RICE UNIVERSITY

THE PHYSIOLOGY OF TORPOR IN *Perognathus hispidus*

by

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Abstract

*Perognathus hispidus* can thermoregulate and remain homeothermic between ambient temperatures of 5.0 to 34.0 °C. Above 34 °C., animal became hyperthermic and death occurred at $T_a$ of 37 °C. In the normothermic animal, the minimum oxygen consumption follows Newton's law of cooling, the thermal conductance is 0.201 cc O$_2$/gm/hr/°C. The thermoneutral zone extends from $T_a$ of 30.5 to 33.5 °C. and oxygen consumption within the thermoneutral zone is 1.25 cc O$_2$/gm/hr. Heart rate and respiratory rate increased with the decrease of ambient temperature below $T_a$ of 30 °C. Shivering was not observed until $T_a$ was below 20 °C.

Occasional spontaneous torpor with food and water present were observed throughout the year in the laboratory. However, the typical response is normothermia under the presence of food and water over a range of ambient temperatures from 5-24 °C. When food supply was withheld or restricted, *P. hispidus* invariably became torpid within 24 hours at $T_a$ between 4 and 24 °C.

During entrance into torpor, heart rate decreases prior to the decrease of oxygen consumption and body temperature. Skipped heart beats and irregular apnea are characteristics during the entry period. Intermittent shivering were
observed electrically during entrance. Cooling rate was slower in the normal entrance than the cooling of dead animal.

During torpor, minimum heart rate was between 25-60 beats/min and respiratory rate was irregular with prolonged apnea. Oxygen consumption decreased to 2-13% of the normothermic value. Body temperature was within 2 °C. of the ambient above $T_a$ of 14 °C.; below 14 °C., delta T increases as $T_a$ decreases. The length of torpor in a single bout was less than 24 hours and it decreases as $T_a$ decreased from 17 to 1.5 °C.

During arousal, the maximum heart rate was between 420-570 beats/min and respiratory rate around 200 breathes/min. Maximum oxygen consumption usually doubles the normothermic value and is characterized by an overshoot. Body temperature rewarmed to within normothermic range after arousal and moderate neck-abdomen temperature difference was found during arousal. The arousal rate was 0.51 °C./min.

Animal can reduce 2/3 of its energy requirement by using torpor than remain normothermic at $T_a$ of 16 °C.. Field observations indicate torpor was occured in *P. hispidus* under natural conditions. It is concluded that daily torpor represents a physiological adaptation to the environment in *P. hispidus*. 
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I. Introduction

A. General Aspects of Torpidity

A relatively constant body temperature independent of environmental temperatures is characteristic of homeotherms. The actual value varies from species to species and from individual to individual. Generally, a core temperature (rectal) of 37.0 °C is taken to be the value in the mammals. However, body temperature may fluctuate in individuals between sleeping and wakeful states and varies with activity of the animal. Hammel (1965) found a relatively constant hypothalamic temperature of 39.0 ± 0.2 °C is maintained for all the environmental temperatures between 20 to 35 °C in the rhesus monkey. During sleep, a drop of 2.3 °C in hypothalamic temperature was found when animal was at an ambient temperature of 30.0 °C. Rectal temperature in man normally rises to 40.0 °C during exercise as a result of heat accumulation by muscular contraction (Dubois, 1948). Therefore, normal body temperature in mammals is not a fixed value but a spectrum of temperatures which varies with the state of the animal.

There is abundant evidence (Von Euler 1961, Hardy 1961, Hammel 1965) which shows that the preoptic region in the rostral hypothalamus is essential for the regulation of body temperature in mammals. Experiments conducted by Hammel et al (1963, 1965) have shown that the preoptic region of unanes-
thetized mammals responds to local heating by inducing panting and vasodilation and to local cooling by evoking shivering and vasoconstriction. Nakayama et al (1963) used low voltage radio frequency current (3 mega cycle/sec) as heating device have also shown that there are temperature sensitive neurons in the preoptic region whose electrical discharges are in proportion to the radio frequency of the stimuli. In addition to the neurons in the preoptic region, the peripheral temperature sensitive receptors also play an important role in temperature regulation. They furnish afferent information to the preoptic neurons to determine the functional "set point" temperature (Hammel 1965). As was postulated by Hammel (1965), the difference between the hypothalamic temperature and the functional set point temperature elicits the proper responses, i.e. shivering, vasoconstriction, panting, vasodilation etc. for the regulation of body temperature.

Certain mammals living in cold environments have physiological adaptions to their environments. They abandon the homeothermic state, i.e. permit their body temperature to drop and approach to that of the environment (Lyman 1963). Body temperature can decline to two or three degrees above freezing and heart rate, metabolic rate and other physiologic functions fall to correspondingly minimal levels (Hoffman 1964). They can also generate enough heat and restore their normal body temperature from the torpid state without the aid of any external heat source. This phenomenon is called hibernation.
Among the living mammals, at least six orders contain species which hibernate. These are the spiny anteater (Monotremata) (Schmidt Nielsen et al. 1966, Griffith 1965), the opossum (Marsupialia) (Bartholomew and Hudson 1962), the hedgehog (Insectivora) (Kayser 1961), probably two lemurs (Primates) (Kayser 1961), many bats (Chiroptera) (Hock 1951, Kayser 1965) and many species of Rodentia such as ground squirrels, hamsters, woodchucks and dormice etc. (Lyman and Chatfield 1955, Kayser 1961, Hoffman 1964). Many of the hibernators e.g. ground squirrels hibernate only in definite seasons of the year even when they were kept in the laboratory where no seasonal cue can be obviously encountered (Lyman 1963). During the spring and summer they remain active and homeothermic. When exposed to cold, they increase their food consumption and metabolic rate and maintain their warm-blooded body temperature (op. cit.). As fall approaches, they become lethargic and increase their fat deposit. If exposed to cold, they will enter hibernation within a very short time (op. cit.). Hibernators in this category are called seasonal hibernators. Recent studies reveal evidence of endogenous rhythm of circannual cycles in the seasonal hibernators such as *Citellus lateralis* (Strumwasser et al. 1964, Pengelley and Kelley 1966), *C. tridecemlineatus* (Strumwasser et al. 1964), *Tamias striatus* (Panuska 1959), *Eutamias sp.* (Cade 1963, Jamson 1964) and five species of *Citellus* (Pengelley and Kelley 1966) etc. Presumably, the endogenous rhythm of the hibernator governs the
onset and termination of the hibernating cycle in each individual and certain environmental cues or zeitgebers viz. temperature, light, food, water and activity may influence this circannual cycle and thus change the pattern of hibernation (Pengelley 1965). However, more experimental evidence is needed before the establishment of this internal master switch concept in the seasonal hibernators.

In a dry hot environment, some species of mammals have developed physiological capabilities which enable them to use summer dormancy or estivation for their survival in the nature. Field observations on disappearance of the animal have been interpreted to indicate that many members in the genus *Citellus* estivate during the summer seasons, e.g. *C. spilosoma*, *C. townsendi*, *C. beebeyi*, *Cynomys fulvus* (Hudson and Bartholomew 1964). Episodes of summer dormancy was also found in *C. tereticaudus* in the laboratory (Hudson 1964). In *Citellus mohavensis*, which is only active above ground during spring and early summer, showed torpidity in the laboratory at room temperature in most of the summer, fall and winter days (Bartholomew and Hudson 1960). Other groups which exhibit estivation are tenrec *Centetes ecaudatus* (Kayser 1961), pocket mice *Perognathus longimembris* (Bartholomew and Cade 1957), kangaroo mice *Microdipodops pallidus* (Bartholomew and MacMillen 1961), and etc.. The physiological changes of the animal in estivation have been studied by Bartholomew and Cade (1957), Bartholomew and Hudson
(1960) and Hudson (1964). They found estivation and hibernation to be physiologically similar phenomena i.e. both are the functions of body temperatures and the latter is in turn depended on ambient temperature (Bartholomew and Hudson 1960).

There is a group of animals which show marked daily fluctuations of body temperatures in the laboratory: birch mouse *Sicista betulina* (Johansen and Krog 1959), some species of bats, e.g. *Myotis lucifugus* (Hock 1951), kangaroo mouse *Microdipodops pallidus* (Bartholomew and MacMillen 1961), at least 12 species in *Perognathus* (Bartholomew and Cade 1957, Cade 1964, Tucker 1962, 1965), pygmy mouse *Balomys taylori* (Hudson 1965) and many species in the genus *Peromyscus* (Morhardt and Hudson 1966).

Within this group, some can only be induced into torpor after starvation. This is best seen in the genus *Peromyscus* (Morhardt and Hudson 1966). No spontaneous torpor with ample food supply to the animal has been found. Some of the others exhibit daily torpidity in the presence of food, water and without any environmental temperature stress; *Sicista betulina* (Johansen and Krog 1959), *Perognathus longimembris*, *P. xanthonotus*, *P. formosus*, *P. penicillatus* and *P. fallax* (Bartholomew and Cade 1957) are the representatives. Many others show daily torpor at either low ambient temperature or the absence of food or both. Examples are *Perognathus californicus* (Tucker 1965).
**Microdipodops pallidus** (Bartholomew and MacMillen 1961)

and etc.. There was no qualitative difference in physiologic parameters found during the torpor cycle in these animals capable of exhibiting daily torpidity (Hudson 1965, Tucker 1965, Johansen and Krog 1959).

