

# BIOLOGY OF *MYOTIS THYSANODES* AND *M. LUCIFUGUS* (CHIROPTERA: VESPERTILIONIDAE)—I. THERMOREGULATION

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**Abstract**—1. Thermoregulatory patterns and levels of controlled body temperature ( $T_b$ ) in adult female *Myotis thysanodes* and *M. lucifugus* throughout their stay in maternity colonies are significantly affected by stage of reproduction and even more by stage of pregnancy, but are not affected by abundance of body fat or age.

2. It is impossible to distinguish regulating bats from conforming bats in ambient temperatures ( $T_a$ 's) above 20–24°C, with bats of both species becoming partially hyperthermic above these  $T_a$ 's.

3. Minimum  $T_b$  required for initiation of flight averages 30.3 and 24.3°C, for *M. lucifugus* and *M. thysanodes*, respectively, while neonates of these two species begin to regulate at about 9½ and 4½ days after birth, respectively.

4. Behavioral aspects of thermoregulation may be as important as physiological thermoregulation in the biology of these species.

## INTRODUCTION

KULZER (1965a) stated that in relation to their abilities to thermoregulate, bats are a non-homogeneous group. This may be considered to be something of an understatement. Within the order Chiroptera, some species have been described as homeothermic (Bartholomew *et al.*, 1964; Arata & Jones, 1967; Carpenter & Graham, 1967; Leitner & Nelson, 1967; McNab, 1969; Morrison & McNab, 1967; etc.) or nearly homeothermic, as vampires (Wimsatt, 1962; Lyman & Wimsatt, 1966; McNab, 1969) and some molossids (Leitner, 1966; Morrison & McNab, 1967; Studier & Wilson, 1970). Other species show either homeothermic or poikilothermic thermal responses (Kulzer, 1965b; Herreid & Schmidt-Nielsen, 1966; Herreid, 1963; Bradley & O'Farrell, 1969; etc.), dependent on the level of activity at the time. In other species, body temperature ( $T_b$ ) may approximate ambient temperature ( $T_a$ ) in daytime lethargy (Hock, 1951; Kulzer, 1965a). Still other species exhibit extremely variable thermal responses (Herreid, 1963; Kulzer, 1965a; Studier & Wilson, 1970). In view of the non-homogeneity of thermoregulatory abilities in bats, a confusing nomenclature for chiropteran thermal responses has arisen.

To complicate matters further, such factors as season (Menaker, 1962; Dwyer, 1964; Henshaw & Folk, 1966; Mejnar & Jansky, 1967; Stones & Wiebers, 1967), reproductive condition (Stones & Wiebers, 1967), acclimation (Stones & Wiebers, 1966), nutrition (McNab, 1969), habitat selection (Twente, 1955), grouping (Kolb, 1950), behavior (Licht & Leitner, 1967a), etc. may have significant effects on the thermoregulatory patterns of bats. Although temperature regulation in bats has been reviewed (Reeder & Cowles, 1951; Stones & Wiebers, 1965b; Henshaw, 1970; Lyman, 1970), thermoregulatory patterns in bats are still not well understood.

The present study presents data on thermal relationships of *Myotis lucifugus* and *Myotis thysanodes* collected in conjunction with an intensive study of the biology of these two species of vespertilionid bats.

