detectable in animal B88 (fig. 2) when it weighed 43.0 g, whereas when it weighed 26.0 g it was torpid for 5.0 h.

The regularity of dormancy varied with individuals. For example, B79 (fig. 3) was torpid for 11 consecutive nights at a T_a which was between 12 and 20 C, and these cycles were so well adjusted to the food ration that there was only a 1.2-g drop in body weight between the first and eleventh days as the W_b went from 27.3 to 26.1 g. Among other individuals, torpor occurred sporadically, and A41 became torpid only on January 20, 28, and 30, 1978, at body weights of 30.0, 26.0, and 26.6 g, respectively, although the food ration

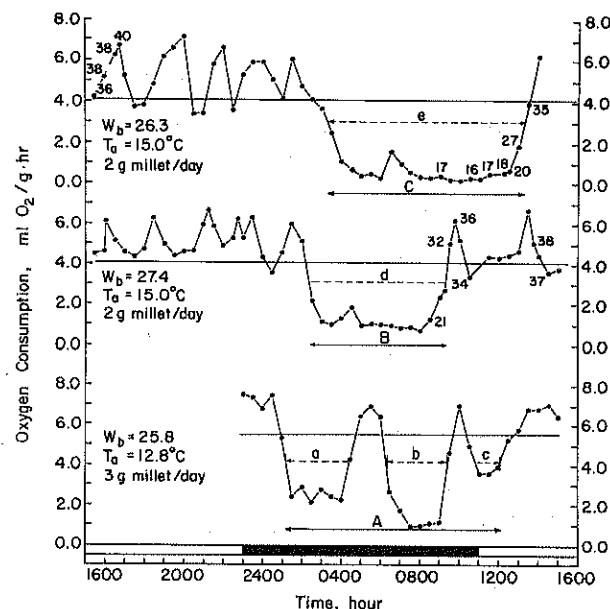


FIG. 3.—Episodes of torpor in one animal (B79) exposed to two different T_a 's (12.8 and 15.0 C). W_b is body weight in grams. Solid horizontal line is the level of resting metabolism measured during the day, while the dashed line is a level 25% below expected. Lines labeled A, B, and C represent the total length of torpor, and lines a, b, c, d, and e represent individual bouts. T_{re} 's were determined with a transmitter.

and T_a were the same for the duration of the experiment.

Body temperature.—The T_{re} of mice on regimens of restricted food is more labile than when animals are fed ad libitum. Measurements made at random among animals in the oxygen analyzer at a T_a of 19–20 C ranged between 22.0 and 37.2 C with an average of 34.5 ± 0.3 (1 SE_m). Among a group of 13 animals given 2 g millet/day, nine had at least one bout of torpor within 8 days, and the remaining four mice were no longer losing weight (implying some undetected torpor) and had a mean T_{re} of 34.1 ± 0.4 C. The food ration of these four mice was reduced to 1 g millet/day, and all four mice became torpid within 3 days. Prior to becoming torpid, the T_{re} alternately decreases and increases, with each successive decrease reaching a lower temperature until the plane of torpor is reached where the T_{re} remains relatively constant for several hours (fig. 4).

Length and depth of torpor.—When the T_a at which animals were torpid was above 16 C, the T_{re} was typically within 1.0 C of the T_a (fig. 5A). At T_a 's below 16 C, the gradient between the T_{re} and T_a increased (fig. 5A). This increase in difference between T_{re} and T_a was also reflected in the oxygen consumption, which was higher at T_a 's below 16 C than it was at T_a 's above 16 C during torpor (fig. 5B). There is an inverse correlation between length of torpor and level of metabolism (fig. 6). At T_a 's below 16 C, the length of the torpor period was longer but more frequently interrupted, as evidenced by the brevity of each bout within a single period of torpor (figs. 3 and 7). The T_a at which torpor became interrupted varied with individuals; however, most mice showed repeated episodes of uninterrupted torpor at 20 C.