In spite of the dissimilarity in torpid pattern of animals showing daily torpor from those of the estivator and hibernator's, Hudson (1965), Tucker (1965), MacMillen (1965) and Morhardt and Hudson (1966) have demonstrated a physiologic resemblance between daily torpor to estivation and hibernation.

The terms hibernation and estivation can also be applied to describe the dormancy in cold blooded vertebrates and invertebrates. Yet, the physiology behind those phenomena may be distinctly different from that of the mammalian and avian estivation and hibernation. To avoid the possible confusion between the quality of these two phenomena, Bartholomew and Hudson (1960) have suggested to use the term "facultative hypothermia" to describe the physiological changes of birds and mammals when they estivate and/or hibernate. Since estivation, hibernation and daily torpor are respectively utilized by the animals for the common purpose of energy conservation, also they share many of the same mechanisms of physiology, the term "torpodity" has been used by many authors (Tucker 1965, Hudson 1964, Morhardt and Hudson 1966) as a general description for the phenomenon of facultative hypothermia. By virtue
of its completion and pertinence to description, the term "torpidity" will also be used throughout this thesis to describe the phenomenon of facultative hypothermia in the experimental animal.

B. Objectives

Natural hibernation among the mammals has long been observed in the antiquity. Aristole (384-327 B.C.) and Pliny (79 A.D.) knew that the marmot and the dormouse were hibernators (Kayser 1965). In 1938, Benedict (1938) studied extensively on the physiology of the hibernating and nonhibernating marmot which has stimulated many of the later researches in the hibernation physiology (Lyman and Chatfield 1955). The physiology of hibernation has been reviewed by Lyman and Chatfield (1955), Kayser (1961), Hoffman (1964), Lyman (1965) and Kayser (1965). Due to the inevitable variations among species and individuals, a simple conclusive description on the physiology of hibernation for all the hibernators is not feasible. However, certain physiological changes are found in common in many hibernators and presumably are characteristics of all the hibernators in the hibernating cycle.

During the entrance into hibernation, a decrease of heart rate prior to the decline of body temperature has been described in the woodchuck (Lyman 1958) and in Citellus beecheyi (Strumwasser 1960). Decrease of oxygen consumption is also preceded the decline of body temperature when
woodchuck enters hibernation (Lyman 1958). Shivering has been recorded in C. beecheyi (Strumwasser 1960) and in the woodchuck (Lyman 1958) during the entry into hibernation. According to these authors (op. cit.), shivering serves as a brake to prevent too fast a drop of the body temperature during enter into hibernation. It has also been found that the cooling rate of body temperature is much slower in a hibernator enters hibernation than it is chilled under anaesthesia (Lyman 1958). All these experimental data indicate that the entrance into hibernation is an actively controled process but not passively abandon the homeothermic state of the animal. As the animal enters deep hibernation, heart rate, respiratory rate and oxygen consumption showed further decrease and reached their minimal level before the plateau of the body temperature (Lyman 1958). Minimal heart rate of 2-16 beats per minute has been recorded in many hibernators during deep hibernation (Dawe and Morrison 1955, Lyman 1958, Kayser 1961, 1965) and oxygen consumption as low as 0.012-0.05 cc O₂/gm/hr has been found in many hibernators during deep hibernation (Lyman 1948, 1958, Kayser 1961, 1965). Body temperature in hibernation depends on the ambient and is regulated during hibernation (Lyman 1948). Body temperature of 3-4 °C. has been recorded in the hibernating hedgehog (Kayser 1961) in the thirteen-lined ground squirrel (Lyman 1959) and 0.5-4 °C. in the arctic ground squirrel and in the Franklin ground squirrel (Dawe and Morrison 1955). When
ambient temperature is lowered below 0 °C., the hibernating hamster increases its oxygen consumption and maintained a 1.7 to 3.4 °C. gradient above the surrounding (Lyman 1948). If the ambient temperature is changed to too low to be "optimal" for hibernation, either arousal initiates or death eventually occurred in the hibernating animal (Lyman 1948, Kayser 1965). The ability of rewarming body temperature from the deep hypothermic to normothermic level without the aid of external heat characterized the hibernators (Lyman 1963). During the onset of arousal, heart rate increases and peripheral resistance decreases (Lyman 1960). Respiratory rate and oxygen consumption also rise markedly (op. cit.). In the early stage of arousal, shivering is noticeable only from EMG recording, as the arousal in progress, it soon becomes apparent that the whole anterior part of the animal is shaking violently (Lyman 1961). The rewarming rate of body temperature is much faster in the anterior portion than the posterior region as a result of differential vasoconstriction of the posterior part in the arousing hibernator (Lyman and O'Brien 1960, Bullard and Funkhouser 1962). The role of the cardiovascular system and its nervous control in the hibernating ground squirrel has been studied by Lyman and O'Brien (1960, 1963). They found out that the parasympathetic system has a regulatory but not essential effect on the heart rate as the animal enters hibernation and has only minimal effect during hibernation and arousal (Lyman and O'Brien 1963).
The sympathetic system on the other hand is responsible for the general vasoconstriction during hibernation and is essential for the precisely timed vascular changes involved in arousal (op. cit.).

The physiology of estivation has been investigated by Bartholomew and Cade (1957) in the pocket mice, by Bartholomew and Hudson (1960) in the ground squirrel and reviewed by Hudson and Bartholomew (1964). They found the physiologic changes when animal enters estivation are essentially the same as those of the hibernators entering hibernation, i.e. oxygen consumption, respiratory rate are markedly reduced and body temperature approaches to that of the environment. Since estivation is found in the animals which live in hot dry environment, the body temperature when animal is torpid is much higher than that of the hibernator's in hibernation because of the higher ambient temperature. During arousal from estivation, no conspicuous anterior-posterior differential vasoconstriction was observed in the Mohave ground squirrel (Bartholomew and Hudson 1960). However, the cardiovascular mechanism of differential rewarming still presented in this species (op. cit.). It is concluded by the authors (Bartholomew and Hudson 1960, Hudson and Bartholomew 1964) that estivation and hibernation are physiologically similar phenomena. The choice of terms is depended on the ambient temperature at which torpidity of the animal is observed (op. cit.).
The physiology of daily torpor has been studied by Tucker (1962, 1965), MacMillen (1965), Hudson (1965), Morhardt and Hudson (1966) and recently reviewed by Hudson (1965b). Generally speaking, the physiologic changes in the daily torpor cycle is quite similar to those recorded in the hibernating cycle (Bartholomew and Cade 1957, Johansen and Krog 1959, Hudson 1965, Tucker 1965, Morhardt and Hudson 1966). However, many aspects are found different in animals capable of daily torpor from the classical hibernators. First of all, the lowest critical body temperature tolerable in torpor is much higher in animals exhibiting daily torpor than that of the hibernators (Tucker 1962, Hudson 1965, MacMillen 1965, Morhardt and Hudson 1966). *Perognathus californicus* can not survive if body temperature is below 22.0°C. (Hudson 1965) and the lowest critical body temperature recorded in *Peromyscus sp.* was between 13.4 - 19.0°C. (Morhardt and Hudson 1966). The inability to withstand low body temperature in the animals capable of daily torpor is not known. The second difference between daily torpor and hibernation is the length of torpor. Investigations showed the length of torpor is less than 24 hours in most of the animals exhibiting daily torpor (Tucker 1962, Hudson 1965, Morhardt and Hudson 1966). It is not known what triggering mechanism is involved in preventing longer torpid period. The third difference is that animals capable of daily torpor seem do not need a
specialized preparation period before the commence of torpor (Hudson 1965b). Thus they can exhibit daily torpor at any time of the year whenever the environmental stress is potent enough to trigger the onset of torpor. The fourth one is that the rewarming rate is faster in the animals aroused from daily torpor than those aroused from hibernation (Hudson and Bartholomew 1964, Hudson 1965b). This faster rate is not weight dependent as has been compared between the pygmy mouse Biomys taylori and the birch mouse Sicista betulina (Hudson 1965b).

Study of the isolated heart from various species capable of exhibiting daily torpor has revealed unexpected data (Hudson 1965b). In Peromyscus sp. the lowest cut out temperature i.e. the temperature at which the ventricle stops beating for the isolated perfused heart is between 3.6 - 7.0°C. (op. cit.) yet, the intact animal can not survive if body temperature is below 13 - 19°C. (Morhardt and Hudson 1966). In Perognathus hispidus, the cut out temperature is 2.0°C, while the lowest tolerable body temperature is probably around 10.0°C. (Hudson 1965b). In Biomys taylori, the cut out temperature is 1.5°C, but the animal can not withstand body temperature below 22.0°C. (op. cit.). Therefore, the heart itself, with respect to its cut out temperatures seems not to be the factor that restrains the lowest tolerable body temperature in daily torpor since the cut out temperature is comparable to that of the
hibernators (Hudson 1965, Lyman and Blinks 1959).

Therefore, although hibernation, estivation and daily torpor are all physiological adaptations to the environment for the common purpose of energy conservation, the mechanism involved between hibernation and daily torpor may be different in many respects.

It is the effort of this research to investigate systematically the temperature regulation in an animal capable of exhibiting daily torpor; at its normothermic level, its heterothermic state and its biological significance in environmental adaptation. Emphasis will be put on the recording of simultaneous changes of the selected physiological parameters and the physiological control in a daily torpor cycle, thus a comparative study can be made with the known physiological changes in hibernation. After the basic knowledge on daily torpor physiology have been obtained, the animal can then be used as a valuable tool for further studies on daily torpor physiology at the mechanistic level.