### MATERIALS AND METHODS

At nearly weekly intervals from 19 April 1970 until 25 September 1970, six or more *Myotis thysanodes* and *Myotis lucifugus*, if available, were collected from the attic of Montezuma Seminary, Montezuma (elevation ca. 6600 ft), San Miguel Co., New Mexico, for laboratory study. A total of about eighty adults and thirty young of each species was studied. Bats were collected at least 1 hr prior to sunrise with routine summer collections at 04.00 hr Mountain Daylight Savings Time (M.D.S.T.). Bats were immediately brought into the laboratory, sexed, weighed, aged (using a tooth wear scale of 1-4) and prepared for study. Three bats were equipped with plastic restrainers (Fig. 1). These restrainers had no significant effects on the parameters measured. Flexible thermistor probes were inserted rectally about 2 cm and taped in place. A Yellow Springs Telethermometer, Model 44TZ, was used to monitor deep body temperature ( $T_b$ ). Leads for recording breathing and heart rates, consisting of small (No. 14) fish hooks, were then inserted under the axial skin on the ventral side of each shoulder. Signals from these leads were fed into an E & M Instruments impedance pneumograph coupled to a hi-gain preamplifier and recorded on a Physiograph Six (E & M Instruments). These three bats thus provided data on heart and breathing rates, and body temperature in addition to the other measured parameters. The three bats thus prepared and three other bats not encumbered in any way were then placed into vertical, cylindrical, glass exposure chambers (dia. 43 mm, height about 100 mm). A strip of  $\frac{1}{4}$ -in. mesh hardware cloth along one side and the bottom of the exposure chambers allowed footing for the bats so they could hang in a normal head down position, and the hardware cloth also prevented bats from contacting a layer of mineral oil covering the bottom of the exposure chamber. The six exposure chambers thus prepared were then immersed in a constant temperature water-bath at an ambient temperature ( $T_a$ ) of 16°C.

Air from compressed air tanks was passed through a drying column containing Drierite and then through a predictability flowmeter (Manostat Corp.), and through a 1-m section of  $\frac{1}{4}$ -in. aluminum tubing in the water-bath for equilibration with water temperature. Air then entered the bottom of the exposure chambers. Normal air flow was maintained at about 150 cm<sup>3</sup>/min, a volume approximating that of the exposure chamber. Air leaving the exposure chamber passed through a column of Drierite, then a column of Ascarite, through another flowmeter and finally into a Beckman Model C-2 Paramagnetic Oxygen Analyzer.

After bats were prepared, placed in exposure chambers and subjected to a  $T_a$  of 16°C,  $T_b$  of the three bats equipped with rectal probes was periodically monitored until body temperature stabilized at which time readings were begun, provided the bats had been exposed to a  $T_a$  of 16°C for at least 2 hr. Figure 2 shows a single example of a typical  $T_b$  stabilization pattern. The intermediate equilibrium  $T_b$ 's reached by two of the bats represented in Fig. 2 were not unusual and such intermediate  $T_b$ 's were maintained by some bats for periods of 10-12 hr at  $T_a$ 's lower than 16°C. Of the parameters measured, only two,

$T_b$  and oxygen consumption (OC), have been analyzed in the present study. Oxygen consumption was determined by standard methods (see, for example, O'Farrell & Studier, 1970) with readings taken for at least 5 min or until readings stabilized.  $T_b$  was monitored throughout, but recorded at the end of oxygen consumption measurements. After these

