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TEMPERATURE REGULATION IN THE VAMPIRE BAT *DESMODUS ROTUNDUS*

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FOREWORD

The research reported in this paper was prepared under contract AF 41(609)-2296 (Project 8237, Task 823703) with the Department of Zoology, Cornell University, Ithaca, New York, and was supported in part by an N.S.F. research grant (G-24043) to W. A. Wimsatt. This interim report covers research carried on from September 1963 to June 1964. Air Force program monitor is Dr. Eugene Evonuk, ALRP, Arctic Aeromedical Laboratory.

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This technical report has been reviewed and is approved.

HORACE F. DRURY
Director of Research

ABSTRACT

Body temperature and oxygen consumption were measured at various environmental temperatures in a series of captive and wild caught vampire bats, *Desmodus rotundus*. The response to changes in ambient temperatures was unpredictable and could not be correlated with the age or sex of the animals, their nutritional condition, or the length of their captivity. Body temperature varied greatly, but generally did not fall below 30° C when the ambient temperature was above 25° C. At lower ambient temperatures, some bats increased their metabolism and maintained a high body temperature for varying periods, while others showed little or no increase in metabolic rate, and their body temperatures declined. Below about 20° C body temperature, bats were unable to rewarm themselves without exogenous heat. Calculations indicate that vampires did not drink sufficient blood to maintain a homeothermic condition at the temperatures of temperate zone hibernacula. Bats could tolerate ambient temperatures of 33° C or more for only short periods. It is suggested that *Desmodus* is limited from spreading northward because of its inferior temperature regulation.

I

INTRODUCTION

As the comparative studies of temperature regulation continue, it becomes obvious that small eutherian mammals cannot be divided into "homeotherms" on the one hand and "hibernators" on the other. In both the bats and the rodents there are species which do not maintain a steady body temperature yet could hardly be described as "deep" hibernators in the sense which one of us attempted to delineate (1). It is conceivable that there are some advantages to this physiologic middle ground, but it is also possible that the condition is disadvantageous in itself and is forced on the animal because of some anatomical or physiological peculiarity.

The anomalous temperature regulation in bats may be associated not only with their small size, but also with the vascular wing membranes, which impose a problem that is not inflicted on any other order of mammals. While it has been clearly demonstrated that the leathery wings of Pteropus can act as an insulator (2), the paper-thin wings of smaller bats can give but little protection even if properly oriented to the body, and must serve as a source of heat loss (3). Even if vasoconstriction is maximal, some blood must course through the wings and must return to the body chilled to near the temperature of the environment.

On the other hand, wings also give bats an ability to travel distances which would be impossible for terrestrial mammals of similar size. In spite of this ability, many species of bats are very limited in their distribution (4), and the great majority are confined to tropical and semi-tropical regions. The very wings which provide bats with their wide range may actually limit some species from distribution to colder regions, but generalizations cannot be made with our present knowledge, and other factors such as food or adequate shelter may often be of greater importance. Certainly with the large variation in homeothermism among the order as a whole, it is not possible to predict whether a given species would be tolerant to a cold climate. The present study examines these problems in the vampire bat Desmodus rotundus which is a moderately sized species with a sharply limited northern distribution.

The genera Desmodus, Diphylla and Diaemus comprise the only group of true vampire bats. Desmodus ranges throughout Central America, but is not known to occur further north than upper Sonora and Tamaulipas in Mexico. There are no obvious physical barriers to a more northern distribution. Since these bats roost in a variety of places, a lack of shelters could hardly be a limiting factor. Their prey consists of almost any mammal of suitable size, including cattle, and there is an abundance of food well north of their present range. In view of these facts, an inability to survive in low prevailing temperatures appears to be the most likely reason for their restricted northerly range.

A captive colony of vampire bats permitted a series of metabolic measurements to test the responses of this species to extremes of temperature. In addition, similar tests were carried out on a small series of specimens freshly caught in the field in order to be sure that the captive colony had not changed due to prolonged "domestication". The results of these tests lead us to conclude that temperature regulation is poorly developed in this species.

II

MATERIALS AND METHODS

A series of 22 adult and subadult vampire bats (Desmodus rotundus murinus) were used in 26 metabolic tests lasting 1 to 9 hours each. Sixteen individuals came from the captive colony at Cornell University and were tested at an altitude of 815 ft. above sea level while the remainder were newly captured wild animals from Mexico and were tested at 7415 ft.

