Thermoregulation in Bats Exposed to Low Ambient Temperatures. (31008)

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Unlike most mammals bats do not maintain body temperatures within narrow limits. The body temperature of inactive Microchiroptera is slightly above ambient(1). Many species of Microchiroptera are hibernators. During exposure to temperatures of 5-10°C these bats enter a state related to hibernation at any time of the year. Some hibernators increase their metabolism without arousal in response to lowering of ambient temperature below 4°C(2,3), indicating the presence of a regulatory mechanism to avoid a further drop of body temperature. However, in hibernating bats body temperature is considered to follow ambient temperature even during cooling to subzero levels(4). Tissue freezing and death of the bat is apt to occur when ambient temperature approaches —5°C(5). Data concerning the metabolic response of bats to temperatures below zero are not available. Since some species of bats hibernate in sites exposed to occasional low temperatures(6,7), we decided to study the response of these species to similar temperature conditions in the laboratory. Rectal temperature and heart rate were measured in dormant bats at different levels of ambient temperature below 10°C.

Materials and methods. Experimental animals: Twelve little brown bats (*Myotis lucifugus*) and 10 red bats (*Lasiurus borealis*) were studied. All animals were captured in Kentucky during September. The little brown bats were found in an attic and the red bats netted outdoors. They were of both sexes. Body weights were 7-10 g for the little brown bats and 10-13 g for the red bats. Following capture the bats were placed in a temperature controlled room at 5°C. The animals were restrained by taping their wings to wooden blocks. A few bats were placed individually in jars and allowed to remain unrestrained.

Temperature and heart rate recording: One junction of a copper-constantan thermocouple was inserted 10-12 mm into the rectum of each restrained bat and the lead fastened with tape to the wooden block to prevent the junction from changing position. In the unrestrained bats the thermocouple junction was put in place and the lead taped to the body after the bats had entered the dormant state. Another thermocouple junction was located within a distance of 30 cm from the bats to show ambient temperature. All leads were connected to a Brown electronic potentiometer. Heart rates were determined from the electrocardiogram of the bat recorded with a Sanborn recording device (Models 350-1600 and 150-1100AS). The connecting leads for the electrocardiogram were fastened to the skin of the bat with alligator clips. With all leads in place the bats were left overnight at an ambient temperature of 5°C.

Changing of ambient temperature: By adjusting a thermostat placed outside the temperature controlled room the temperature of the room could be changed and maintained at any desired level between —15°C and 15°C. The temperature fluctuated within a range of 2-3°C at each level of thermostat setting. The fluctuations were due to delay in turning on and off the cooling unit and occurred regularly with 8-12 min periods. The temperatures listed as ambient in this paper are average room temperatures. These were obtained by recording the rectal temperature of dead bats which gave sufficient damping to show nearly complete elimination of the fluctuations. During an experiment care was taken to insure that the only stimulus imposed on the bats was the change in ambient temperature. The temperature was changed stepwise in either direction from 5°C in the range between —5°C and 10°C.

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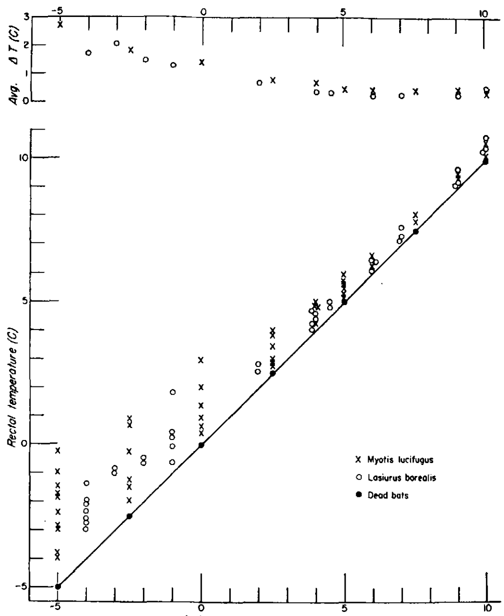

FIG. 1. Lower part of graph shows rectal temperatures (T_r) in dormant, restrained bats exposed to ambient temperatures (T_a) below 10°C. Upper part shows average difference (ΔT) between T_r and T_a ($\Delta T = T_r - T_a$) at each level of ambient temperature.

Each step represented 2-5°C. Experiments on some bats were repeated over several days. For each change to a new level of ambient temperature, the bats were allowed to establish thermal balance (heat production = heat loss) with their environment before a second temperature change was imposed. Constant rectal temperature indicated that such a state had been reached.