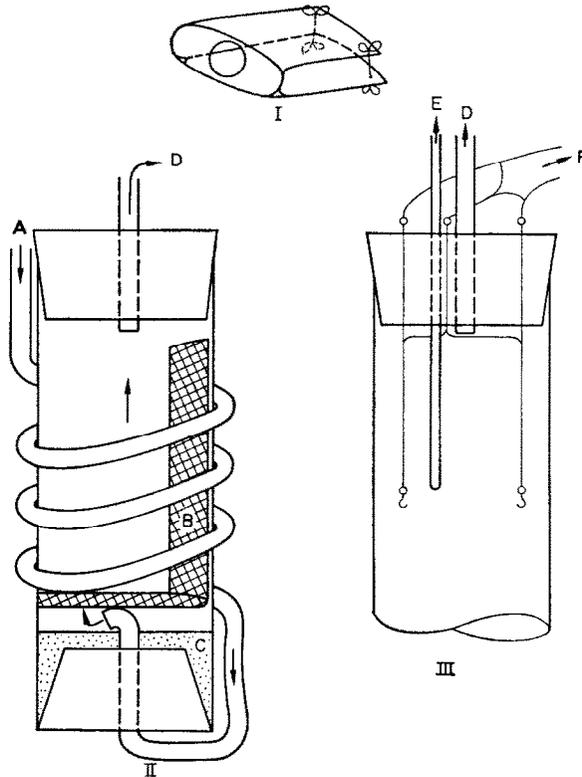


FIG. 1. Detail of parts of the apparatus—(I) Restraining harness, bat's head passes through anterior hole, sewed through plagiopatagium adjacent to the posterior lateral abdomen; (II) Exposure chamber, A—1-m section of aluminum tubing for temperature equilibration, (B)  $\frac{1}{4}$  in. mesh hardware cloth upon which bats roost, (C) layer of mineral oil, (D) tubing carrying air out of exposure chamber to oxygen analyzer; (III) Exposure chamber for monitoring body temperature, heart and breathing rates, (D) same as above, (E) rectal thermistor probe, (F) grounded leads for recording heart and breathing rates.

determinations were made for each bat at a  $T_a$  of 16°C,  $T_a$  was rapidly raised (time required about 5 min) to 20°C.  $T_a$  was maintained within 0.3°C of the desired temperature.  $T_b$  was again monitored until it stabilized or for a minimum of 30 min, and readings were again taken. Bats were examined as described at 4°C intervals from a  $T_a$  of 16°C to a  $T_a$  of 40°C. During a few early studies, bats were run at 4°C intervals beginning at 14°C to a maximum  $T_a$  of 38°C. After exposure to the final  $T_a$ , bats were removed from the exposure chambers, sacrificed, weighed and frozen for use in other studies. Initial and final

body weights were averaged for use in calculation of OC. All oxygen consumption measurements were corrected to STPD. Additionally, during many hours of field observation,  $T_b$ 's of individuals and  $T_a$ 's of roosts of both species were measured sporadically in their normal roosting sites using a Model PRT-10 I.R. field thermometer (Barnes Engineering Co.) and a Schultheis quick-registering rectal thermometer. Finally, the minimum  $T_b$  required for flight in the laboratory was determined using the procedure of Bradley & O'Farrell (1969), except that bats were studied on the day of capture.

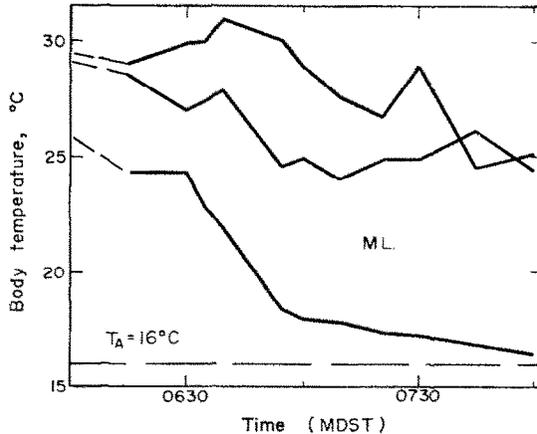


FIG. 2. Sequential body temperature of three *M. lucifugus* at an ambient temperature of 16°C (dashed line). Exposure was begun at 0510 M.D.S.T. with  $T_b$ 's of all three bats above 30°C. These data were collected on 24 May 1970 and are typical of the thermal responses of *M. lucifugus* and *M. thysanodes* throughout the summer.

Laboratory experimentation was performed precisely in the manner described so that a minimum of stress would be placed on the bats under study. Hart (1957) discusses several of the criticisms generally applied to laboratory studies and their application to the response of natural populations. Most of the criticisms center around the placement of animals into stressful environments and exposing those organisms to grossly unnatural conditions. In these studies, bats were nearly always collected long before dawn but after cessation of their regular nocturnal activity. Since experimentation on all bats was begun within an hour of the time of capture, we feel that no nutritional stress was placed on the subjects. Also, because food passage in bats is so rapid, effects of the specific dynamic action of food should be negligible and bats in this study are considered to be post-absorptive. Bats were studied only during their normal roosting periods. The confining nature of the exposure chambers should not place undue stress on the bats since both species exhibit strong positive thigmotaxis and normally roost in confined quarters. The testing of bats as individuals and not as groups does have some effect on oxygen consumption and evaporative water loss (Studier & O'Farrell, unpublished data), which is to be expected in view of the gregarious roosting habits of both species. Bats were exposed and studied in the laboratory in  $T_a$ 's which exist in their normal roost (Fig. 3); i.e. laboratory exposure temperatures were programmed to coincide with normal roost site temperatures. This was also done in an attempt to reduce any conflicts between laboratory studies and naturally existing thermal relations.

