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FALL METABOLISM IN RELATION TO AMBIENT TEMPERATURES IN THREE SPECIES OF *MYOTIS*

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Abstract—1. A zone of thermoneutrality exists for adult female *Myotis thysanodes* in early September in an ambient temperature range of 32·5–34·5°C with minimum metabolism of 1·74 cm^3/g per hr.

2. A transition from a homeothermic to a non-homeothermic metabolism to ambient temperature relation is evident by late September in adult female *M. thysanodes*.

3. In early September, some adult female *M. yumanensis* exhibit a homeothermic metabolism to ambient temperature relation while others exhibit a non-homeothermic relation.

4. In early September, adult *M. lucifugus occultus* of both sexes exhibit a non-homeothermic relation.

5. At ambient temperatures above 32·5°C, metabolism in *M. thysanodes* increases at a significantly more rapid rate than in *M. lucifugus occultus*.

6. A critical thermal maximum ambient temperature of 44·5°C has been found for each of these three species.

INTRODUCTION

OXYGEN consumption and temperature regulation for many species of *Myotis* have been studied extensively (Hock, 1951; Reite & Davis, 1961; Henshaw & Folk, 1966; Stones & Wiebers, 1965, 1967). Recently, Licht & Leitner (1967) reported metabolic activity for *Myotis yumanensis* in high ambient temperatures. Stones & Wiebers (1967) reported seasonal oxygen consumption in *M. lucifugus*. Although *M. lucifugus* has been dealt with frequently, only the eastern subspecies has been used. The present study is concerned with *M. lucifugus occultus* (Findley & Jones, 1967), *M. yumanensis* and *M. thysanodes*. These species roost sympatrically in maternity colonies from late spring to early fall in the attic of Montezuma Seminary, Montezuma, San Miguel Co., New Mexico (Studier, 1968). Variations in metabolism–ambient temperature relationships may indicate physiological species differences coinciding with morphological differences within the three species.

MATERIALS AND METHODS

Adult bats of both sexes were routinely collected at about 08.00 hr from the attic of Montezuma Seminary on various dates from 9 to 25 September 1969. Bats were immediately brought to the laboratory where four were weighed and placed in the exposure chambers under dim light conditions. Air was conducted through a drying column before entering the apparatus, and metabolism was determined using the technique of Studier *et al.* (1967). *Myotis thysanodes* were studied at intervals of 4°C throughout the ranges of 26·5–46·5°C, 28·5–44·5°C, 24·5–4·5°C and 22·5–6·5°C. Four animals were studied in each ambient temperature (T_a) range resulting in a total of sixteen animals studied at 2°C intervals from 4·5 to 46·5°C. Ambient temperature in the exposure chambers was maintained within 0·3°C of the desired level. Eight *M. lucifugus occultus* and four *M. yumanensis* were tested in T_a's from 16·5 to 44·5°C. A final group of four *M. thysanodes* was tested in late September in T_a's from 32·5 to 4·5°C. Bats were found to come to constant metabolic rate about 2 hr after their introduction into the metabolic chambers. Data were collected at 10-min intervals until readings stabilized for three successive readings. T_a was then changed by 4°C and readings begun again. Upon conclusion of each experiment, bats were reweighed and mean body weight determined and used to calculate oxygen consumption. All data were corrected to dry air at standard temperature and pressure. Regression lines were calculated using mean oxygen consumption of all bats tested at any given T_a except where indicated otherwise.