Results. When kept overnight at 5°C the bats entered the dormant state. Except for slow and irregular respiratory movements, signs of muscular activity were absent. No observable change in the appearance of the bats could be induced by changing the ambient temperature to any level between 5°C and 10°C. They seemed to rewarm passively to establish thermal balance at the new level. However, if a downward change in ambient temperature from 5°C was imposed on the bats, their appearance changed markedly. At an ambient temperature of about zero the respiratory movements became faster and more regular than at 5°C. Unrestrained red bats covered the ventral part of their body completely up to the neck with their tail membrane and thus formed an air pouch between the tail membrane and the body. This response took place immediately upon lowering of ambient temperature.

The rectal temperatures (T_r) of the bats were 0.1-1°C above ambient at temperatures (T_a) of 5-10°C. However, this difference ($\Delta T = T_r - T_a$) increased with decreasing ambient temperature (Fig. 1). All temperature readings were performed 40-50 min after ambient temperature had been changed to the new level. This time was sufficient for the bat to establish thermal balance (constant rectal temperature). A few of the little brown bats and one of the red bats responded to lowering of ambient temperature to below zero by attempting to arouse from dormancy. Instead of establishing thermal balance they showed steadily increasing rectal temperatures. These bats were excluded from Fig. 1. Possible factors determining whether bats will respond by arousal from dormancy or by maintaining an increased ΔT will be discussed elsewhere(8).

Lowering of ambient temperature below 5°C caused an increase in average heart rate (Fig 2). The data represent measurements from one little brown bat during a series of stepwise elevations of ambient temperature to 10°C and stepwise lowering to −5°C. Although different in magnitude the nature of the response was similar both when re-

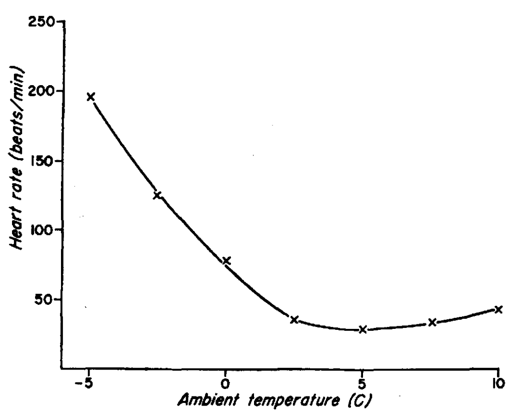

FIG. 2. Relationship between ambient temperature and heart rate in the dormant little brown bat (*Myotis lucifugus*) during exposure to cold. Symbols show average heart rate within one or more periods of room temperature fluctuations.

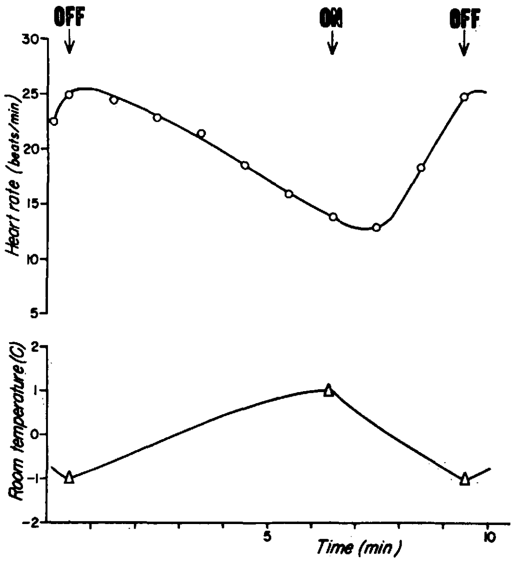

FIG. 3. Periodic heart rate changes in the dormant red bat (*Lasiurus borealis*) as related to a single cycle of the periodic temperature fluctuations at an average ambient temperature of 0°C. Each symbol represents mean values based on the frequency of 10 successive heart beats.

peated over several days in the same bat and when repeated in another animal of the same species. The latter individual showed an increase in heart rate from 26 beats/min at 5°C to 100-130 beats/min at —5°C. The 2 red bats in which the response of the heart to a lowering of ambient temperature was studied showed an increase in heart rate from 12-16 beats/min at 5°C to 25-40 beats/min at —2°C. Each level of ambient temperature seemed to correspond to a certain heart rate, and the response was not dependent on the direction of the change in ambient temperature. At any level of ambient temperature the application of stimuli other than the thermal one would initiate arousal from the dormant state. Thus pinching of a limb or touching the head of a bat kept at low temperature caused a further increase in heart rate and the rectal temperature began to increase.