The increase in metabolism of torpid animals at lower T_a 's and the increased difference between T_{re} and T_a demon-

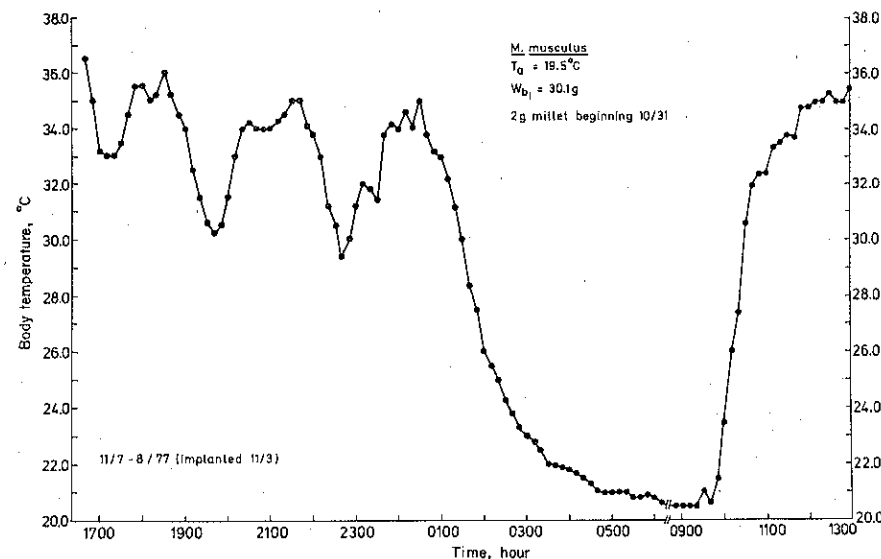


FIG. 4.—The T_{re} measured with an implanted thermocouple during a single episode of torpor. The time scale between 0600 and 0900 has been condensed. Arousal was initiated by disturbance.

strate that at T_a 's below 16–19 C animals regulate to prevent a further drop in body temperature. This ultimately results in a reduction in the length of torpor (fig. 7) and supports the observation that the "critical T_{re} " is about 16–19 C.

Arousal rates.—The rate at which

Mus musculus restores its T_{re} to normothermic levels is between 0.11 and 0.25 C/min (table 2). Some arousals were spontaneous in the sense that no external disturbance was evident, whereas some arousals occurred as a result of noise or moving the animal chamber. It is, of course, unknown to what extent

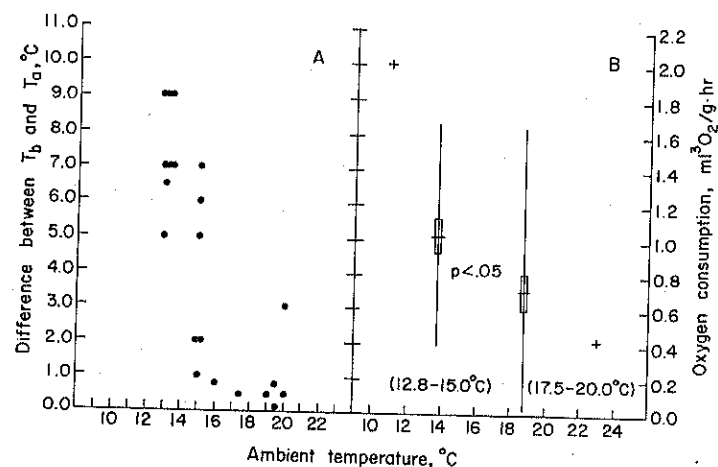


FIG. 5.—The relationship between T_a and either T_{re} (panel A) or oxygen consumption (panel B) of torpid *Mus musculus*. The oxygen consumption has been averaged for T_a intervals noted on graph and given as a mean (horizontal line) and range (vertical line). The rectangles are ± 1 SEM. The + represents single values. A P of less than .05 indicates a significant increase in oxygen consumption with a decline in T_a .