RESULTS

The relationship of oxygen consumption (OC) to T_a in *M. thysanodes* in early September (Fig. 1) is a homeothermic response. A zone of thermoneutrality exists in a T_a range from 32·5 to 34·5°C with mean experimental OC of 1·74 cm³/g per hr

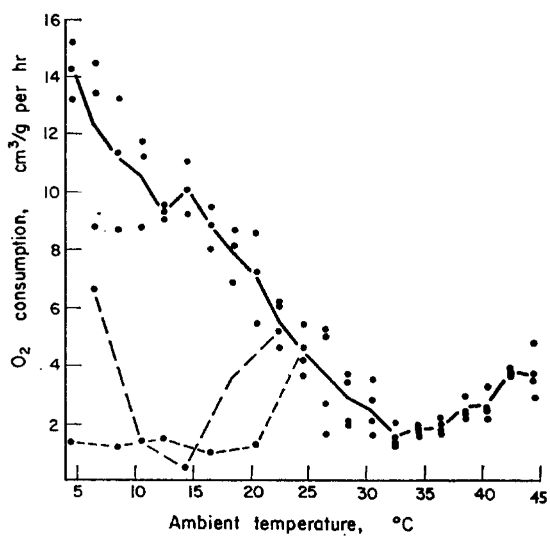

FIG. 1. The relationship of OC–T_a in adult female *M. thysanodes* taken in early September. Each dot represents an individual reading. The solid line connects the means excluding several aberrant readings; these aberrant readings are separated by individual bats and connected by the dotted lines.

(S.E. $\bar{x} = 0{\cdot}092$; $n = 8$). A regression line, calculated by the method of least squares, for T_a-metabolism data of *M. thysanodes* below and above the zone of thermoneutrality, results in the respective equations:

$$OC = 15{\cdot}5 - 0{\cdot}429\ T_a \quad (1)$$

and

$$OC = 0{\cdot}239\ T_a - 6{\cdot}61. \quad (2)$$

Solving these equations simultaneously, one finds a calculated minimal metabolic rate of 1·30 cm^3/g per hr at a thermoneutral point of 33·1°C. Maximum measured metabolism in the *M. thysanodes* ranged from 13·3 to 15·2 cm^3/g per hr at 4·5°C. Critical ambient temperature and upper critical temperature (Stones & Wiebers, 1967) are 30·5 and 38·5°C, respectively.

Responses of *M. thysanodes* to high temperatures were uniform. At 40·5°C these bats started showing signs of wetness on the fur and when T_a reached 44·5°C all bats showed signs of distress. The fur was wet and matted, although lapping of the fur was not observed, and water was observed in the tubes leading out of the exposure chambers. *M. thysanodes* died within a $\frac{1}{2}$ hr at 44·5°C. Post-mortem examination revealed that the prime areas of wetness were the middle of the back and the abdomen, with some moisture about the shoulders.

Although most *M. thysanodes* exhibited homeothermic-like metabolism, two individuals tested at low T_a's in early September were not included in the calculations inasmuch as they exhibited a non-homeothermic-like metabolism. This physiological transition is nearly complete for *M. thysanodes* by late September (Fig. 2). At that time, *M. thysanodes* did not exhibit a thermoneutral zone. They do, however, exhibit increased OC at T_a's below 10°C, reaching a mean peak metabolism of 6·87 cm^3/g per hr at 4·5°C.

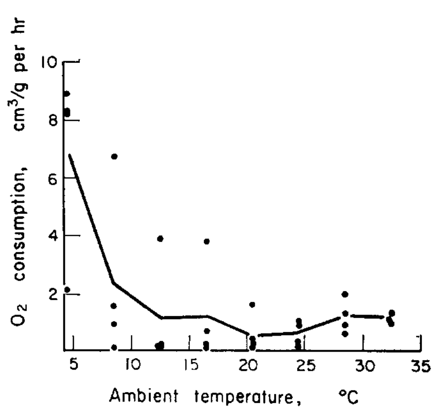

FIG. 2. The relationship of OC–T_a in adult female *M. thysanodes* taken in late September. The symbols used are the same as in Fig. 1.

The relation of OC and T_a in *M. lucifugus occultus* in mid-September is shown in Fig. 3. Like the late-September *M. thysanodes*, this species exhibits a non-homeothermic-like metabolism–T_a response. A few individuals showed unusually high OC at 16·5°C, which may be valid measurements or a case of non-equilibrium at the initial tested T_a.