Torpidity in the genus *Perognathus* of the family *Heteromyidae* was observed by Scheff (1938) and Hall (1946). However, physiology of temperature regulation in this genus has only recently been investigated (Bartholomew and Cade 1957, Tucker 1962, 1965, Morrison and Ryser 1962). Because of its accessibility in this region, *Perognathus hispidus* is used for this research.
II. Materials and Methods

*Perognathus hispidus* (Family Heteromyidae) was one of the largest animals in this genus (Morrison and Ryser 1962). The external measurements are 198 - 223; 25 - 28 (Hall and Kelson 1959). This group is widely distributed in the North America; north up to North Dakota and Minnesota, south down to Mexico City, east extends to Louisiana and west to Las Vegas (op. cit.). The *Perognathus hispidus* used in this study were collected at the Welder Wildlife Refuge, San Patricio County, Texas, between October, 1964 and August, 1965. The weight of the animal varied usually between 30 - 50 grams depends on maturity and nutritional state. Animals were kept individually in the plastic cages (8.0" x 10.5" x 6.0") with San-I-Cel beddings. The photoperiod was kept at 13 hours and the room temperature was 23 \( \pm 1.0^\circ C \). Animals were given sun flower seeds, wild bird food, purina lab chow and water ad. libitum. Survival was excellent.

Continuous records of body temperature (\( T_b \)) were obtained from copper-constantan thermocouples (30 gauge) implanted in the abdominal cavity posterior to the kidneys. In the case of double implantation, thermocouple was also implanted in the dorsal neck muscle between the two scapulae. A plastic saddle was sutured on the neck skin to sustain the thermocouple leads. A piece of rubber tubing was used to protect the thermocouple leads from being chowed by the animal. Ordinarilly, thermocouple could remain in place for 15 - 30
days before they were destroyed by the animal. Thermocouples were connected to a Leeds and Northrup Speedomax G Recorder to record body temperatures continuously. Body temperature was also measured by inserting thermocouple (30 gauge, sheathed with polyethylene tubing) rectally into a depth of approximately 2.0 cm and read from a Leeds and Northrup portable potentiometer.

Minimum oxygen consumption was measured by putting the thermocouple implanted, postabsorptive (no food overnight) animal in a small plastic can (1350 ml) and kept in a constant temperature cabinet. The ambient temperature surrounded the animal could be controlled with an accuracy of ± 0.5°C. Air supplied by a compressor, was dried, passed through a flow meter into the small can. The outlet air was redried and the CO₂ absorbed by passing through a drying tube of silica gel and ascarite mixture before entering the Beckman G-2 Paramagnetic Oxygen Analyzer with a Brown Strip Chart Recorder. Only those minimum oxygen consumption values at which the simultaneously measured body temperature was within the normothermic range, were used for calculation. Oxygen consumption was calculated by the method of Depoca and Hart (1957).

Heart rate and respiratory rate of the animal were recorded by soldering the double implanted thermocouple wires to two bipolar switches. Thermocouple wires from each region were connected to the Leeds and Northrup Recorder.
and two additional copper wires from the bipolar switches were connected to a impedance pneumograph which was in turn connected with a cardiac preamplifier and a four channel E & M physiograph. By switching on and off the bipolar switch, body temperature, respiratory rate and heart rate can be recorded alternatively and continuously.

Muscle electrical activity (EMG) was detected by two constantan electrodes (0.004 inch diameter) implanted in the m. Gluteus medius of the rump. The electrode leads were connected to a cardiac preamplifier and then to a four channel E & M physiograph. In all cases, thermocouple was also implanted in the abdominal cavity thus EMG and body temperature can be recorded continuously and simultaneously.

Comparison of cooling rates between dead animal and animal entering into torpor was made in an implanted individual at a constant $T_a$ of 15.5°C. After two successive torpors have been obtained, the animal was killed with overdose Nembutal at its normothermic state. When $T_b$ of the freshly killed animal has reached 19.0°C., it was taken out and rewarmed to 38°C. in a separate temperature box. The rewarmed dead animal was then put back to $T_a = 15.5°C.$ for one more determination.

The relation between length of torpor and ambient temperature was studied in one un implanted individual. The length of torpor was obtained from continuous record of
oxygen consumption in a daily torpor cycle. The time lapse between the beginning of final drop in oxygen consumption during entrance and the first increase in oxygen consumption during arousal was taken as the length of torpor. The body weight of the animal was kept constant by supplying measured amount of food and the selected ambient temperature range was between 17.0 and 1.5°C. inclusive.
III. Results

A. Field observation

*Perognathus hispidus* is nocturnal in habit and has been collected in the southern Texas during January, April, August, September, October and November between 1965 and 1966. In the field, one *P. hispidus* was found torpid in an exposed shallow burrow in the late afternoon of October 31, 1965. The torpid animal was picked up easily by the investigator as the animal was motionless in the hole. The animal rewarmed spontaneously to normothermia within 30 minutes after being transferred to the cage. In the next morning, seven out of ten *P. hispidus* were found torpid in the traps while the ground temperature around midnight was 5 °C. All the torpid pocket mice aroused spontaneously to normothermia after being transferred to the cages.

B. Laboratory observation

1. Normothermic mice

   (1) Body temperature

   Body temperature (*T_b*) is *Perognathus hispidus* at its normothermic level ranges from 34.5 to 39.5 °C. at room temperature (23 °C.). It fluctuates with activity of the animal. Body temperature at 0400 was significantly higher than at 1600 (*p < .05*) (fig. 1). Body temperature is higher at night (mean = 37.4 °C.) than during day time (mean = 37.0 °C.) consonant with their nocturnal habits. The mean body tempera-
Figure 1

Body temperature of *P. hispidus* at different time of the day

N is equal to the number of measurements made on 10 animals. All body temperatures were recorded from implanted thermocouple in the abdominal cavity. Ambient temperatures were between 11.0-25.0 °C. inclusive.

Vertical line indicates range, horizontal line the mean. Rectangular box is ± 2 standard errors of the mean.
ture of *P. hispidus* was maintained between 36.4 and 37.1 °C after exposure to ambient temperatures between 5.0 and 25.0 °C. inclusive (fig. 2). Animals were capable of regulating their body temperatures and remained homeothermic during prolonged exposure at cold environment (5 °C.) provided food was available. Four out of six individuals remained in normothermic state for at least 30 days when they were kept in the cold room (5 °C.) with food and water ad libitum. The other two individuals showed occasional torpors throughout the period (see next section for torpid mice). *P. hispidus* became hyperthermic when $T_{a}$ exceeds 34 °C. (fig.2). After prolonged exposure at $T_{a}$=34 °C. for a few hours animals extended their limbs and showed apparent lethargy. Neither panting nor licking of fur was observed. One individual at 37 °C. was dead after three hours exposure. The body temperature was 42 °C. just before death.

Thermocouples implanted in both neck and abdomen showed a difference of 0.2-2.0 °C. between the two regions. The neck temperature was often lower than the abdominal when animal was at its normothermic level. However, neck temperature exceeded the abdominal temperature when the animal was arousing from torpor and shortly after arousal (see next on arousing animal).

(2) Oxygen consumption

Basal oxygen consumption decreased linearly as ambient temperature increased from 3.0 to 30.5 °C. inclusive.
Figure 2

Body temperature of *P. hispidus* at different ambient temperatures

N is equal to the number of measurements made on a total of 14 animals. All body temperatures were recorded from implanted thermocouple in the abdominal cavity. Measurements were made both at day and night.

Vertical line indicates range, horizontal line the mean. Rectangular box is ±2 standard errors of the mean.
The least squares equation fitted to the data over this range of ambient temperatures is:

\[
\text{metabolic rate} = 7.4 - 0.201 T_a \quad \text{(fig. 3)}
\]

The slope of the line is equal to the thermal conductance of 0.201 cc O2/gm/hr/°C. The thermoneutral zone, ambient temperatures at which metabolism is lowest, extends from 30.5 to 33.5 °C. Oxygen consumption at thermoneutrality is 1.25 cc O2/gm/hr. When \( T_a \) is above 33.0 °C., body temperature increases with increased \( T_a \) and oxygen consumption increases slightly.

(3) Heart rate, respiratory rate and muscle electrical activity

Continuous recording of heart rate, respiratory rate and EMG from implanted electrodes showed a pattern similar to oxygen consumption, i.e., the rates and electrical activity increased when ambient temperature decreased. Heart rate and respiratory rate were different in (a) different individuals at the same ambient temperature; (b) in the same individual with different activity. In one representative individual (fig. 4), the minimum heart rate was 280 beats/min at a \( T_a \) of 30.0 °C.. Between 30.0 and 34.0 °C, the heart rate increases with the elevation of ambient temperature. In the same individual the minimum respiratory rate of 51 breath per minute was recorded at \( T_a=34.0 \) °C.. Both heart rate and respiratory rate increased abruptly when \( T_a \) exceeded 34.0 °C. (fig. 4). After the animal had become hyperthermic, both
Figure 3

Minimum oxygen consumption in the normothermic *P. hispidus* as a function of ambient temperature

The equation for the statistically fitted line is:

\[
\text{Metabolic Rate (cc O}_2/\text{gm/hr)} = 7.4 - 0.201 T_a
\]

with the slope of the line equal to the thermal conductance of 0.201 ccO\(_2\)/gm/hr/°C. This line intercepts the abcissa at \(T_a=36.8 \, ^\circ\text{C}\).
Figure 4

A representative record of simultaneous recording of body temperature, heart rate and respiratory rate of normothermic animals as a function of different ambient temperature.