The animals were housed as previously described (5). They were fed their daily meal of defibrinated blood in the evening, and, since the tests were started either the next morning or afternoon, the bats were presumably in the post-absorptive state. After the bat was weighed, a thermistor was inserted into the rectum to a depth of two cm, and held in place with a restraining device of light brass which loosely circled the body at pelvis and neck. With this device, the bat could move its legs and body freely and partially extend and completely fold its wings. It could not walk freely about the metabolism chamber, which was too small for full extension of the wings. Temperature of bat and chamber were recorded with a YSI tele-thermometer having an accuracy of $\pm 0.5^{\circ}$ C which was calibrated periodically against mercury thermometers (Yellow Springs Instrument Co. Inc., model 44, 12 channel). In six bats of the series, metabolic measurements were made without encumbering thermistor and harness, and rectal temperature was measured manually at the beginning and end of the experiment.

The metabolism chamber was an airtight glass jar of 80 mm diameter and 100 mm height, with a weighted cap through which the chamber and rectal thermocouples had been threaded and sealed. With bat in place, the cap was screwed tight and the jar sunk upside down in a thermostatically controlled water bath. Movement of the bat could be seen through the water and glass. Soda lime on the floor of the chamber served to absorb expired CO_2 and was separated from the bat by wire mesh. A tube from the chamber led to a spirometer of 80 ml capacity which was filled with pure oxygen, and refilled manually when necessary. Readings from the spirometer and the thermistors were usually made every five minutes. Bats were routinely exposed to temperatures between 25 and 34° C until reasonably steady readings were obtained. The bath was then refrigerated and a series of readings made at the new steady temperature. The bat was weighed again at the end of the experiment and the two weights averaged for calculations. All oxygen consumptions were corrected to dry gas at 0° and 760 mm Hg.

III

RESULTS

The bats used in these experiments were either subadult, sexually immature animals, or adults. The bats varied in weight from 18.0 to 42.5 gm, with an average of 30.0 gm. During the test they usually lost less than 1 gm of weight, though losses up to 2 gm were recorded in a few cases, probably due to urination. Rectal temperatures (T_B) taken at the start of the experiment averaged 37.3° C, but varied greatly, the highest being 40.2° C and the lowest 30° C.

The metabolic response of vampires could be characterized by the notable absence of a steady state and a large and unpredictable variation in response from animal to animal. Although the T_B averaged near the expected normal for homeothermic mammals, the animals showed little tendency to regulate their body temperature at this level. If the T_B was near 37° C at the start of the experiment, it almost invariably declined after an indefinite period, even if the ambient temperature (T_A) was as high as 33° C. The rate of the decrease of T_B depended, of course, on the T_A and the metabolic rate, but the latter varied from animal to animal, as well as in the same animal on different days.

Figures 1 and 2 depict the extremes observed in the reactions of the vampires to changes in T_A. In Figure 1 there is little evidence of thermoregulation, and Figure 2 illustrates the maximum thermoregulatory effect recorded in this series of experiments. As illustrated in Figure 1, the T_B started at 33° C and declined slowly to 27°, which was two degrees above the T_A. T_B remained at this level until T_A was reduced, when T_B again declined, and a further reduction in T_A was again followed by a decline in T_B. Each drop in T_A caused a slight rise in metabolic rate and the bat was observed to move briefly in the chamber, but the increase in oxygen consumption did not compensate for the gradient between T_B and T_A, and T_B continued to decline. At the end of the experiment, with a T_B of 17° C the animal could move very slowly and retained the grasping reflex of the hind legs. It regained its normal, active state when removed from the chamber and exposed to room temperature.

Figure 2 illustrates the other extreme. Here the animal had a low metabolic rate at a T_A of 30 to 33° C, and the T_B declined from 39° C. However, when T_A was reduced drastically, the animal increased its metabolic