Continuous recording of the electrocardiogram from bats showed constant heart rate at an ambient temperature of 5°C. However, when ambient temperature was kept at a level near or below zero, the heart rate showed periodic fluctuations which followed the previously described fluctuations in room temperature but were out of phase (Fig. 3). For each time the cooling unit was automatically turned off the heart rate showed a slow decrease lasting for 6-7 minutes followed by a rapid increase to the starting level when the cooling unit was turned on again.

At low temperatures the ECG-recording for short periods took the picture of an electromyogram. This change occurred concomitantly with the periodical increase in heart rate. A similar picture was obtained by recording the electrocardiogram from shivering bats at higher temperatures during their arousal from the dormant state. No visible shivering or other muscular movements were observed in bats exposed to low temperature unless they were disturbed by mechanical stimuli.

When restrained bats had been kept at an ambient temperature of —4°C to —5°C for 3-4 hours they apparently stopped regulating their body temperature. Rectal temperature dropped to ambient, and the bats were unable to rewarm spontaneously. Unrestrained bats could be kept overnight at this temperature. These bats still maintained body temperatures close to zero and responded to mechanical stimuli by spontaneous rewarming.

Discussion. There is a marked increase in the difference (ΔT) between the rectal temperature of the bats and ambient temperature as the latter decreases. This is evident for both species of bats studied. There is a corresponding increase in heart rate with decreasing ambient temperature. The increase in ΔT and heart rate indicates that the metabolism of the bats increases when they are exposed to low ambient temperatures. If the bats were poikilothermic one would expect a decrease in ΔT and heart rate. The observed response apparently is an attempt to maintain thermal homeostasis. It is different from responses where increased heat production is associated with or secondary to changes in the physiological state of the animal as is the case during arousal from dormancy.

Although it is generally agreed that the bats we studied are hibernators, we prefer to use the term dormancy for the physiological state entered by the bats kept overnight at an ambient temperature of 5°C. The physiological distinction between dormancy in bats exposed to low temperatures and true hibernation is not clear(1,9,10). All bats tested by us were able to rewarm and arouse from the dormant state whenever an appropriate stimulus was imposed, but Menaker(11) found a seasonal difference in the ability of the little brown bat to rewarm spontaneously at low ambient temperatures, the ability being absent in summer.

The promptness with which the red bats change their posture to diminish heat loss when exposed to subzero temperatures is suggestive that the thermoregulatory mechanism of dormant bats is triggered by peripheral receptors. The periodical changes in heart rate corresponding to periodical fluctuations in ambient temperature within a range of 2-3°C also show the alertness of this mechanism. Moreover it indicates that we are dealing with a true regulatory process and not an unsuccessful attempt to rewarm and arouse from the dormant state. Once triggered the process of arousal is followed by a continuous increase in heart rate and thus is different from the response described here.

The restrained bats were regulating body temperature for 3-4 hours at an ambient temperature of —5°C and subsequently fell into hypothermia. Bats in their natural habitat would probably be able to maintain body temperatures above ambient for extended periods during similar temperature conditions. This view is supported by the observation that unrestrained bats which stayed overnight at —4°C to —5°C still maintained rectal temperatures close to zero.

The observations presented here strongly suggest that the species of bats studied possesses thermoregulatory ability during dormancy. No other reports are available on the metabolic response of bats to subzero temperatures, but a few observations on bats in their natural habitat and laboratory studies at temperatures slightly above zero support this point of view. Although uncertain whether the studied bats were in the process of arousal, both Kayser(12) and Hock(1) found an increased oxygen consumption at ambient temperatures near zero compared to the values found at 5°C. Mislin and Vischer(13) studied a clustered colony of hibernating noctule bats *(Nyctalus noctula)* during the winter and found that while ambient temperature occasionally was as low as —17°C the temperature among the bats never went below —4°C and was always higher than ambient.

Summary. Heart rates and rectal temperatures (T_r) were recorded from inactive bats exposed to stepwise changes in ambient temperature (T_a) in the range between —5°C and 10°C. An increase in heart rate and in the difference (ΔT) between rectal and ambient temperature ($\Delta T = T_r - T_a$) with decreasing ambient temperature below 5°C was found. The bats remained in the dormant state but were able to arouse from dormancy in response to mechanical stimuli. The results indicate that the species of bats studied possess thermoregulatory ability during dormancy and that this ability is a homeostatic mechanism and thus different from the process of arousal.

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