The lines are fitted by eye. The symbols are as follows:

○ Abdominal temperature (°C.)
○ Neck temperature (°C.)

▲ Heart rate (beats/min)
▲ Respiratory rate (breath/min)
Respiratory Rate

Ambient Temperature °C

Heart Rate

Temperature °C
heart rate and respiratory rate decreased to values only slightly higher than thermoneutral values. The relative frequency and the maximum intensity of shivering both increased when the ambient temperature decreased from 20.0 to 3.0 °C. inclusive. Above $T_a$ of 20.0 °C., no bursts of shivering can be detected by the EMG electrodes implanted in the rump muscle of the experimental animal (fig. 5).

2. Torpor with food present

Occasionally, animals were torpid in the plastic cages at day time with both food and water available at room temperature of 23 ± 1.0 °C. At least thirty spontaneous torpor from four out of five animals were observed throughout the year. Body temperature may be only 0.2 to 2.0 °C. above the ambient temperature (i.e. $T_b=22.6$ when $T_a=22.4$). Episodes of torpor were also found in animals kept at 15 and 5 °C. environment with excess food and water in the cage. However, their body temperatures were usually more than 1 or 2 °C. above the ambient temperature (see next section on body temperature of torpid mice). However, the majority of animals remained active and homeothermic at these ambient temperatures if food and water were provided ad libitum.

Arousal starts either spontaneously or by disturbance with handling the individual. Twenty to sixty minutes was usually necessary for the individual to restore body temperatures to normal levels depending on how low the body tempera-
Figure 5

Relative frequency and maximum intensity of shivering vs. ambient temperature

A representative record of the relative frequency and maximum intensity of shivering as a function of ambient temperature. A standard unit of shivering is defined as a burst of shivering with a length of 3.0 mm on the recording at a paper speed of 66.8 cm/min (it is assumed that the speed controller on the physiograph was functioning consistently through out the experiment). The 3.0 mm length is then corresponding to a lasting of 0.26 second for each standard unit of shivering. Measurements of shivering have been made in three P. hispidus.

Symbols for the relative frequency and maximum intensity of shivering are as follows:

- Relative frequency of shivering (standard unit/min)
- Maximum intensity of shivering (mV) (each point represents the averaged maximum intensity of 10 highest peaks of shivering recorded within 30 sec. interval at each selected ambient temperature)

Vertical line indicates the range, horizontal line the mean.
ture from which they start to arouse was. The mean of the fastest arousal rate for arousal induced by disturbance was 0.55 °C./min (table 1). (The fastest arousal rate was defined arbitrarily as the increment of body temperature within the 15 minute period during the fastest arousal period).

Animals did not usually become torpid when food was supplied in excess and animal implanted with thermocouple. Among the various ambient temperatures tested—6.0, 13.0, 15.0, 18.0, 20.0, 23.0 °C., implanted individuals remained in active state with body temperature fluctuating between 36-38 °C. over a period of several days. Yet if food was deprived, the implanted animal became torpid usually within 24 hours at these same ambient temperatures. Table 2 compares the influence of food on the episodes of torpor in P. hispidus.

No records of heart rates, respiratory rates, oxygen consumption and muscle activity were obtained due to the difficulty in securing spontaneous torpor.

3. Torpor without the presence of food

Torpor can be induced in both thermocouple implanted and unimplanted P. hispidus from T_a of 2.0 to 24.0 °C. inclusive, by either limiting food supplies (measured amount of sun flower seeds) or appropriate starvation (water provided ad libitum in both cases). No animal lost more than 16% of its original value before an episode of torpor was observed. Commonly, the weight loss was around 0-10%.
Table 1
Rewarming rate of body temperature
(animal aroused by disturbance)

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For the convenience of description, the torpor cycle is broken into three phases, namely, entry into torpor, torpor itself and arousal from torpor:

(1) Entry into torpor

A. Heart rate and respiratory rate

As *P. hispidus* entered torpor, heart rate decreased prior to the decrease of oxygen consumption and body temperature (fig. 6). Heart rate was unstable during entrance, a difference of 80 beats/min can be found within one minute interval. During early entrance, heart rate decreased sharply, i.e. a very low heart rate (180 beats/min) can be found at fairly high body temperature (33.2 °C.) (fig. 7). As body temperature dropped below 30.0 °C., the heart rate decreased at a much slower rate (fig. 7). Thus there are two slopes to the heart rate/body temperature curve during entrance. Between $T_b = 30 - 17$ °C., the slope $Q_{10}$ value is 1.95 while between $T_b = 35 - 30$ °C., the corresponding $Q_{10}$ for the slope is 4.27.

Skipped heart beats have been recorded in all experimental animals during the entrance into torpor. Prolonged apnea and interspersed bursts of breathing were observed in all experimental animals during the entrance period (fig. 8,9).

B. Oxygen consumption

Oxygen consumption fluctuated during entrance into torpor. Oxygen consumption usually alternately decreased and increased successively during entry with each reduction
Figure 6

Simultaneous recording of heart rate, oxygen consumption and body temperature during the entrance into torpor to demonstrate their sequential changes.

The symbols are as follows:

- ▲ Heart rate
- ○ Oxygen consumption
- ● Body temperature
Figure 7

Relationship between heart rate and body temperature during entrance into and arousal from daily torpor in *P. hispidus*

The symbols are as follows:

- ○ Heart rate vs. abdomen temperature during entrance
- ○ Heart rate vs. neck temperature during entrance
- ▲ Heart rate vs. abdomen temperature during arousal
- ▲ Heart rate vs. neck temperature during arousal
Figure 8

Simultaneous recording of heart rate, respiratory rate, oxygen consumption and body temperature during a daily entrance into and arouse from torpor
Figure 9

Representative records of the changes in heart rate and respiratory rate at successive times during the entrance into torpor

$T_b$ of chamber declined from 12.5 to 12.0 °C, as animal became torpid. Upper tracing is the EKGs, middle tracing is the respiratory rate, lower tracing is the time interval (5 seconds between two marks). Numbers below represent heart rate (beats/min) and respiratory rate (breath/min).

A. Time 0343 $T_b$=35.9 °C.
Animal prior to the entrance into torpor (normothermic)
HR=357  RR=129

B. Time 0415 $T_b$=33.7 °C.
Animal entering torpor. Heart rate and respiratory rate also began to decline. Note the unevenly spaced heart rate on EKG record.

C. Time 0428 $T_b$=31.2 °C.
Heart rate and respiratory rate have decreased to 207 and 72 respectively.

D. Time 0437 $T_b$=27.9 °C.
Intermittent electrical activities were observable between the 3rd and 6th and between the 17th and 19th heart beats when counted from left to right on the EKG record. These are probably intermittent muscle activity found during the entrance period (see fig. 9).
HR=156  RR=52

E. Time 0444 $T_b$=25.9 °C.
Note marked irregularity of heart rate due to skipped beats.
HR=128  RR=44

F. Time 0534 $T_b$=19.3 °C.
Note respiratory apnea.
HR=115  RR=30

G. Time 0604 $T_b$=17.3 °C.
Enterance near its completion. Irregular apnea persists.
HR=98  RR=16

H. Time 0657 $T_b$=15.5 °C.
Animal has reached its deepest level of torpor. Irregular heart beats and irregular apnea are characteristics of this animal as well as the others during torpor.
HR=64  RR=15 with apnea
more profound than the previous one (fig. 10). As the entrance continues, the oxygen consumption dropped continuously and smoothly until the final low plateau was reached.

C. Body temperature

Body temperature drops after the decline of heart rate and oxygen consumption (fig. 6). It is also fluctuated before its final drop to the low plateau. The fluctuation may be as great as 2-5 °C, the value depending on the ambient temperature and individual differences. When the animal was deprived of food and exposed to various ambient temperatures, it was usually between 2-15 hours at a $T_a$ of 5.0 to 19.0 °C, before the animal became torpid (table 2). However, lapses of 34, 38, 42, and 92 hours prior to entry into torpor at $T_a = 20.0$, 12.0, 20.0, and 23.0 °C. respectively have been recorded among the animals. Even in the same individual at the same ambient temperature, the time lapse before the occurrence of torpor differed. After the $T_b$ reaches 31 °C during entrance, it will drop to its final plateau as no spontaneous returns to normothermia were ever been found after the $T_b$ had fallen below 31.0 °C during entrance.

D. Shivering

Shivering was observed during the entrance of torpor in *P. hispidus*. Four different patterns of EMG records were found during the entry process (fig. 11): (a) "Quiescence" or the abscence of shivering. This was characterized by its small magnitude and was only observed
Continuous recording of body temperature and oxygen consumption in a single episode of daily torpor to demonstrate the successive decline of oxygen consumption during entrance and the rapid increase during arousal.

Symbols are as follows:

- O Oxygen consumption (cc O₂/gm/hr)
- O Body temperature (°C.)

\[ T_a = 16.8 \, ^oC. \]
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--- no torpor found
+ Torpor found

Table 2
Influence of food on episodes of torpor
Representative sample of continuous recording of muscle electrical activity (EMG) during the entrance into torpor

Four types of EMG record can be observed when *P. hispidus* enters torpor:

1. Little or absence of EMG (quiescence). Usually found during rapid decline of body temperature.

2. Continuous electrical activity of the muscle with no apparent peaks or bursts of shivering observable.

3. Intermittent peaks of shivering with "moderate" magnitude.

4. Intermittent peaks of shivering with "intense" magnitude.

Ta declined from 15.5 to 15.0 °C. during entrance into torpor.