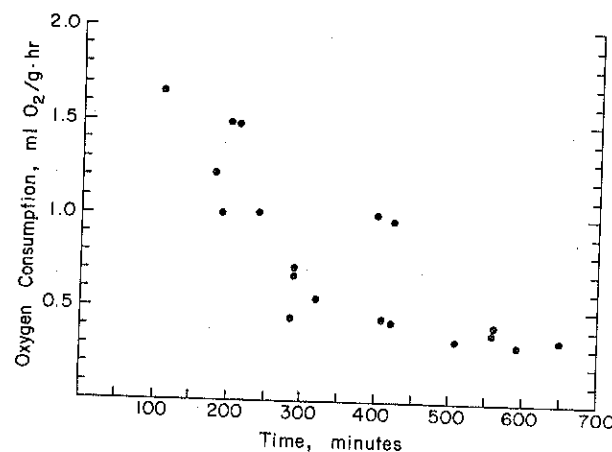


FIG. 6.—The relationship between oxygen consumption and duration of torpor

torpid mice can perceive the various sounds and vibrations which occur in a building filled with many people doing a variety of things.

Behavior.—The behavior of torpid mice supports the observation that they are unable to cope with T_{re} 's below 16.0 C. The minimum T_{re} at which

animals could right themselves, stand, and begin to shiver was 18.0 C. At 24.0 C they were able to gather seeds (millet) and eat them. Between 26.0 and 30.0 C they could walk and run in a manner similar to animals with T_{re} 's of 36–37 C. Thus, it would be easy to miss a significant depression of T_{re} if mobility were

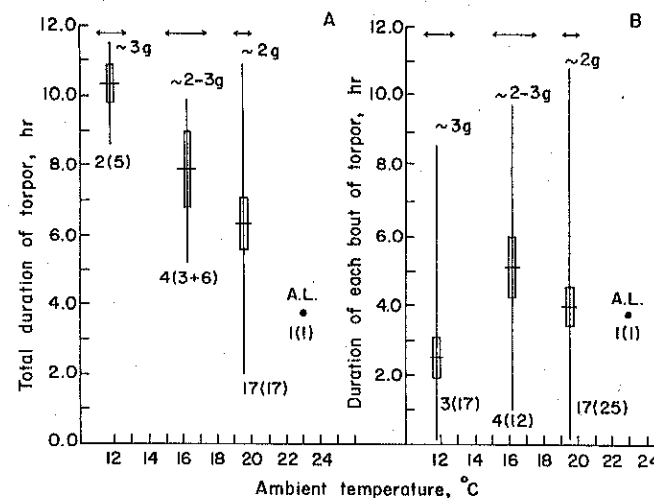


FIG. 7.—The relationship between the length of torpor and T_a given as ranges (double arrows). The ordinate of panel A is the total length of nocturnal period of torpor represented by means (horizontal line), range (vertical line), and \pm SEM (rectangle). The ordinate of panel B is the duration of individual bouts of torpor of which there may be more than one during a nocturnal period of torpor. The numbers above the range (vertical line) are the grams of millet fed each day, while the numbers below the range represent the number of animals. The number of measurements are parenthesized. The numbers 3 + 6 represent one episode from each of three individuals and six episodes from one individual.

TABLE 2
SPONTANEOUS AROUSAL RATES OF "MUS MUSCULUS" VAR. ALBINO FROM
DAILY TORPOR AT VARIOUS AMBIENT TEMPERATURES*

T_a (°C)	T_{re} (°C)	T_{ref} (°C)	Arousal Time (min)	Fastest Rate (°C/min)	Overall Rate (°C/min)
12.8.....	19.5	37.0	90	..b	.19
15.0.....	16.0	35.0	180	.25	.11
	21.0	36.0	75	.20	.18
16.0.....	17.0	35.0	130	..b	.14
16.0.....	19.5	33.0	70	..b	.19
17.5.....	17.5	35.5	105	.21	.17
19.5.....	20.5	35.2	120	.20	.12
20.0.....	20.5	32.0	48	..b	.24

* Animals were induced into torpor by food restriction. Body temperatures were abdominal.

b Not markedly different from overall arousal rate.

the only criterion applied, particularly since torpor most frequently occurs between 0100 and 0800, times when few measurements are likely to be made. Although it is difficult to prove the following assertion, we believe these animals are easily disturbed by sounds which to the human ear may be scarcely detectable; hence, their episodes of torpor coincide with the absence of human disturbance rather than the more typical pattern of early morning to midday dormancy following foraging, or at least coincidental with increased illumination (Morhardt and Hudson 1966).

