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# Temperature Relationships of the Western Pipistrelle (*Pipistrellus hesperus*)<sup>1</sup>

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BATS INHABITING temperate regions commonly avoid the lower environmental temperatures of fall, winter, and early spring by either migration or hibernation. A few exceptions have been noted in the literature for areas in the southwestern United States. In those areas certain species have been found to be active throughout the winter or during the warmer periods of winter (Grinnell, 1918; Alcorn, 1944; Reeder and Cowles, 1951; Twente, 1960; Cross, 1965; and Stones and Wiebers, 1965). O'Farrell, Bradley, and Jones (1967) have reported a significant amount of activity in two species, *Pipistrellus hesperus* and *Myotis californicus*, at low  $T_A$  (air temperature) in the fall and winter months in southern Nevada.

Temperate zone bats exhibit unique thermoregulatory behavior by a daily cycle of homeothermic and poikilothermic states (Kayser, 1939, 1961; Eisentraut, 1960; Hock, 1951; Herreid, 1963; and others). Although exceptions have been noted, especially in tropical and subtropical species, bats which regularly hibernate tend to show an inability to maintain a high and relatively constant  $T_B$  (rectal temperature) when inactive (Burbank and Young, 1934; Morrison, 1959; Bartholomew, Leitner, and Nelson, 1964; Kulzer, 1963; Slonim, 1952; Leitner, 1966; Stones and Wiebers, 1965). Therefore, bats have been more properly classified as heterotherms by Hock (1951), who stated

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that bats are different from other heterotherms because their  $T_B$  approaches  $T_A$ , when inactive, throughout the year. In contrast, active bats are thought to thermoregulate effectively and to maintain a high and relatively constant  $T_B$ . We found bats to be active over a wide range of  $T_A$  and therefore believed further study of thermoregulation was warranted.

The western pipistrelle, *Pipistrellus hesperus*, is ideally suited for such a study. It is the most common bat in southern Nevada and is active at dusk and at dawn. This activity pattern facilitates observation. The species is a weak, erratic flier which is easily captured in mist nets. It is active over a wide range of  $T_A$ . Due to its small size (3.5-5.5 g) and sparsely haired wing and tail membranes, it should have difficulty thermoregulating in flight.

#### STUDY AREA

White Spot Spring, at an elevation of approximately 4,460 ft, is located on the north-facing slope of the Las Vegas Range, Desert Game Range, Clark County, Nevada. The spring flow is contained within a stone tank, which is approximately 11.5 ft square and 2 ft deep. The tank is usually filled with water. The surrounding area consists of rolling hills covered by sparse desert vegetation. The steep cliffs of Fossil Ridge situated approximately 1 mile from the spring are suitable for roosting sites for western pipistrelles.

#### METHODS

*Field study.* A mist net was set over the spring tank for a total of 70 nights during the period of February 1962 to September 1967. The net was set for at least 4 nights for each month of the year. The net was tended for several hours after dusk, or in many instances, for the entire night.

Air temperatures taken at 30-min intervals while netting have been supplemented by recording thermograph records for much of the time since March 1964. Time of capture and  $T_A$  were recorded when each bat was netted. Rectal temperatures of netted bats were taken with a Schultheis quick-registering mercury thermometer inserted 8 mm into the rectum. Their  $T_B$  was taken within 30-60 sec from the time the bat was netted, thereby approximating the  $T_B$  during flight.

*Laboratory experiments.* Bats collected at the study area were transported to the laboratory and kept at room temperature for 1 to 3 days.

The bats were then transferred to a refrigerator that was maintained at approximately 0 C.  $T_B$  was checked periodically and the bat was removed at a  $T_B$  below 15 C.  $T_B$  was usually lowered to this level within 30 min. Most bats shivered excessively upon removal and the  $T_B$  reached 25 C or above within 5 to 10 min. At approximately 1 C intervals the bats were glided out over a net after their wings were stretched. Flight was considered successful when the bat flew around the laboratory without loss of altitude.