A. Time 0930 Tb=35.0 °C. Normothermic *P. hispidus* prior to entry into torpor. Intermittent peaks of shivering in "moderate" magnitude (type 3) can be observed.

B. Time 1026-1042 Tb decrease from 31.8 to 28.0 °C. Absence of EMG (quiescence, type 1). Usually found during rapid decline of body temperature. Note small bursts of muscle activity. EKG can be seen clearly during the "quiescence" period.

C. Time 1140 Tb=22.2 °C. Electrical activity of muscle observed during the entrance into torpor (type 2) and during the deepest state of torpor.

D. Time 1342 Tb=19.5 "Moderate" and "intense" (type 4) shiverings recorded during the entrance into torpor. "Intense" shivering was also found if the ambient temperature was lowered when the animal was in its deepest torpid state.

E. Time 1500 Tb=20.5 °C. Typical EMG record of animal in deepest torpor. Some electrical muscle activity maintained throughout the torpid period. Note EKG trace. HR=60 beats/min.
when body temperature was decreasing sharply. (b) A second type was continuous "muscle electrical activity" with no apparent peaks of shivering observed. This type of EMG was found most of the time either during normothermia, during entry into torpor and in deepest torpor. (c) The third pattern of EMG was characterized by intermittent bursts of shivering of moderate magnitude. (d) The fourth kind was similar to the third type except its magnitude was greater.

From the simultaneous recording of EMG and body temperature the role of shivering during the entry into torpor in *P. hispidus* is as follows (Fig. 11): when one representative animal was induced to torpor at $T_a = 15.0^\circ C$, intermittent peaks of shivering were observed at its normothermic state. At entry, these intermittent shiverings suddenly disappeared and were followed by a prolonged "quiescent" period, when the body temperature drops from 31.5 to 29.9$^\circ C$ within 2.5 minutes. During the decrease of body temperature, intermittent bursts of small magnitude in muscle activity were found scattered among the "quiescent" periods (Fig. 11B). Below $T_b$ of 29.9$^\circ C$, increased muscle electrical activity and intermittent shivering were observed. Body temperature either stopped decreasing or increased slightly (i.e. 0.1 - 0.2$^\circ C$) after episodes of strong shivering (Fig. 11D).

From a comparison of cooling rates between
an animal in its normal entrance into torpor and after this
same animal was overdosed with Nembutal at $T_a$ of 15.5 °C.
(fig. 12), it appears that the fastest cooling rates of
body temperature during the two types of cooling were differ¬
ent. The rate of two normal entrances was .27 °C./min and
the animal's $T_b$ reached 19.0 °C. in 130 and 140 minutes
beginning with a $T_b$ of 33.5 °C.. A faster cooling rate was
found in a dead animal than a normal animal during entry into
torpor (.36 °C./min) and reaching 19.0 °C. in 80 minutes.
When the corpus was rewarmed to 38.0 °C. and returned to a
15.5 °C. environment, the cooling rate was even faster than
the freshly killed animal (.38 °C./min). It reached 19.0 °C.
in 63 minutes.

(2) During torpor

A. Heart rate and respiratory rate

Heart rate during the torpid period was not
evenly spaced. There were occasional accelerations of heart
rate. Heart rate at $T_b$'s between 12.0-20.3 °C. had minimum
values of 25-60 beats/min, 1/7 to 1/16 of the normothermic
value. The lowest recorded heart rate was 25 beats/min and
it was obtained from an torpid individual with $T_b=12.0$ and
$T_a=11.0$ °C.. Respiratory rate is characterized by prolonged
apnea and irregular bursts of breath during torpor. The
lowest rate obtained was 12 times/min recorded in an animal
with a $T_b$ of 15.6 at a $T_a$ of 11.5 °C.. The longest apnea
recorded was 40 seconds found at a $T_b$ of 12.5 at $T_a$ of 10.0 °C..
Figure 12

Comparison of cooling rates during entrance into torpor and after overdose of Nembutal at a constant ambient temperature

The comparison of cooling rates in the same animal was made at a constant ambient temperature but under different conditions. $T_a=15.5\,^\circ\text{C}$.

The symbols are as follows:

- ∙ Entering torpor run No. 1
- ○ Entering torpor run No. 2
- ▲ Killed with Nembutal
- △ Rewarmed to 38.0 °C.
B. Oxygen consumption

Oxygen consumption was markedly reduced during torpor. The lowest oxygen consumption recorded was 0.12 cc O$_2$/gm/hr at $T_a=8.0$ °C. The $Q_{10}$ value for oxygen consumption between $T_b$ of 13.0 to 37.0 °C. was between 2.4-4.0. This was calculated by comparing the oxygen consumption of the torpid mouse to that of its normothermic value at the same ambient temperature.

C. Body temperature

When $T_a$ was equal to or greater than 14.0 °C., $T_b$ usually falls within 0.2-2.0 °C. above the ambient. When $T_a$ was less than 14.0 °C., there was usually an increase in $T_b - T_a$ gradient (delta T) as ambient temperature decreases (fig. 13). The lowest $T_b$ at which spontaneous arousal could still occur was 8.1 °C. at $T_a=7.8$ °C.. Newly captured summer animal (August, 1965) exhibited torpor and $T_b$ declined to 11.0 °C. with spontaneous arousal. In one individual $T_b$ declined to 3.0 °C., and survived for 50 hours (by EKG record) but never aroused from torpor and died eventually.

D. Length of torpor

Among approximately 150 episodes of torpor observed in the laboratory, only one instance was found in which the torpid period exceeded 24 hours. The length of torpor in most P. hispidus was less than 24 hours (table 3). The relationship between length of torpor and ambient temperature was studied in one unimplanted animal (fig. 14). Between $T_a$ of 1.5 to 17 °C., the length of torpor increased with the
increase in ambient temperature. No systematic measurements have been made in this animal above $T_a$ of 17 °C.

E. Muscle electrical activity

Electrical activity of the muscle was observed in the torpid *P. hispidus*. Intermittent bursts of shivering of the rump muscle have been found in the torpid mouse at $T_b$ of 12.5 °C. Strong shivering was invariably observed in the torpid animal when the ambient temperature was lowered after the animal has in its deepest torpid state (fig. 11D).

(3) Spontaneous arousal

A. Heart rate and respiratory rate

Heart rate and respiratory rate increased rapidly during arousal (fig. 8, 15). Maximum heart rate was between 430-570 beats/min when the animal aroused at $T_a$'s between 6.5 and 18.0 °C. Inclusive. In one representative individual, at a $T_b$ of 17.0 and $T_a$ of 16.8 °C, the heart rate was 36 beats/min. During arousal the heart rate reached its maximum of 468 beats/min within 50 minutes (fig. 15).

Skipped heart beats were observed during the early arousal. In all cases skipped beating lasted less than 20 minutes after the initiation of arousal. Skipped heart beats have been recorded at various $T_b$'s between 13.0-14.1, 17.9-22.0, and 21.1-22.4 °C. as the animals aroused from 13.0, 17.9 and 21.1 °C, respectively. Short apnea and irregular bursts of breathing were found during early arousal before the distinct
Figure 13

The difference between body temperature and ambient temperature as a function of ambient temperature during torpor in *P. hispidus*

Body temperatures obtained from chronically implanted thermocouple in 17 *P. hispidus* which became torpid.
Table 3

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<th>Time at Onset of spontaneous arousal</th>
<th>Length of torpor (Hour)</th>
<th>Length of torpor in <em>P. hispidus</em></th>
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Representative records obtained from 10 animals implanted with thermocouple in the abdominal cavity. Animals were induced to torpor by food deprivation.
Figure 14

The length of torpor in one *P. hispidus* at different ambient temperatures
and continuous rise of respiratory rate appeared in the later stage (fig. 15). In the same individual described above, a maximum rate of 200 breathes/min was recorded after 50 minutes when the animal aroused from $T_b=17.0$ and $T_a=16.8 \, ^\circ C$. (fig. 8). Both heart rate and respiratory rate reached their maxima before the full restoration of body temperature.

B. Oxygen consumption

Oxygen consumption increased abruptly and was characterized by an overshoot during arousal (fig. 10). The maximum oxygen consumption during arousal was between 3.6-9.4 cc $O_2$/gm/hr depending on the body temperature and ambient temperature at which arousal starts. The maximum oxygen consumption is roughly two times of the normothermic value between $T_a$'s of 12.5 and 24.0 $^\circ C$. As one representative individual aroused from $T_b=17.0$ and $T_a=16.8 \, ^\circ C$, a maximum oxygen consumption of 8.57 cc $O_2$/gm/hr was attained 42 minutes after the initiation of arousal. It is approximately twice the normothermic value and about 34 times greater than its consumption during the deepest torpid state. After arousal, oxygen consumption remained at a higher than normothermic level for one to two hours before it returned to its normothermic value.

C. Body temperature

Implanted thermocouples in both neck and abdominal regions showed moderate temperature difference during all the arousals. Temperature of the neck region rose
Continuous recording of heart rate and respiratory rate during arousal

A representative record of heart rate and respiratory rate during arousal as a function of body temperature. Upper trace EKGs lower trace respiratory rate. Numbers below represent heart rate (beats/min) and respiratory rate (breath/min). Ta increased from 16.8 to 17.3 °C. by the arousing animal.