Oxygen consumption.—There is a Q_{10} relationship of 4.9 between T_{re} and oxygen consumption at T_{re} 's at or above 31°C (fig. 8), while at lower T_{re} 's the oxygen consumption tends to remain relatively constant (not graphed). Like T_{re} , the oxygen consumption prior to torpor exhibits alternate decreases and increases, with a progressive decline in the lowest level until the plateau is reached (fig. 2).

The oxygen consumption at any par-

ticular T_{re} is greater during arousal from torpor than it is during entry into torpor (fig. 9). The marked drop in metabolism during entry suggests that heat production may be suppressed. The abrupt decline in oxygen consumption is represented by a Q_{10} of 7.6 as the T_{re} declined from 36.0 to 32.0°C, whereas the Q_{10} was only 2.1 as the T_{re} declined from 29.5 to 28.0°C. During early arousal, the oxygen consumption increased little as the T_{re} increased from 18 to 22°C, but then there was a steep increase in oxygen consumption, represented by a Q_{10} of 3.3 as the T_{re} increased from 22 to 35°C.

The white mouse appears to exhibit an overshoot in oxygen consumption during arousal (fig. 3, middle panel). A maximum oxygen consumption of 6.2 ml/g·h at a T_{re} of 36.0°C was attained 1 h and 45 min subsequent to the initiation of arousal. After the animal was fed, the oxygen consumption was 3.5 ml O₂/g·h at a T_{re} of 37.0°C within 5 h after arousal. Typically, the decline in oxygen consumption following an overshoot is ac-

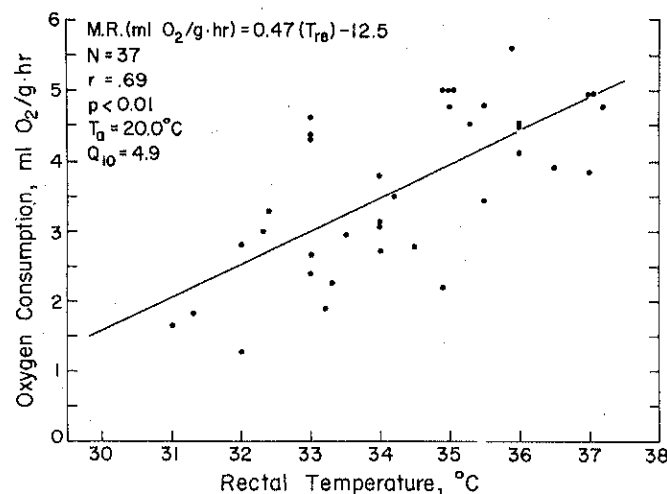


FIG. 8.—The relationship between oxygen consumption and T_{re} of *Mus musculus* exposed to T_a 's of 19.0 and 20.0°C.

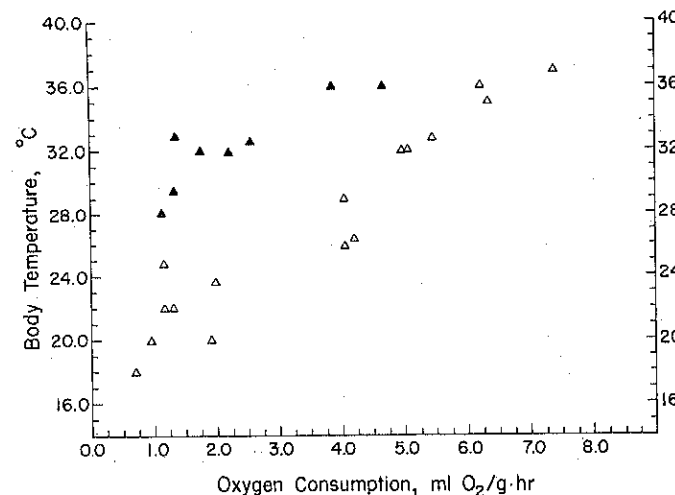


FIG. 9.—The relationship between oxygen consumption and T_{re} during entry into torpor (closed triangles) and arousal from torpor (open triangles) at T_a 's of 15–23°C.

companied by a fall in T_{re} (fig. 3), which differs from the response of the classical hibernator. The T_{re} and oxygen consumption decreased from 36.0°C and 6.2 ml O₂/g·h to 34.0°C and 3.3 ml O₂/g·h, respectively (fig. 3), within 40 min subsequent to arousal, and this was followed by a slow increase in both T_{re} and oxygen consumption over a period of several hours.