Inactive bats were placed in a reconditioned refrigerator with a wide range of  $T_A$  from below 0 to above 55 C. Both  $T_A$  and  $T_B$  were obtained with a Yellow Springs telethermometer. Thermister probes were inserted 8 mm into the rectum and held in place by cementing the hairs around the rectum to the probe.

#### SEASONAL ACTIVITY

Seasonal activity over the spring area is indicated in Figure 1. A total of 648 *P. hesperus* (214 ♂ and 434 ♀) were netted during the study period. Larger numbers were netted in the warmer months of June, July, and August than at other times of the year.

Various factors may influence activity or net captures over water. Cockrum and Cross (1964) have pointed out that pregnant and especially lactating females may require more water than males and may be unable to maneuver and avoid a mist net as readily as nonpregnant females or males. Jones (1966) has shown seasonal population shifts that are correlated with precipitation and availability of water. These factors may help explain the preponderance of females captured from June to August. Air temperature remains, however, as one of the more important environmental variables influencing activity.

Western pipistrelles exhibit some activity throughout the night, but have an activity peak approximately 1 hr after sunset (Cockrum and Cross, 1964; Mumford, Oakley, and Zimmerman, 1964; Jones, 1965; and O'Farrell et al., 1967). Cross (1965) observed that flying is restricted to the evening hours during the winter. O'Farrell et al. (1967) found no evidence of morning activity during the fall and winter.

A peak of activity shortly after sunset is apparent for all months of the year (Fig. 2). From December to March, activity over the spring is concentrated mainly in the 2 hr after sunset. A slightly more prolonged period of activity is indicated for May and September-November. The nights on which we have netted at the spring in April

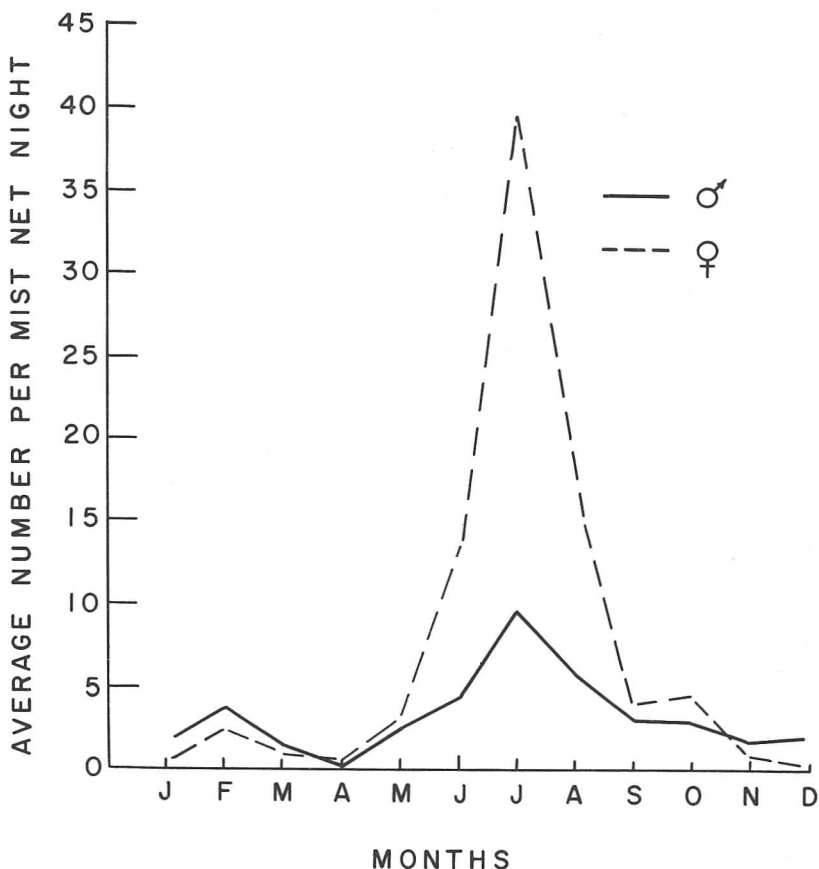


FIGURE 1. The average number of *Pipistrellus hesperus* netted per mist-net night for monthly periods.