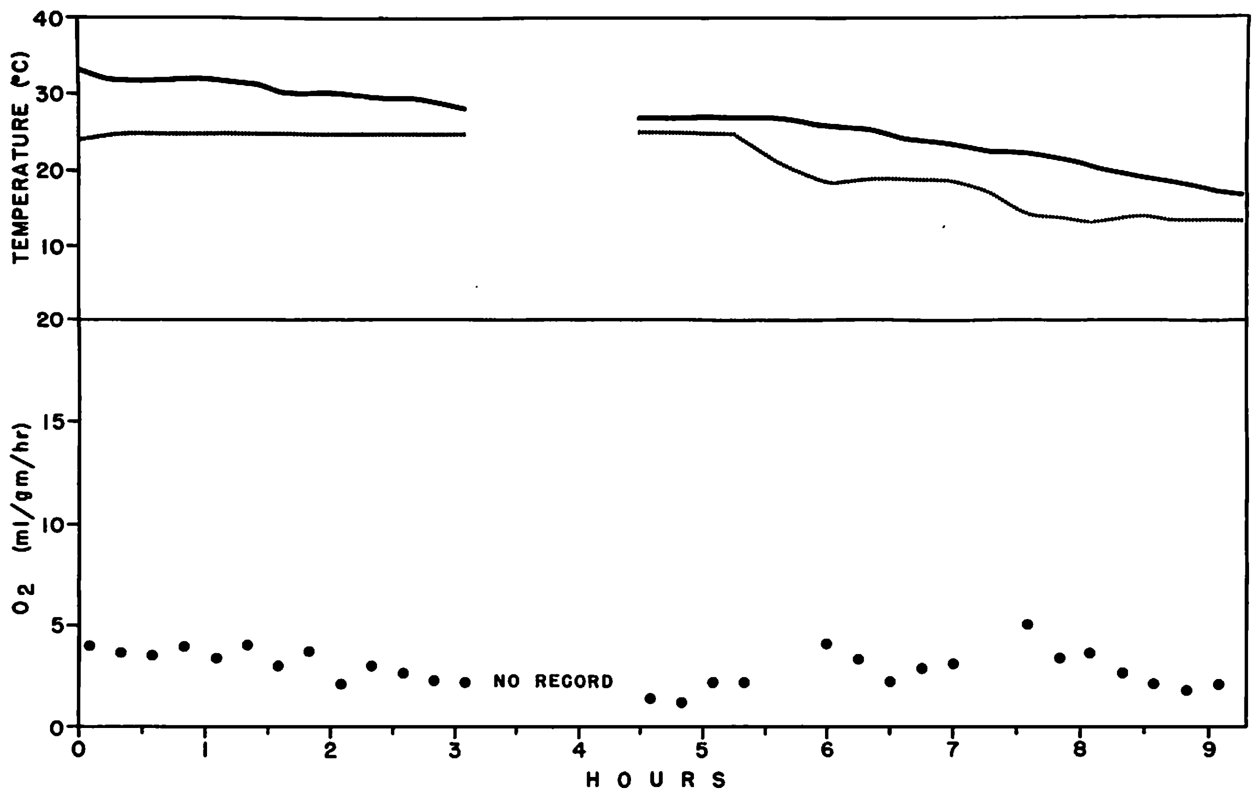

FIGURE 1

Oxygen consumption, rectal temperature (black line) and environmental temperature (dotted line) of a vampire bat, showing minimal temperature regulation. Oxygen consumption = average of three readings taken at five minute intervals.