A. Time 0930 T_b=17.0 °C.
   Typical EKG record and irregular apnea of torpid P. hispidus.
   HR=36.

B. Time 0950 T_b=18.2 °C.
   Early stage of arousal. Note muscle activities between the first three, between the 12th and 16th and between the last four heart beats when counted from left to right on the EKG trace. Skipped heart beats found in the early arousal. Respiratory rate still irregular.
   HR=93.

C. Time 0954 T_b=20.3 °C.
   Skipped heart beats and apnea still present.
   HR=174 RR=82

D. Time 1004 T_b=24.3 °C.
   Heart rate and respiratory rate both increased as arousal continues.
   HR=246 RR=142

E. Time 1011 T_b=27.5 °C.
   Occasional slowing down of breathing rate has been found common in many animals during arousal.
   HR=310 RR=142

F. Time 1016 T_b=30.4 °C.
   Arousal near its completion.
   HR=384 RR=192
earlier and was higher than abdominal temperature during arousal (fig. 16). A maximum difference of 3.7 °C. has been recorded in one individual 20 minutes after arousing from a \( T_b \) of 15.0 °C. After the completion of arousal, neck temperature dropped below abdominal temperature as was described at its normothermic state. Generally, body temperature was maintained at its normothermic level after arousal with only little fluctuations.

D. Shivering

The sequential changes of EMG during arousal are shown in figure 17. No apparent burst of shivering was observed in the earliest stages of arousal. There was an increase in muscle activity associated with increased heart rate in the latter stages of arousal. In one representative individual arousing from a \( T_b \) of 20.6 °C., no burst of shivering was found until body temperature had reached 21.4 °C.

Beyond 21.4 °C., the intensity of shivering increased continuously. Between 24.0 to 30.4 °C., the animal was shivering at its maximal intensity. The fastest increment of body temperature was found associated with the strongest shivering during arousal. When \( T_b \) reached 30.4 °C., the intensity of shivering reduced again.

E. Arousal rate

Animals aroused from torpor either by disturbance or spontaneously. Since there is no standard index for the degree of disturbance, comparison of arousal rates
Figure 16

Maximum difference in neck-abdominal body temperature in arousal
$T_a = 16.8 \, ^{\circ}C$

*P. hispidus*

No. 26  Run No. 4

Weight = 40.5 - 39.5 Gm
Figure 17
Continuous recording of EMG during arousal from daily torpor

$T_a$ increased from 15.5 to 17.0 °C. by the arousing animal.

A. Time 1534 $T_b=21.4$ °C. (aroused from $T_b=20.0$ °C.)
EMG at the early stage of arousal. Muscle electrical activity increased but no bursts of shivering observed.

B. Time 1543 $T_b=23.0$ °C.
Bursts of shivering of moderate magnitude (less than 250 µV in a single burst of shivering) appear as arousal continues.

C. Time 1601 $T_b=29.1$ °C.
Bursts of strong shivering (250-500 µV in a single burst of shivering) recorded in the middle way of arousal. The fastest rate of increase in body temperature was often found to be correlated with strong shivering during rewarming.

D. Time 1611 $T_b=33.2$ °C.
Bursts of shivering reduce magnitude when body temperature reached 30.0 °C.

E. Time 1630 $T_b=35.5$ °C.
EMG record right after arousal has been completed.
were restricted to spontaneous arousals. Table 4 shows the mean arousal rates calculated from all spontaneous arousals. The fastest arousal rate was 0.51 °C/min when aroused at $T_b$'s below 15.0 °C. and 0.46 °C./min with arousals commencing at $T_b$'s above 15.0 °C.. There was no significant difference in arousal rates when aroused either above or below $T_b$ of 15.0 °C..
Table 4
Rewarming rate of body temperature
animal aroused spontaneously.

<table>
<thead>
<tr>
<th>Animal No.</th>
<th>Fastest arousal rate (°C./min)</th>
<th>Animal No.</th>
<th>Fastest arousal rate (°C./min)</th>
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<td>Initial $T_b$ above 15.0 °C.</td>
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<td>mean</td>
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IV. Discussion

A. Normothermic *P. hispidus*

1. Body temperature

The labile body temperature of *P. hispidus* is similar to that of other pocket mice (Bartholomew and Cade 1957, Tucker 1965). The body temperature of many other small rodents viz. birch mouse (Johansen and Krog 1959), pygmy mouse (Hudson 1965), kangaroo mouse (Bartholomew and MacMillen 1961) was also found to be labile and fluctuated with ambient temperature and activity. It is therefore not surprising to find a range of normal body temperatures existed in *P. hispidus*. It is advantageous for the animal to maintain a lower body temperature while possessing the capability of normal functions because of the reduced energy requirements.

The absence of panting and licking of the fur as an emergency way for heat dissipating in this species, as been described in the antelope ground squirrel (Hudson 1962), indicates poor regulation at high ambient temperature. The high lethal temperature of *P. hispidus* was the same as *P. californicus*, $T_l=37.0\, ^\circ C$. (Tucker 1965). This is a low value when compared with *Balomys taylori* because this animal has the lowest heart rate at 37 $^\circ C$. (Hudson 1965).

2. Oxygen consumption

From figure 3, the statistically fitted line for minimum oxygen consumption intercepts the abcissa at 36.8 $^\circ C$. According to the biological application of Newton's law of
cooling (Scholander et al 1950) this temperature represents the body temperature of the experimental animal. The simultaneously measured $T_b$ of the animal at $T_a=30.0 \, ^\circ C$ was $37.0 \, ^\circ C$, which was in good correlation with the extrapolated value of $36.8 \, ^\circ C$. Therefore, the relation between heat loss and ambient temperature following Newton's law of cooling in $P. hispidus$.

The basal metabolism of $P. hispidus$ was only 81% of the theoretical value when equation $3.8 W^{0.27}$ ($W=39.5 \, \text{gm}$) was used for calculation (Morrison, Ryser and Dawe 1959). Morrison (1960) derived the following equation for the small mammals:

$$T_b - T_{ac} = 4 W^{0.4}$$

Where $T_{ac}$ is the lower critical temperature of the thermo-neutral zone and $W$ is the body weight of the animal in gram. When body weight of $39.5 \, \text{gm}$ was inserted for calculation, the $T_{ac}$ turned out to be $27 \, ^\circ C$, which is about $3 \, ^\circ C$ lower than the empirically measured value in $P. hispidus$.

Hudson (1964) noted that a 25% reduction of basal metabolism will elevate the lower critical temperature from $2.5$ up to $6 \, ^\circ C$, depends on the thermal conductance of the animal. With a lower basal metabolism, animal can conserve energy requirements and producing less waste. An elevated lower critical temperature facilitate entry into torpor at relatively high ambient temperature since the animal need only reduce the amount of shivering or muscle activity nece-
ssary for maintaining normal body temperature below the lower critical temperature (op. cit.). Morrison suggested (1960) that active reduction of resting metabolism may be a distinguishing physiological characteristic of estivators. In P. californicus (Tucker 1965), Microdipodops pallidus (Bartholomew and MacMillen 1961) and in Baiomys taylori (Hudson 1965) a reduction of 41%, 38% and 12% of basal metabolism have been found respectively and all three species showed daily torpor phenomenon. In the P. hispidus studied, there was a 3 °C. elevation of the lower critical temperature, a 19% reduction of basal metabolism in the thermoneutral zone which allows this species to enter torpor at relatively high ambient temperatures.

3. Heart rate, respiratory rate and muscle electrical activity

Heart rate of P. hispidus within the zone of thermoneutrality varies with body size and activity. As was shown in the Result part, a representative 40 gram animal had an average heart rate of 285 beats/min. This was considerably lower than the theoretical value of 517 beats/min when calculated by using H.R. = 1400 W^{–0.27} (Clark 1927 cited by Hudson 1965). Reduction of heart rate was found in Baiomys taylori (300 vs 863, Hudson 1965) and also in the masked shrew (600 vs 1020, Morrison, Ryser and Dawe 1959). The respiratory rate was around 55 breathes/min in the same individual at thermoneutrality. Both minimum heart rate and
respiratory rate were close to the thermoneutral range when
determined by oxygen consumption.

Shivering can not be detected from the rump muscles
when $T_a$ has exceeded $20\,^{\circ}\text{C}$. It is assumed that either non-
shivering thermogenesis alone is adequate for the thermo-
regulatory response between $20$ to $30\,^{\circ}\text{C}$, or the muscle of the
rump region do not shiver unless the ambient temperature is
below $20\,^{\circ}\text{C}$.

B. Heterothermic $P.\ hispidus$

1. Preparation for torpor

In the $P.\ hispidus$ studied, spontaneous daily
torps have been observed through out the year at the presence
of food. The animals can also be induced to become torpid at
any time of the year. Therefore, it is similar to the other
pocket mice (Bartholomew and Cade 1957, Tucker 1965) and the
birch mouse (Johansen and Krog 1959) that little if any pre-
paration prior to the onset of torpor is needed in this
species.