have all been unusually cold or windy and this has resulted in a low number of captures and a reduced span of activity. In the fall, winter, and early spring the activity peak coincides with the highest  $T_A$ . During the warmest months of the year, activity occurs throughout the night and is probably due to optimum  $T_A$  and an increased need for drinking. The additional food and water requirements of pregnant or lactating females may also prolong activity.

Activity around the spring occurs over a wide range of  $T_A$ , with pipistrelles being netted from  $-5$  to  $31$  C. Figure 3 shows the number

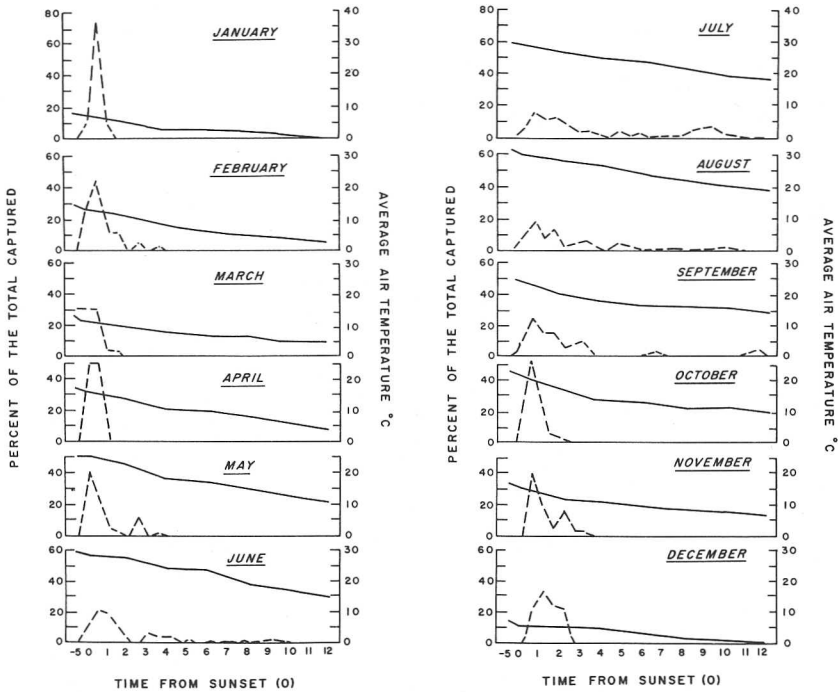


FIGURE 2. The relationship between average monthly air temperature (solid line) and time of activity (broken line) of *Pipistrellus hesperus* for different times (in hours) following sunset.

of pipistrelles netted per mist-net hour at  $T_A$  intervals of 3 C. It is readily apparent that activity is greatly reduced at  $T_A$  from -5 to 12 C. Optimum  $T_A$  for foraging and drinking seems to be between 16 and 30 C. This optimum range may extend above 30 C where instances of higher  $T_A$  are encountered.

BODY TEMPERATURES

The low  $T_A$  at which pipistrelles fly in the fall and winter would increase food requirements and place severe strain on the bats for effective thermoregulation. The  $T_B$  of 248 pipistrelles (89 ♂ and 159 ♀) were grouped by monthly intervals in relation to the  $T_A$  at which they were netted (Fig. 4). There appears to be a positive relationship between the mean monthly  $T_A$  and  $T_B$ . Mean  $T_B$  varied from 24.8 C