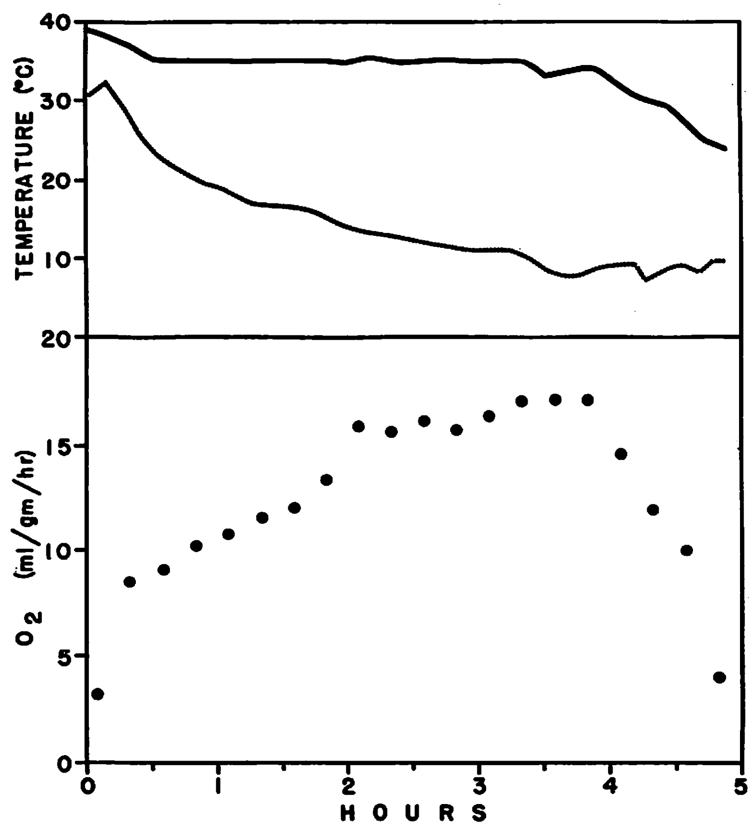

FIGURE 2

Response of bat with good temperature regulation. Symbols as in Figure 1

rate and maintained its T_B above 32^o for more than 3 hours. At the end of this time a reduction of T_A from 11^o to 7.5^o C resulted in a brief increase in O_2 consumption and a slight rise in T_B. After this the T_B began to drop rapidly and the experiment was terminated.

Between the two extremes illustrated here, so many variations occurred that generalizations are difficult. No bat maintained its T_B above 36^o C for longer than 3.25 hours even when the T_A was as high as 32^o. In all cases in which the T_A was held steady for long periods, the T_B eventually declined to a level which was 2 to 3^o above T_A, and remained at that temperature until T_A was changed. The amount of oxygen consumed in this semi-poikilothermic state was temperature-dependent, being less at the lower body temperatures. Below a T_B of about 25^o C the bats offered little resistance to further cooling, and oxygen consumption rarely increased at all when the T_A was lowered further. It is probably significant that there was definite deterioration of muscular coordination at about this T_B.

Muscular coordination showed no obvious impairment at rectal temperatures of 32 to 33° C. At 31° the movements were noticeably slower, although one animal responded to a visual stimulus of bright light by turning its head. There was no response to this stimulus at 29°, though bats moved and struggled against the harness at body temperatures varying from 25 to 19.5°C. The lowest T_B recorded was 17° C, as described above, but several animals recovered from body temperatures between 23 and 20° C. However, two other animals died at higher body temperatures, one at 27° C. There is no evidence that the thermocouple harness limited the ability of the bats to respond to cold, for unharnessed bats always had lower body temperatures after the experiment than at the start.

In the series of 22 bats, a total of 9 were able to attain metabolic rates of at least 10 ml/gm/hr for periods of 20 minutes to 3-1/2 hours, the highest recorded metabolic rate being 18.5 ml/gm/hr. On the other hand, five bats showed no tendency to maintain a high body temperature by increasing their metabolic rates. The responses of the remaining bats fell between these two extremes. There was no correlation between the size of the animal and its ability to increase its metabolic rate when challenged by a low T_A, nor was the state of nutrition a factor, for the reaction of animals tested in the morning was the same as those tested in the afternoon. The unpredictability of the response may be emphasized by the observation that some animals maintained a low oxygen consumption and allowed their T_B to decline at one T_A, while they increased their metabolic rate at a lower T_A. There was no evidence, however, that ambient temperatures near 0° C more consistently stimulated the metabolic rate than temperatures between 10 and 20° C.

Of the nine bats which attained an oxygen consumption above 10 ml/gm/hr, seven were females and the sex of the other two was undetermined. It is doubtful, however, that females are capable of a higher metabolic rate than males, since in our sample the females outnumbered the males two to one due to chance. Furthermore, several other females showed no increase in their metabolic rates when exposed to a lower ambient temperature. There was also no evidence that bats kept in captivity responded less vigorously than those recently captured from the wild.

Bats were more apt to struggle against the restraining harness at ambient temperatures below 25° C, and shivering occasionally occurred before the bats became moribund from cold. The wings were usually partially extended, and not wrapped around the body for insulation. We made no measurements of blood flow in the wings, but, even in bats which were moribund, the small vessels were suffused with blood and there was no gross evidence of vasoconstriction. In the captive colony and in the wild, vampires often but not invariably huddle together when at rest, so that behavioral thermoregulation may occur.

Because of the variable response to changes in T_A it was not possible to establish a basal metabolism, thermal neutral zone or critical temperature. However, in considering the ecology and energetics of the species it is desirable to have some estimate of the metabolic rate during natural "rest", even in the absence of a steady state. Previous measurements (6) had established that the temperature of vampire roosts varied between 21 and 27° C. In our series, eight vampires remained at ambient temperatures between these limits for periods of 30 minutes to 5 hours. Some of these animals were "regulating" their T_B above that of the environment while others were not. The average O_2 consumption for this group was 3.0 ml/gm/hr, while the high and low averages for the individuals over the particular period were 4.3 and 2.4 ml/gm/hr respectively.