DISCUSSION

The standard metabolic rate of *Mus musculus* var. albino occurs at T_a 's between 31 and 35°C and is 103% of the level predicted from the equation $MR = 3.8 W^{-0.27}$ (Morrison, Ryser, and Dawe 1959) and close to the level Morrison (1948) observed for albino mice (94% of predicted). This is unusually high. Hart (1971) concluded from his review of desert rodents that their metabolism is 15% below that expected for mammals of comparable size. Although not specifically stating so, Fertig and Edmonds (1969) imply that domestic house mice were derived from desert ancestors. And

it has been thought (Hudson and Bartholomew 1964) that a low metabolism would be advantageous, particularly for small mammals, because it raises the lower critical temperature and allows small mammals to become torpid at the high T_a 's typical of desert habitats. In spite of this rather typical metabolism for a small mouse engaging in a daily torpor, its lower critical temperature is 4°C above the 27°C predicted by the equation $T_{lc} = T_{re} - 4 W^{0.25}$ (Morrison 1960), and its conductance gradually increases from T_a 2.5 to 31.0°C (from 0.15 to 0.26 ml O₂/g·h·°C). Thus, with a higher conductance near the thermal neutral zone, the $(T_{re} - T_a)$ factor in the equation $MR = C(T_{re} - T_a)$ must decrease, which means a higher T_a (or critical temperature) since T_{re} is relatively constant.

The upper lethal T_a is unusually low for a species which appears to have had its evolutionary origins in the desert although since it is a nocturnal animal it may not be subjected to the high daytime temperature of the desert. Also, the

of drinking water in the chamber excludes the dry air more typical of most measuring procedures.

The extent to which daily torpor served in a variety of rodents is due "starvation" is difficult to assess. Moseley and Dill (1971) report that body temperature decreases from 7.8% to 1.7% in survivors and to 1.0% in individuals which died when *Dipodomys merriami* became torpid during exposure to 13–15 C while eating 2 g millet/day. The average weight loss of surviving individuals was 15%, whereas those which died under this regimen lost 25% of their body weight. Various species of *Peromyscus* lost between 9% and 27% of their body weight during periodic episodes of torpor, which Morhardt (1970) attributed to the unusually high weights incurred in the laboratory prior to torpor. Although no analysis of fat was made in our study, it is likely that heavy animals were fat; therefore, the relatively small weight loss prior to the onset of torpor at the time food was either withheld or given in limited rations indicates that white mice had not depleted their energy reserves prior to torpor. Torpor in white mice appears for the most part to be a response to a postabsorptive condition rather than starvation. Some food-restricted individuals did not become torpid but reduced their T_{re} and oxygen consumption to the point that they no longer lost weight. Thus, mice with a T_{re} of 32.0 C had a metabolism 50% of air normothermic levels, which accomplished the necessary savings of energy without jeopardizing survival because of a low T_{re} .

White mice arouse from torpor at a rate conspicuously slower than observed in other species of comparable body weight (Hudson 1967). Significantly, the brown fat of the white mouse is only 65% that of the deer mouse,

Peromyscus sp. (Chaffee and Roberts 1971). This may mean that the capacity for nonshivering thermogenesis is not very great in the white mouse, hence the arousal rate is slow.

The difference in oxygen consumption levels for a specific T_{re} of white mice depending on whether they are entering or arousing from torpor suggests that oxygen consumption has been suppressed as the animal becomes torpid in a manner analogous to the suppression of heart rate during entry of *Peromyscus leucopus* into torpor (Morhardt 1970). The simplest interpretation is to assume that there is a reduction in shivering, normally required to maintain normothermic T_{re} 's, during entry into torpor in a manner similar to the California ground squirrel, *Spermophilus (Citellus) beecheyi* (Strumwasser 1959).