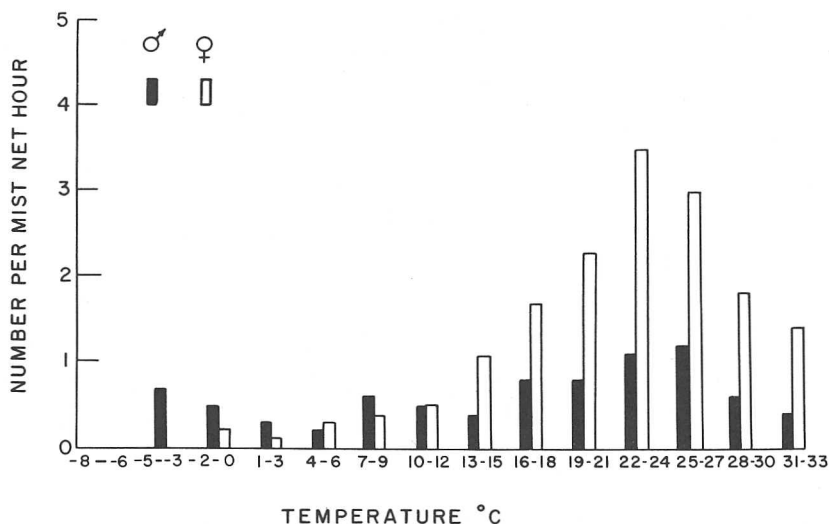


FIGURE 3. The average number of *Pipistrellus hesperus* netted per mist-net hour at different temperature intervals.

in April to 35.5 C in August, a range of 10.7 C. The mean  $T_A$  varied from 8.0 C in April to 23.8 C in August, a range of 15.8 C. Western pipistrelles do not exhibit effective thermoregulation during flight over a wide range of  $T_A$ .

In Figure 5 the  $T_B$  of both netted and inactive bats are plotted against  $T_A$ . The correlation coefficient of 0.880 for netted pipistrelles is significant ( $P < 0.01$ ). The line for inactive bats is based on the  $T_B$  of four females which were used in laboratory experiments to determine warming and cooling rates. Since the  $T_A$  in the modified refrigerator varied at a rapid rate,  $T_B$  did not have sufficient time to stabilize at a given  $T_A$ . However, the close approximation of  $T_B$  to  $T_A$  for inactive bats is well known (Stones and Wiebers, 1965). The present data allow a comparison between the curves for active and inactive pipistrelles. Both curves, although they differ considerably in slope, do show a positive correlation between  $T_B$  and  $T_A$ . These differences are greatest at the lower temperatures. At low  $T_A$  the inactive bat is dormant and the flying bat has a steep thermal gradient between body and air. Poor thermoregulation of pipistrelles in flight at lower  $T_A$  is clearly indicated.