A systematic study of rewarming after chilling was not undertaken. Animals whose T_B was in the mid-twenties were able to rewarm at room temperature. One animal warmed from a T_B of 28.5 to 35° C at a T_A of 27° in 85 minutes. Animals with body temperatures of 20° C or below were so sluggish that they could be rewarmed in the hands without fear of being bitten, and it seems most unlikely that any natural stimulus could cause them to rewarm without heat from exogenous sources. In no case did the rewarming approach the rapidity of the arousal of vespertilionid bats from hibernation.

Vampires tolerated high ambient temperatures better than was to be expected from earlier observations (7). During part of the routine metabolic tests 10 bats withstood ambient temperatures of 31 to 34° C for periods lasting from 15 to 30 minutes with no apparent ill effects. Another animal appeared normal after 130 minutes at 33 to 34° C, but still another died after exposure to 32 to 33° C for 150 minutes. In all but one of these 12 observations the T_B was between 37.5 and 40° C at the start of exposure to the warm temperature and declined 0.5 to 2° C during this time. In the other case the T_B was 36° C and rose to 40° C in 15 minutes. No behavioral reaction such as salivation or fanning of wings for heat dissipation occurred in any animal.

IV

DISCUSSION

Some Megachiroptera and Microchiroptera can be regarded as highly specialized as far as temperature regulation is concerned. Among the Megachiroptera, the relatively small-sized Syconycteris (2) and Rousettus (8) and the large Pteropus (2, 9, 10) can maintain reasonably stable T_B as adults, usually using their wings either as an insulator or a heat dissipation mechanism.

In contrast, the small microchiropterans of temperate climates usually, but not invariably, lower their body temperature with cessation of activity (11), and enter into prolonged periods of hibernation during the winter months. This type of temperature regulation has often been regarded as poikilothermic, yet the bats are capable of rewarming themselves spontaneously using only endogenous heat. The physiology of hiberation in bats has not been thoroughly documented, but it is reasonable to assume that it involves many of the same adaptations as in rodents and insectivores, including tolerance to very low body temperatures (12) and precise control of circulation during arousal from hibernation. Thus this group has met the problems of small size and cold climate with definite specializations.

A third group of bats cannot be classified as homeotherms or as hibernators, and, though they have some of the attributes of both, they have the specializations of neither. Here we would include the vespertilionid bent-wing bat, Miniopterus (9), the molossid free-tailed bat, Tadarida (13), two species of Rhinolophid horse-shoe bats (9), the phyllostomid leaf-nosed bat, Macrotus (14), and the desmodontid vampire bat studied here.

The vampire has some ability to control its body temperature, but it is clear that T_B is not "set" near 37° C. In all of the bats tested, T_B dropped below 37° C soon after the start of the experiment, and there was a wide variation in T_B of animals taken at random from the colony. Though vampires usually reacted to a low T_A by increasing their metabolic rate, the response was not invariable, and there was no evidence that a certain ambient or body temperature set the heat production mechanisms in motion. Miniopterus also has a labile body temperature, but Morrison has shown that these bats tend to maintain their T_B above 30° C, and quotes Slonim's similar evidence for another species of Miniopterus, for Myotis myotis and, to a lesser extent, for Rhinolophus. Herreid (13) found that freshly caught Tadarida mexicana invariably increased their oxygen consumption at environmental temperatures below 30° C and that most individuals maintained their T_B above this temperature, even at T_A of 5° C. Macrotus californicus maintains a T_B of about 36° at a T_A as low as 25° C, but cannot maintain this T_B below a T_A of 20° C (14). In Miniopterus, Tadarida, and Desmodus, a T_B of approximately 30° C is a critical one, for below this coordination deteriorates rapidly and the animals are unable to fly. In spite of this, Desmodus makes no extra effort to hold its T_B above 30° C. Captivity impaired the ability of Miniopterus and Tadarida to maintain a high T_B, suggesting that thermoregulation is in delicate balance in these animals. Desmodus, with its less precise and predictable thermoregulation, is apparently unaffected by captivity.