2. Entrance into torpor

As was described by Lyman (1961) "entrance into
hibernation is under precise physiologic control, with heart
rate, respiratory rate and oxygen consumption slowing before
a decline in body temperature". In $P.\ hispidus$ this was also
the case after simultaneous recording of these parameters
when the animal was enterig into torpor (fig. 6, 7). The
sharp decline of heart rate during the early entrance was
similar to that reported in the California ground squirrel (Strumwasser 1960). Strumwasser (op. cit.) has pointed out that the cooling rate of body temperature during the entrance was partly determined by the amount of shivering generated by the animal during the entry process. His concept on "shivering as a brake during entrance into hibernation" was confirmed in *P. hispidus* after continuous recording of EMG during the torpor cycle. The animal shivered intermittently during entry into torpor and body temperature either increased slightly or stop decreasing after episodes of strong shivering occurred. Comparison on the cooling rates between entrance into torpor and the cooling of freshly killed animal indicates that the cooling of body temperature during entrance was actively controlled. In *P. californicus* (Tucker 1965) and *P. longimembris* (Bartholomew and Cade 1957), visible shivering was not observed when the animals entering torpor. However, no EMG recordings have been reported in these two species.

Skipped heart beats and irregular respiratory apnea were found during the entrance into torpor as was shown in figure 8. In the ground squirrels, golden hamster, marmots (Lyman 1965) and in *Baiomys taylori* (Hudson 1965), skipped heart beats and irregular apnea were also found during the entrance into torpor. According to Lyman (1965), the skipped heart beats and prolonged asystoles are served to maintain a more exact correlation of heart rate with temperature and time when the animal is entering into.
hibernation. The skipped beats are induced by parasympathetic actions, because atropinization abolishes skipped beats and get faster heart rate at any body temperature during the entrance into torpor (op. cit.) (Hudson and Morhardt unpublished).

3. In torpor

During torpor, heart rate, respiratory rate and oxygen consumption were greatly reduced. Minimum heart rate of *P. hispidus* during torpor was considerably higher than the 2-16 beats/min reported in many deep torpid hibernators (Lyman 1958, Kayser 1961). This is probably due to the relatively higher body temperature of *P. hispidus* during torpor as well as its relatively smaller body size than the hibernators. In the birch mouse (Johansen and Krog 1959), minimum heart rate of 30 beats/min was found at $T_b = 4 - 8^\circ C$. In the pygmy mouse (Hudson 1965), heart rate of 78-100 beats/min was recorded when the animal was torpid between $T_a$ of 15.5 to 20.1° C. Occasional accelerations of the heart rate, prolonged apnea and irregular bursts of breathes were typical during torpor in this species as was also observed in the torpid *Peromyscus sp.* (Hudson and Morhardt unpublished).

The increase of muscle activity and intense shivering in the torpid *P. hispidus* indicates the animal was maintaining the $T_b - T_a$ gradient through active thermoregulation. The *Q_10* value of oxygen consumption was between...
2.4 and 4.0 in P. hispidus. $Q_{10}$ value of 2.4 for oxygen consumption has been reported in P. californicus (Tucker, 1965). In the little brown bat, Myotis lucifigus $Q_{10}$ values as high as 5.09 has been recorded between $T_b$ of 20 to 30°C, and 5.54 between $T_b$ of 10 to 20°C. (Hock 1951).

The increase of delta T with the decrease of ambient temperature below 14°C. during torpor indicates P. hispidus was actively thermoregulating even at low body temperatures. Similar thermoregulatory response has been observed in the torpid Peromyscus sp. (Morhardt and Hudson 1966). In contrast however, the delta T of torpid Peromyscus eremicus decreases as the ambient temperature decreased from 25 to 10°C. (MacMillen 1965). Torpid Peromyscus eremicus can not survive if $T_b$ is below 16°C. (op. cit.). Therefore, the capability of maintaining $T_b - T_a$ gradient during torpor probably reflects the thermoregulatory ability at low body temperatures among the small rodents capable of exhibiting daily torpor.

Lyman (1965) stated that in most hibernators, temperature was about the same in all parts of the body during deep hibernation which implies an even blood flow with no differential vasoconstriction over certain parts of the body. Thus in the torpid P. hispidus it is physiologically similar with the other hibernators during hibernation.

The lowest recorded critical body temperature - 38 -
(8.1°C.) in *P. hispidus* was relatively lower than most small rodents exhibiting daily torpor whose critical body temperature varies between 10 - 22°C. (Bartholomew and MacMillen 1961; Tucker 1965; Chew, Lindberg and Hayden 1965; Hudson 1965; Morhardt and Hudson 1966). However, in the European birch mouse, spontaneous arousal has been recorded with $T_b$ as low as 4.5°C. (Johansen and Krog 1959). According to Hudson (1965), the ability to tolerate low body temperature in the torpid animal was probably a reflection of the environment in which the animal lives. *P. hispidus* can tolerate much lower body temperature than the pygmy mouse (Hudson 1965) yet, the two were collected from the same locality in the southern Texas. However, since the northern range of *P. hispidus* extends to Minnesota, it is possible that genotypical difference might have been existed between the two species. Comparative studies on the lowest critical body temperature in *P. hispidus* between the northern and southern populations would elicit the influence of ecological factors as well as the role of acclimatization on torpidity.

Length of torpor in *P. hispidus* was mostly less than 24 hours with only one exception. In *P. longimembris* torpid period longer than 24 hours has been observed under food deprivation and cold stress (Chew, Lindberg and Hayden 1965). In the hibernators, length of torpor between periodical arousals was usually between one week in
the golden hamster to several weeks in the ground squirrels and woodchucks (Lyman and Chatfield 1955). In the little brown bat *Myotis lucifugus* torpid period was between 1 - 5 days at $T_a$ of 3 - 5°C, but continuous torpor of 80 - 90 days have been recorded (Menaker 1964). In *P. hispidus*, the length of torpor decreases with the decrease in ambient temperature (fig. 14). In contrast, in the golden-mantled ground squirrel the length of torpor increases as ambient temperature decreased from 25 to 2°C. (Twente and Twente 1965). In *P. hispidus*, the delta T increases in the torpid animal as the ambient temperature approaches zero therefore more energy is consumed to maintain the higher delta T gradient at lower ambient temperatures. Consequently, the length of torpor is shortened at low $T_a$'s. In the golden-mantled ground squirrel, the delta T during torpor was 2°C. of the ambient at all temperatures tested (op. cit.). Therefore, the lower the body temperature during torpor the less the energy will be consumed and consequently the length of torpor is lengthened.

4. Arousal

In the arousing *P. hispidus*, continuous recording of heart rate, respiratory rate, oxygen consumption, muscle activity and body temperature showed qualitatively similar changes to those of the classical hibernators and estivators in arousal. Skipped heart beats were recorded in *P. hispidus* usually within 20 minutes after the initiation...
of arousal. Chatfield and Lyman (1950) found in the arousing hamster there was A-V dissociation in the early arousal but the mechanism was not known. It is speculated that because of the rapid increase in heart rate and relatively little change in stroke volume (Bullard and Funkhauser 1962), the rapid increase in cardiac output and venous return may stretch the baroreceptors in the aortic arch, vena cava and in the atria. This in turn elicits the buffer reflex and exerts vagal inhibition on the heart. However, experimental evidence is needed to verify this speculation.

When heart rate was plotted against body temperature during arousal (fig. 7), the increase in heart rate showed $Q_{10}$ values of 7.7 and 1.2. Since these values are beyond the 2-3 value normally found in the biological system, it is indicative that the increase in heart rate during arousal was not temperature dependent. Chatfield and Lyman (1950) found that the increase in heart rate in the arousing hamster was not temperature dependent but was being driven at its maximum rate by the sympathetico-adrenal system.

The maximum oxygen consumption during arousal is approximately two folds of its normothermic value in the arousing P. hispidus. In contrast, the maximum oxygen consumption during arousal was often less than its normothermic value in Peromyscus crinitus (Hudson and Morhardt unpublished).
and its body temperature was often below the normal active level (Morhardt and Hudson 1966). After given food to the newly aroused *P. crinitus*, the oxygen consumption showed further increase and the body temperature restored to its normal active level (Hudson and Morhardt unpublished). In *Peromyscus eremicus* however, oxygen consumption was higher than normothermic value during arousal and the animal often rises its body temperature to within the normal active range (MacMillen 1965). It therefore appears that the maximum metabolic rate during arousal was under active control according to the animal's own energy budget. Since all these small rodents mentioned above have a range of normal body temperatures, to conserve energy by rising its body temperature only to the lower range, represents an adaptive feature for survival.

The moderate neck-abdomen temperature difference (3.7 °C.) observed in the arousing *P. hispidus* qualitatively resembles that of the arousing hibernators. The marked antero-posterior temperature difference (27 °C.) in the arousing 13-lined ground squirrel was due to a differential vasoconstriction of the posterior part in the early arousal (Lyman and O'Brien 1960, Bullard and Funkhauser 1962). Although possessing the ability of differential vasoconstriction, there was no A-P difference observed in the arousing *Citellus mohavensis* probably due to the relatively high $T_b$ from which they start to arouse (Bartholomew and
Hudson 1960). In the birch mouse, even when aroused from $T_b$ of 6°C., the maximum A-P difference was only around 6°C. (fig 4, Johansen and Krog 1959). The neck-abdomen temperature difference in the arousing $P. \text{hispidus}$ suggests that either a moderate differential vasoconstriction occurred in the posterior part or heat generating sources were near the neck region. However, since the neck temperature was either higher or equal to the abdomen temperature during torpor, and the two temperatures were increased in a parallel fashion (i.e. no lag behind of the abdominal temperature) during arousal, it is assumed that heat generating sources (e.g. brown fat) were near the neck region which produce the neck-abdomen temperature gradient during arousal.