The response to high T_a in *M. lucifugus occultus* was similar to that observed for *M. thysanodes*. All *M. lucifugus occultus* died within a ½ hr at T_a of 44·5°C. One bat had a wet back, while the others had a wet muzzle and throat, with a damp to wet abdomen. No water was observed in the tubes leading from the chambers.

The relationship of OC to T_a in *M. yumanensis* in mid-September is shown in

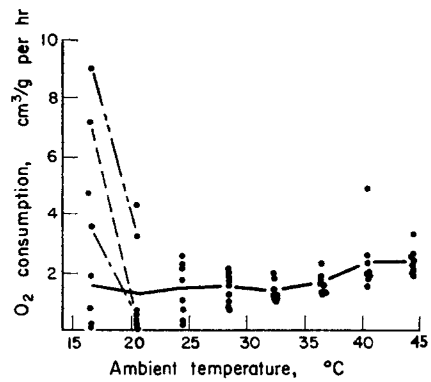

FIG. 3. The relationship of OC–T_a in adult *M. lucifugus occultus* taken in early September. Two females and six males were used. The symbols used are the same as in Fig. 1.

Fig. 4. This species demonstrated a highly variable metabolic state during this time of year. One animal showed a thermoneutral zone of 32·5–36·5°C and the remainder of the bats were at various stages of losing their homeothermic-like response.

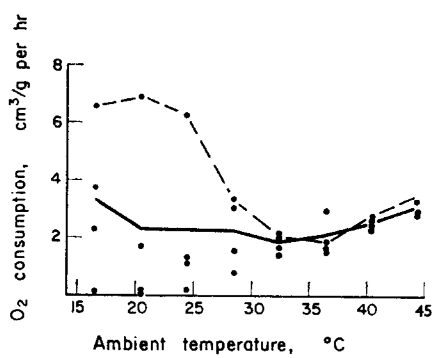

FIG. 4. The relationship of OC–T_a in adult female *M. yumanensis* taken in early September. The symbols used are the same as in Fig. 1; the dotted line indicates an individual that exhibited a homeothermic-like response.

High T_a response for *M. yumanensis* is grossly similar to that of the other two species tested. *Myotis yumanensis* died within 40 min exposure to a T_a of 44·5°C. These bats were wet over the muzzle and entire ventral surface, but only damp on the back.

DISCUSSION

M. lucifugus and *M. yumanensis* in the attic decreased in number rapidly around the first week in September; however, *M. thysanodes* is very abundant until the end of September. Temperatures fluctuated greatly within the attic during September. A recording hygrothermograph, suspended in the attic next to a large group of *M. thysanodes* from 9 to 15 September, showed T_a ranges from 12·2 to 41·1°C; mean maximum $T_a = 36{\cdot}9$°C and mean minimum $T_a = 13{\cdot}5$°C. Relative humidity did not exceed 16% with large fluctuations occurring daily.

During the first part of September *M. lucifugus* and *M. yumanensis* were in deep torpor in the morning. When these bats were picked up they were not capable of much movement for approximately 15 min. On the contrary, *M. thysanodes* at this time appeared torpid, but if touched were capable of flight immediately. By the end of September, *M. thysanodes* were very torpid in the morning. It would take around 15 min for these bats to attain flight. In the afternoon, however, all bats were very active.

In early September, fourteen out of sixteen *M. thysanodes* exhibited a thermoneutral zone and a T_a–OC pattern identical to winter–spring *M. lucifugus* (Stones & Wiebers, 1967). It is unusual that in early September, post-lactating *M. thysanodes* should exhibit a T_a–OC pattern similar to early-pregnant *M. lucifugus* instead of one similar to their post-lactation pattern which is decidedly different. Also, in early September, two of sixteen *M. thysanodes* did not exhibit a homeothermic-like T_a–OC pattern. It would appear that a transition was occurring from a homeothermic-like to a non-homeothermic-like state, presumably a physiological reorientation preparatory for hibernation. By the end of September this physiological switch was almost complete. All bats entered torpor as T_a was lowered, but below 10°C the metabolic rate started to increase. Reite & Davis (1961) reported increased OC at T_a's below 5°C in *M. lucifugus* and *Lasiurus borealis*. By 6 October, the transition to non-homeothermic-like metabolism appeared complete, for ten individuals of this species were placed in a refrigerator ($T_a = 4$°C) and hibernation was achieved at this time.