The failure of a low T_A to stimulate oxygen consumption in some vampires is reminiscent of a hibernator entering hibernation. The similarity ceases here, however, for no vampire, whether it resisted chilling or not, was capable of rewarming itself from a T_B below 20° C, without heat from external sources. Furthermore, unlike the typical hibernator, a T_B below 30^o C was unfavorable and two animals died during the chilling experiments. One must conclude that the low body temperatures are simply a manifestation of imperfect temperature regulation.

The unpredictability in response to cold seems typical of this species, and has previously been noted even in vampires which were supplied with food (7). With such variations, calculations of the energetics can have no precision, yet they may offer clues concerning the vampire's metabolic budget. The figures indicate (see Results) that bats under our experimental conditions metabolized at an average rate of 3.0 ml/gm/hr at ambient temperatures between 21^o and 27^o C, which is the temperature of their roosts. This compares to an average rate of 2.0 ml/gm/hr for Myotis lucifugus at T_A 30^o C (15), 2.2 to 5.8 ml/gm/hr for Eptesicus fuscus which remained active for 24 hours or more at T_A 25^o to 30^o C (11), 1.67 ml/gm/hr for Tadarida brasiliensis at T_A 30^o C (16) and 1.9 ml/gm/hr at its thermal neutral point of 33^o C for the small megachiropteran, Syconycteris australis (2).

Wimsatt and Guerriere (6) have reported that a captive 28 gm vampire ingests 12.7 kcal of digestible energy each day. At 3.0 ml O_2/gm/hr, the metabolic rate of a 28 gm bat is 9.1 kcal/day. Although the closeness of the figures may be fortuitous, still they indicate that the estimate of the basal condition is of the correct magnitude. These calculations do not include the energy involved in night flight for wild vampires. However, the bat used in Wimsatt and Guerriere's calcuations consumed an average of 20.3 ml of blood/day, while another animal of the same weight drank 52 ml in a single day. Thus there is great variation in energy intake, and the calculations and observations agree that the bats can remain in metabolic balance at ambient temperatures of 21^o to 27^o C.

The vampire may respond to lower ambient temperatures either passively or by a maximum effort. If the former occurs, the problem is not one of energy expenditure, but recovery from hypothermia. Oxygen consumption roughly parallels the decline in T_A, but T_B also declines, and the bat is unable to rewarm itself when T_B approaches 20^o C. Under natural conditions it would die unless its roosting place became warmer.

The experiment illustrated in Figure 2 is typical of several cases in which the vampire increased its metabolism in response to cold. The peak metabolism was high (17 ml O_2/gm/hr), though not as high as found in the small shrew, Sorex cinereus (17), and the rapid decline in O_2 consumption after four hours indicates that the animal was exhausted. This 26 gm bat used 7.4 kcal during the five hour period, and at this rate would have used 35.6 kcal in 24 hours. With an intake of about 12 kcal/day the bat would be far short of the needed energy and, even if it equalled the maximum recorded consumption of 52 ml blood (or twice its own weight), it would still be out of balance.

Wimsatt (7) records one vampire that was apparently well at the end of 60 hours' exposure to $3^{\circ} - 5^{\circ}$ C but died a few hours later, while others became moribund within a 24 hour period, one in less than 2 hours. We are unable to explain the variations, and determination of the lowest tolerable T_A for a series of vampires seems pointless, but it is clear that heat conservation in this species is very poorly developed. Certainly a population would be in severe difficulty if the bats were forced to roost at temperatures found in the caves of temperate areas.

As far as tolerance to high ambient temperatures is concerned, our experiments indicate that vampires can live at 33° to 34° C only for short periods. The T_B almost invariably declined in bats exposed to temperatures in this range, even in the animal that died in two hours, indicating that the cause of death was not explosive temperature rise, as is usually the case in animals under heat stress. There was no visible sweating or salivation, but evaporation from the lungs must have been high to cause the body to cool at such high temperatures, and desiccation may have contributed to death.

Thus it may be concluded that Desmodus has some defenses against extremes of temperature, but these defenses are in no way comparable to those of a terrestrial mammal of the same size. As a homeotherm, Desmodus ranks near the bottom of that group of microchiropterans which have not developed the specializations of hibernation. Vampires show no evidence of using their wings for insulation and it is probable that heat loss through them is very high. The temperature regulation of vampires is erratic, and probably the only time it is in a true steady state is during flight. Desmodus is evidently neither a hibernator nor a capable homeotherm, and it may well be that this physiologic weakness alone limits its distribution to tropical and semi-tropical areas. In view of the vampires' adverse effect on the economy and public health, this is indeed fortunate.

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