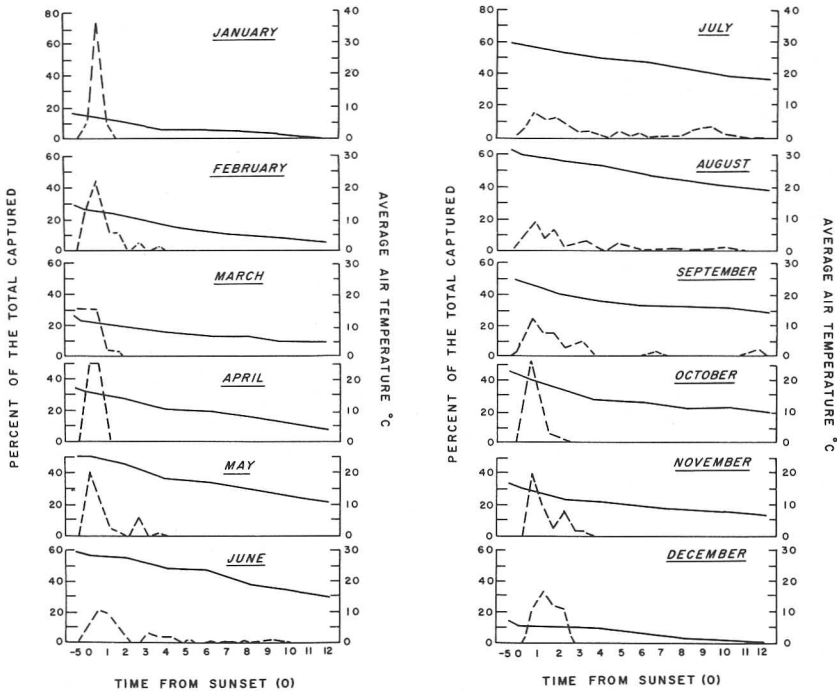


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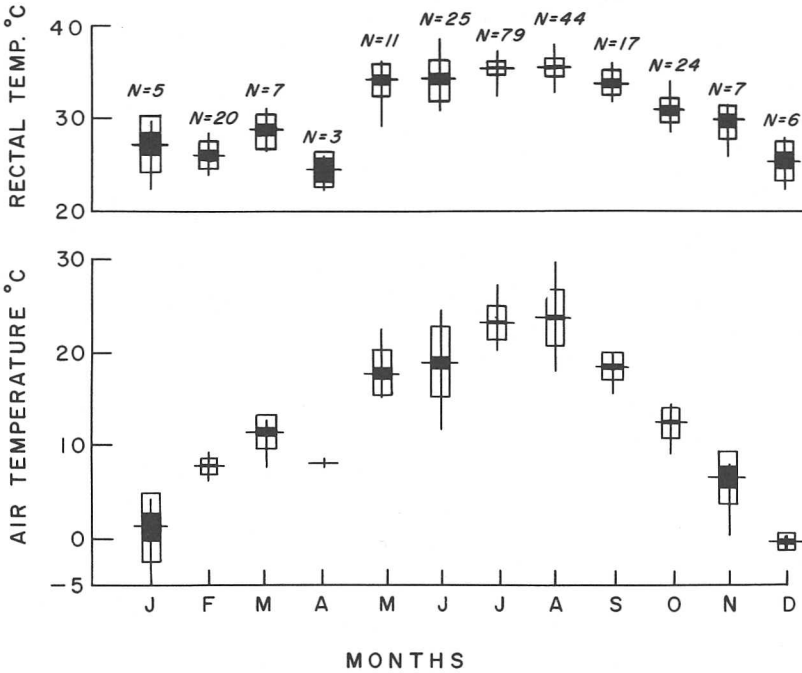


FIGURE 4. The relationship between air temperature and rectal temperature of flying *Pipistrellus hesperus*. Sample size for each month is shown above the range of rectal temperature. Vertical lines indicate ranges; horizontal lines indicate means; hollow rectangles indicate one standard deviation; solid rectangles indicate one standard error of the mean.

However, there is evidence for adequate thermoregulation during flight at higher  $T_A$ . Cowles (1947) and Reeder and Cowles (1951) have observed vasodilation in the wings of bats exposed to high  $T_A$  and consider that wing flapping is an effective means of thermoregulation at high  $T_A$ . In our experiments on cooling and warming rates we have noted extreme vasodilation of the blood vessels in the flight membranes at  $T_A$  above 40 C, and this is accompanied by fluttering of the wings. We have kept pipistrelles in flight in the laboratory for periods of up to an hour; they effectively thermoregulated throughout these periods and had a  $T_B$  close to that of netted bats in the same  $T_A$  range. For example, a female with an initial  $T_B$  of 29.5 C was flown for 25 min. Within 5 min her  $T_B$  had risen to 38.2 C. After an additional 20 min it was 37.8 C. We determined the upper lethal