M. lucifugus occultus, when first tested on 15 September, had completed a transition from a homeothermic-like to a non-homeothermic-like state. This agrees with Stones & Wiebers (1967) in that their late summer bats (after 29 July) had lost the ability to resist torpor.

M. yumanensis appears to be in an intermediate category. At a time when *M. thysanodes* is starting to show a small change towards this transition, *M. yumanensis* appears to be much farther along in the transition. In an admittedly small sample, one individual seemed to exhibit a homeothermic-like response while the other three bats seemed to exhibit a nearly non-homeothermic-like response.

A critical thermal maximum T_a (T_a at which short-term exposure proved lethal) of 44·5°C has been found for these three species. Licht & Leitner (1967) stated that one *M. yumanensis* survived for 60 min at a T_a of 44·5–45°C while two others remained unusually still and panted throughout the test. Stones & Wiebers

(1967) stated that *M. lucifugus* effectively lowered their body temperature at a T_a of 43·4°C by panting and salivating. Hock (1951) stated that *M. lucifugus* died quickly at a T_a of 44°C in the exposure chamber. *Myotis lucifugus* are known to exist in extremely hot nursery colonies at T_a's up to 54°C (Henshaw & Folk, 1966) and 55°C (Davis *et al.*, 1965). The three species of bats in the present study might not have been able to thermoregulate efficiently in the small exposure chambers, which might account for the discrepancy between the critical thermal maximum and actual roost temperatures. These bats, also, may not have been physiologically capable of coping with T_a of this intensity at this time of year.

Panting and wetting of the fur with saliva were observed in all three species and agrees well with observations on *M. lucifugus* (Stones & Wiebers, 1967).

Table 1 gives regression coefficients showing the relationship of OC–T_a at T_a's above the thermoneutral point for the three species tested. Although differences between the species existed, especially between the small-eared *M. yumanensis* and *M. lucifugus* and the large-eared *M. thysanodes*, the regression coefficients are not significantly different.

TABLE 1—REGRESSION COEFFICIENTS SHOWING THE RELATIONSHIP OF OXYGEN CONSUMPTION TO AMBIENT TEMPERATURE AT AMBIENT TEMPERATURES ABOVE THE THERMAL NEUTRAL POINT FOR THREE SPECIES OF *Myotis*

Species	Regression coefficient
M. thysanodes	0·239
M. yumanensis	0·107
M. lucifugus	0·0872

An analysis of variance (Edwards, 1950) was carried out on OC of each species at 4°C intervals from 32·5 to 44·5°C. Results show that T_a has a significant directly proportional affect on metabolic rate ($F = 26{\cdot}3$ for 3 and 39 d.f., $P < 0{\cdot}001$) and, also, that the inter-species metabolic response differences approached significance ($F = 3{\cdot}33$ for 2 and 13 d.f.). Since analysis of variance on OC of each species at 44·5°C showed significant species differences ($F = 13{\cdot}6$ for 2 and 13 d.f., $P < 0{\cdot}01$) and, further, analysis of variance on metabolic differentials of each species (OC at 44·5°C minus OC at 32·5°C) showed significant species differences ($F = 7{\cdot}34$ for 2 and 13 d.f., $P < 0{\cdot}01$), we can conclude that T_a's above the thermal neutral point cause a significantly more rapid rise in OC in *M. thysanodes* than in *M. lucifugus occultus*.

The existence of the physiological and ecological differences between these three sympatric species must act as a species-isolating mechanism.

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Key Word Index—Chiroptera; bats; Vespertilionidae; *Myotis*; metabolism.