Many small mammals arousing from torpor exhibit a metabolic overshoot (Lyman 1948; MacMillen 1965; Tucker 1965; Hammel et al. 1968; Wang and Hudson 1970), which is generally thought to represent the excess heat generated in rewarming the body tissues to their normothermic level. Not all animals exhibit this overshoot (Hudson 1965; Morhardt 1970), which may merely mean that the overall rate of heat production is precisely equal to the heat required for warming body tissues commensurate with the rate of rewarming and to compensate for the increased heat loss as the difference between T_{re} and T_a increases. White mice characteristically exhibit the overshoot, but then they usually let their T_{re} 's fall back to 32–34 C until given food, at which time their T_{re} returns to 36–37 C. This response makes it difficult to know just how much of the first burst of heat production during arousal is related to an anterior-posterior temperature gradient (Lyman 1948).

Like many other small rodents, the white mouse also has a "critical T_{re} " during torpor of about 16–19 C; and, if its T_{re} falls much below this level, arousal may not be spontaneously initiated. The white mouse, by increasing the difference between T_{re} and T_a and by intensifying oxygen consumption at T_a 's below 16–19 C, controls its T_{re} so as not to fall below a critical T_{re} similar to other hibernators (Morhardt 1970; Wang and Hudson 1970, 1971; Pivorun 1976) or mammals utilizing daily torpor (MacMillen 1965; Tucker 1965; Mor-

hardt and Hudson 1966). However, there is considerable difference between various species as to what the critical T_{re} is. It ranges from as low as 5–10 C in the chipmunk, *Tamias striatus* (Wang and Hudson 1971), to 8–12 C in *Perognathus hispidus* (Wang and Hudson 1970), to as high as 16 and 19 C in the white mouse. Presumably, ranges of "critical temperatures" for each species reflect normal variation within populations, and the level at which the range is set for a particular species is related to the habitat in which the animal lives.

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A COMPARATIVE STUDY OF THE FREEZING TOLERANCES OF THE MARINE SNAILS LITTORINA LITTOREA (L.) AND NASSARIUS OBSOLETUS (SAY)¹

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Littorina littorea, which were found in the intertidal zone throughout the year, displayed a seasonal change in freezing tolerance that was greatest during the colder winter months, was dependent on salinity acclimation, and was independent of temperature acclimation and photoperiod. *Nassarius obsoletus*, which avoided the freezing stress by migrating to subtidal areas during the winter months, displayed a seasonal change in freezing tolerance that was greatest during the warmer summer months and was dependent on both temperature and salinity acclimation. Acclimation to lower salinities reduced the freezing tolerances of *L. littorea* and *N. obsoletus*. The temperature-acclimation-dependent differences in the freezing tolerance of *N. obsoletus* and the seasonal changes in the freezing tolerance of *L. littorea* also decreased following acclimation to lower salinities. When collected during the winter months, *L. littorea* possessed a greater freezing tolerance than *N. obsoletus* under all of the conditions examined, but the freezing tolerance of *L. littorea* was lower than that of *N. obsoletus* when collected during the summer and acclimated to warm temperatures and high salinities. Continuous temperature recordings of intact snails exposed to their LD50 temperatures demonstrated that the seasonal and interspecific decreases in lethal freezing temperatures were not due to a lowering of the temperatures at which tissue ice formation occurred. Calorimetric determinations of the amounts of tissue ice formed at LD50 temperatures showed that the seasonal and interspecific decreases in lethal freezing temperatures were due to increased tolerances to greater quantities of tissue ice.

INTRODUCTION

Marine snails (Phylum, Mollusca; Class, Gastropoda) inhabiting the intertidal zone of northern temperate regions may be exposed to air temperature as low as -20 C during low tides. The ability of marine snails to tolerate exposures to such subfreezing temperatures varies among species, and may change seasonally within any given species. Interspecific differences in the freezing tolerances of marine snails are related both to vertical zonation patterns on the shore (Southward 1958; Ibing and

Theede 1975) and to geographic distributions (compare Hargens and Shabica [1973] with Southward [1958]). Marine snails from northern temperate regions which inhabit higher vertical zones or have more northern distribution limits characteristically possess greater freezing tolerances. Seasonal changes in the freezing tolerances of marine snails are variable. In some species, seasonal changes in freezing tolerance have been reported (Somme 1966; Ibing and Theede 1975), while in other species no seasonal changes were observed (Roland and Ring 1977).

The influence of environmental factors on the interspecific and seasonal differences in the freezing tolerances of marine snails is not presently known. Indeed,

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