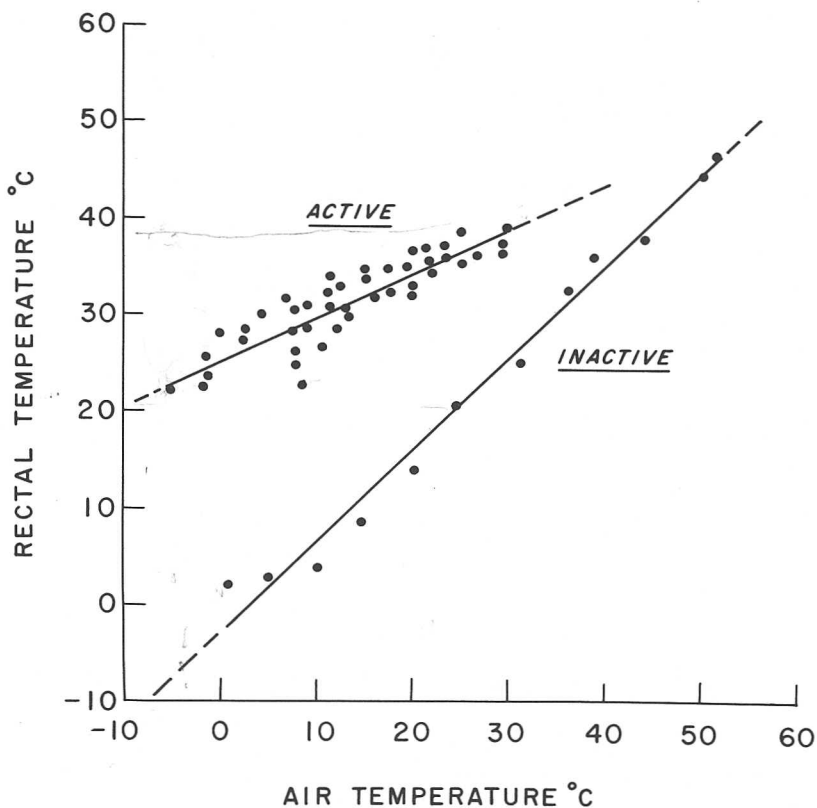


FIGURE 5. The relationship between air and rectal temperatures of active and inactive *Pipistrellus hesperus*.

$T_B$  as approximately 45 to 46 C at  $T_A$  of 55-60 C. A female that appeared near death and had a  $T_B$  of 47 C launched herself from the hand and began flying rapidly around the laboratory. She was captured after approximately 1 min of flight and had a  $T_B$  of 35 C. The loss of 12 C of  $T_B$  is surprising and can be taken as evidence for effective thermoregulation during flight at high  $T_A$ .

#### MINIMUM BODY TEMPERATURES FOR FLIGHT

Observation of low  $T_B$  of flying pipistrelles led to a series of tests designed to ascertain the lowest  $T_B$  at which flight was possible. Bats used for these experiments were captured in both winter and sum-

mer. Pipistrelles of a series captured in August were placed in an environmental chamber at a  $T_A$  of approximately 10 C for a 1-week period and then tested. The results of these experiments are given in Figure 6. The mean  $T_B$  for flight are all above the lowest  $T_B$  (22.2 C) obtained in the field in December. This 22.2 C is lower than any flight-trial  $T_B$  with the exception of one of 20.2 C from a bat that had been in dormancy for a week at 10 C. The low  $T_B$  obtained after dormancy is difficult to interpret. We have no evidence for ability to fly at a lower body temperature in winter than in summer. However, it is possible that pipistrelles can fly at a lower body temperature after a short period of hibernation. The possibility of acclimation to lower winter temperatures should be further studied.