The essential source of heat during arousal is provided by the shivering of striated muscle (Lyman and Chatfield 1950b). However, since the curarized animal can also arouse (op. cit.), shivering is not the only heat source. Lyman (1965) has proposed several heat sources (e.g. brown fat, heart pump viscous blood, glycogen depletion from the liver, shivering) for the arousing hibernator. Zimney and Gregory (1958b) reported that adenosine triphosphate (ATP) was the source of energy during early stages of arousal. In the arousing $P. \text{hispidus}$, shivering of the rump muscle did not appear immediately after the initiation of arousal (fig. 16) yet, strong shivering of the rump muscle was found in the torpid animal.
whenever the ambient temperature was lowered. It is therefore unlikely that the rump muscles can not shiver during early arousal. It is not known whether heat sources other than shivering were utilized for the early rise of body temperature in *P. hispidus*.

The arousal rate in *P. hispidus* is comparable to other pocket mice (Bartholomew and Cade 1957; Tucker 1965) and to kangaroo mouse (Bartholomew and MacMillen 1961). But is slightly slower than the birch mouse (Johansen and Krog 1959) and is relatively higher than the white-footed mice (Morhardt and Hudson 1966), pygmy mouse (Hudson 1965) and round-tailed ground squirrel (Hudson 1964).

In *P. hispidus*, physiological changes in daily torpor cycle have shown qualitative similarities to those of the hibernators and estivators in hibernation or in estivation. However, since in *P. hispidus* and in many other animals capable of exhibiting daily torpor have shown that (1) need no preparation period before exhibiting torpor (2) higher critical body temperature for spontaneous arousal (3) length of torpor usually shorter than 24 hours (Hudson 1965b) and (4) faster arousal rate with no apparent neck-abdomen temperature difference in *P. hispidus*, it is assumed that physiological mechanisms involved for daily torpor may be different in many respects from those of the hibernation.

C. Biological significance of torpidity in *P. hispidus*
Small mammals, because of their high body surface to mass ratio, rate of heat lose is greater than the larger mammals. In *P. hispidus* the lower critical temperature was around 30°C. Since *P. hispidus* is nocturnal and night temperature over 30°C. is not usually encountered by the animal, therefore, much of the animal's life will be spent in an environment with temperatures generally are beyond its thermoneutral range. Thus, in addition to the metabolic burden because of its relatively small body size, *P. hispidus* must render additional metabolic expense for the environmental temperatures they encountered.

The only effective metabolic reserve of the body is depot fat (Morrison 1960). In the wild animals, 50% of the body weight existed as fat were usually observed (Pitts, quoted by Morrison 1960). Morrison (op. cit.) derived the following equation to demonstrate the potentiality of depot fat with respect to the survival time of the animal during prolonged starvation:

\[
\text{survival time} = \frac{f}{m} \times 16 \times W^{\frac{4}{3}} \text{ (days)}
\]

where \(f\) is the fat content (fraction of body weight), \(m\) is the metabolic level (fraction or multiple of basal metabolism) \(W\) is the weight of the animal in gram. When this equation was applied to a 40 gram *P. hispidus*, assuming that exogenous food was temporarily not available and the animal was in a complete resting state at a burrow temperature of 20°C.
(1) If body temperature is maintained at 37°C, metabolic rate at 20°C. = 2.8 times of basal metabolism (fig. 3) i.e.
\[ m = 2.8 \quad f = \frac{1}{2} \ldots .50\% \text{ fat content} \]
survival time = 7 days
(2) If the animal was torpid and body temperature declined to 21°C.
\[ m = \frac{1}{4} \text{ of basal metabolism} \quad f = 50\% \text{ fat content} \]
survival time = 80 days
These theoretical calculations merely show the advantage of using torpor under unfavorable conditions for energy conservation in this species, practically, probably no individual will behave like the assuming way. However, if use the calculated oxygen consumption value of a torpid \textit{P. hispidus} and compares to its normothermic level (fig. 18) as is shown in the following:

(1) In torpor
\[ 3.8 \times 35 + 2.8 \times 11 + 2.3 \times 28 + 1.0 \times 41 + \\
.52 \times 30 + .30 \times 367 + .70 \times 20 + 4.1 \times 15 + \\
8.4 \times 20 + 6.28 \times 18 + 5.5 \times 20 = 861.4 \text{ cc}O_2/\text{gm} \]
in 10.2 hours
(2) In normothermia
\[ 4.1 \times 611 = 2505.1 \text{ cc}O_2/\text{gm} \text{ in } 10.2 \text{ hours} \]
(1)/(2) = 1/3
Therefore, by exhibiting torpor, even as short as 8 hours (including the entry and arousal also one hour after arousal)
The continuous record of oxygen consumption indicating the total metabolism in a daily torpor cycle

$T_a = 16.5 \, ^\circ C$.

The horizontal line indicates the metabolic rate of a normothermic animal at that ambient temperature.

Total metabolism (metabolic rate x time i.e. the area under the oxygen consumption curve in a daily torpor cycle was estimated by taking area sum of the rectangles as an approximation.
only $1/3$ of the energy was needed. Thus viewing from the point of energy conservation, the physiologic modifications for torpor are adaptive for survival in *P. hispidus*. Field observation indicates torpor was occurred in *P. hispidus* under natural conditions. *P. hispidus* can use daily torpor to minimize their contact with the unfavorable environment if necessary and reduce the energy requirement at the same time. Daily torpor also provides the opportunity to the animals of sensing the environment frequently for the favorable conditions.
V. Summary

In the laboratory, *P. hispidus* can thermoregulate and remain normothermic over a range of ambient temperatures from 5 to 34 °C. Hyperthermia was found when $T_a$ exceeds 34 °C, and death occurred at $T_a$ of 37 °C. The poor tolerance of high ambient temperatures in the laboratory correlates with their nocturnal habit in nature where extensive heat is usually not encountered.

The heart rate, respiratory rate and oxygen consumption in the normothermic *P. hispidus* increased with the decrease of ambient temperature below critical temperature of 30 °C. Shivering was not observed in the normothermic animal until $T_a$ was below 20 °C. The metabolic rate at thermoneutral zone, which extends from 30.5-33.5 °C., is 1.25 cc O₂/gm/hr which is 19% less than the theoretical value.

Spontaneous daily torpor in *P. hispidus* with food and water available has been occasionally found in the laboratory at room temperature (23 °C.) throughout the year. However, the typical response is normothermia under the presence of food and water over a range of ambient temperatures from 5-24 °C. When food supply was withheld or restricted, *P. hispidus* invariably became torpid within 24 hours at $T_a$ between 4 and 24 °C.

During entrance into torpor, physiological changes represented by the continuous recording on the simultaneous changes of heart rate, respiratory rate, oxygen consumption,
body temperature and muscle electrical activity were similar to that of the classical hibernators. Heart rate decreases prior to the decrease of oxygen consumption and body temperature during entrance. Both heart rate and respiratory rate were irregular and oxygen consumption showed fluctuations during entrance into torpor. Skipped heart beats and irregular apnea are characteristics during the entry process. Intermittent shiverings were detected by EMG during entrance. Cooling rate was faster in the dead animal than the animal enters into torpor indicates active control of cooling of body temperature during entrance.

During torpor, minimum heart rate was between 25-60 beats/min and respiratory rate was irregular with prolonged apnea. Oxygen consumption decreased to only 2-13% of the normothermic value. Body temperature was within 2 °C. of the ambient above $T_a$ of 14 °C.; below 14 °C., delta $T$ increases as $T_a$ decreases. The selective maintainence of delta $T$ with respect to the ambient temperature represents a physiological thermoregulation during torpor in this species. The length of torpor is less than 24 hours in P. hispidus with only one exception out of approximately 150 instances.

During arousal, the rapid increase in heart rate, respiratory rate, oxygen consumption and shivering were qualitatively similar to that of the hibernators during arousal from hibernation. The maximum heart rate was between 420-570 beats/min and respiratory rate around 200 breathes/min.
Skipped heart beats were found during early arousal. Maximum oxygen consumption usually doubles the normothermic value and is characterized by an overshoot during arousal. Body temperature rewarmed to within normothermic range after arousal and moderate neck-abdomen temperature difference (3.7 °C.) was found during arousal. The mean maximum arousal rate was around 0.51 °C./min in *P. hispidus* which is slower than the birch mouse but is comparable to the other pocket mice and is faster than the white-footed mice and pygmy mouse.

Gross comparisons on a 10 hour energy expenditure at $T_a$ of 16 °C. yield 2505 cc $O_2/gm$ is needed for a resting normothermic animal while only 861 cc $O_2/gm$ is necessary if the animal spends 8 hours in torpor (including entrance and arousal and one hour after arousal for a total of 10 hours). Thus only 1/3 of the energy is needed if animal exhibits torpor. It is therefore energetically advantageous for *P. hispidus* to use torpor in the field under unfavorable conditions.

In *P. hispidus*, physiological changes in daily torpor cycle have shown qualitative similarities to those of the hibernators and estivators in hibernation or in estivation, but quantitatively, there were differences in many respects. Thermoregulatory capabilities enable *P. hispidus* to remain active above ground at cold nights with near freezing temperature. By using daily torpor *P. hispidus* can minimize their contact with the unfavorable environment if necessary, and reduce their energy requirements at the same time.
VI. Bibliography