In former studies the generalization has been made that the minimum  $T_B$  for flight in bats is about 30 or 31 C (Morrison, 1959; Herreid, 1963; Burbank and Young, 1934; Twente and Twente, 1964;

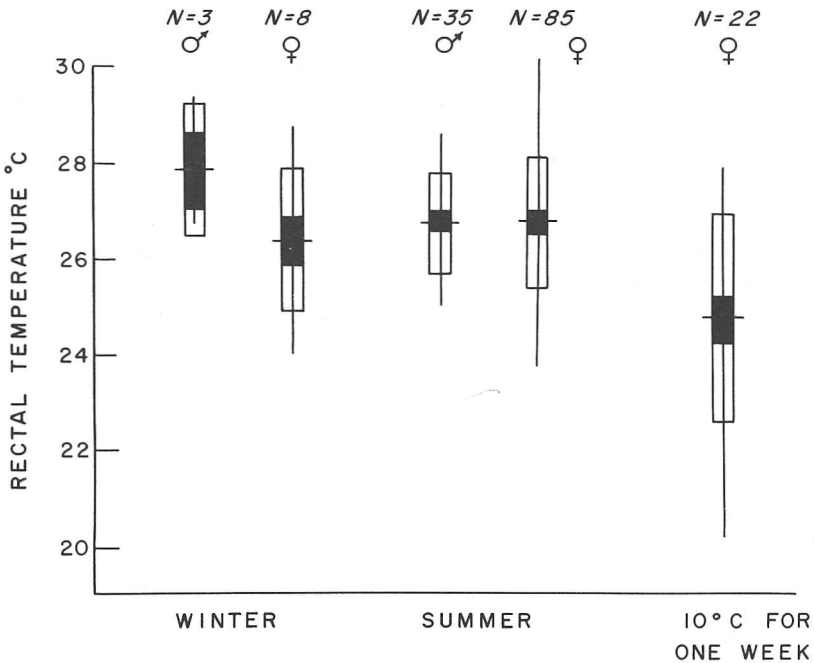


FIGURE 6. Minimum rectal temperatures for flight of *Pipistrellus hesperus*. The mean, range, one standard deviation, and one standard error of the mean are given. Symbols as in Figure 4.

Reeder and Cowles, 1951). Birds have been known to fly at  $T_B$  of 34 C (Miller, 1950; Marshall, 1955). However, Reeder and Cowles (1951) reported a minimum flight temperature of 24.3 C for *Plecotus townsendi* and this is near the temperatures that we report for *Pipistrellus hesperus*.

#### DISCUSSION

Pearson (1948) has pointed out that reduced size, large surface area, and metabolic requirements of flight place some bats in a precarious position with respect to energy requirements. Hibernation and daily dormancy, with a reduction in metabolic rate, result in a corresponding saving of energy. The lower  $T_B$  of active western pipistrelles represents additional conservation of energy not only from a reduction in metabolism during flight but also from a lowering of the temperature gradient between body and air.

The typical roost for this species is a rock crevice which apparently does not provide the lower, relatively constant  $T_A$  and high humidity typical of most cave hibernals (Twente, 1955; Cross, 1965). Twente further suggested that  $T_A$ 's averaging above 12 C would exhaust the fat reserves of the smaller-bodied species of bats and therefore would be unsuitable for hibernation. It is probable, then, that western pipistrelles which roost in crevices do not enter into prolonged periods of hibernation but must leave the roost during the winter to obtain both food and water. This may be a logical explanation for the low activity levels throughout the colder months.

Eisentraut (1960) considered hibernating bats to be the most imperfect thermoregulators among mammals. He and others have suggested that mammals which possess labile  $T_B$  are primitive (Eisentraut, 1960; Hudson and Bartholomew, 1964; Cade, 1964). However these so-called primitive mammals span several orders and include such diverse groups as monotremes, marsupials, insectivores, edentates, rodents, and bats. McNab (1966) has suggested that low  $T_B$  accompanied by thermal lability may be considered as ecological specialization and therefore convergent evolution. Twente and Twente (1964) have argued quite convincingly that heterothermy in bats was derived from homeothermy. This heterothermy, so characteristic of temperate-zone bats, has given them a selective advantage through thermal and metabolic economy, over other homeothermic mammals.

McNab (1966) has used the term *facultative poikilothermy* to de-

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