Statistical treatment of data primarily follows Simpson *et al.* (1960). Sample size in each instance is the number of separate individuals involved in the specific statistic; i.e.

when more than one point was generated by the same individual, the number of individuals involved, not the number of points generated, is used as the sample size.

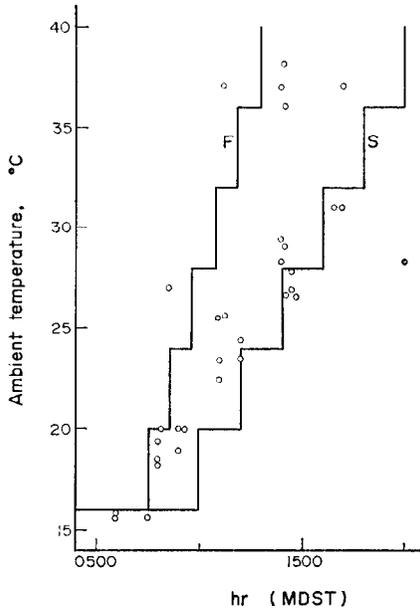


FIG. 3. Ambient temperature (circles) in natural roost sites of *M. lucifugus* and *M. thysanodes* taken primarily from spring and fall and experimental exposures (solid lines). Fastest (F) and slowest (S) experimental runs are indicated.

## RESULTS

Since  $T_b$ 's of both species studied were extremely variable in relation to  $T_a$  in routine laboratory studies, only two illustrations (Figs. 4 and 5) are shown. In view of the variability of the data, it is of critical importance to distinguish bats with controlled body temperatures (regulators) from those bats which did not control their body temperature (conformers). We will use the terms "regulators" and "conformers" throughout the balance of this paper in the hope of avoiding conflicts in semantic problems associated with the large literature vocabulary which has evolved to describe thermoregulation in mammals. An attempt was made to graphically segregate regulators from conformers by plotting  $T_b$  to  $T_a$  differential against oxygen consumption (see Figs. 6 and 7). It is possible to distinguish regulators from conformers at  $T_a$ 's of 16 and 20°C for *M. lucifugus* and at  $T_a$ 's of 16, 20 and 24°C for *M. thysanodes*. Conformers are those bats in which  $T_b - T_a$  was less than 2°C or, within the  $T_a$  ranges just listed, are bats not equipped with rectal probes in which oxygen consumption was less than 1.0 cm<sup>3</sup>/g per hr. We do not intend to imply that the classifications of regulators and conformers used in this paper indicate any genetically based differences in the bats under study. The

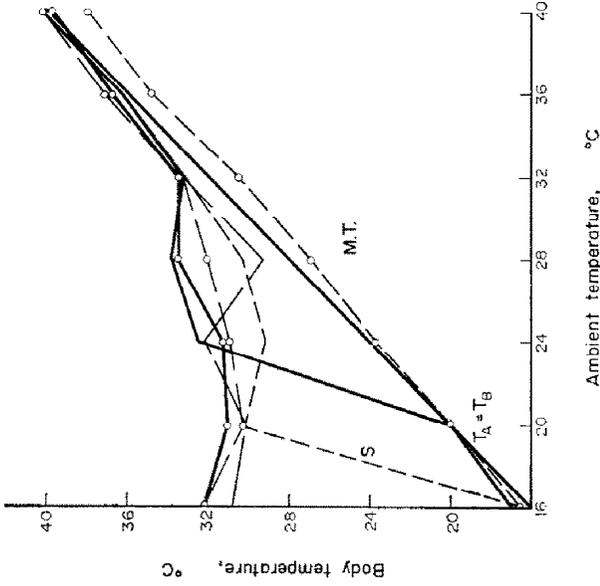


FIG. 5. Body temperatures of six pregnant *M. thyssanodes* at various ambient temperatures on 12 and 19 (circles) June 1970. An individual classed as a shifter is indicated with an S.

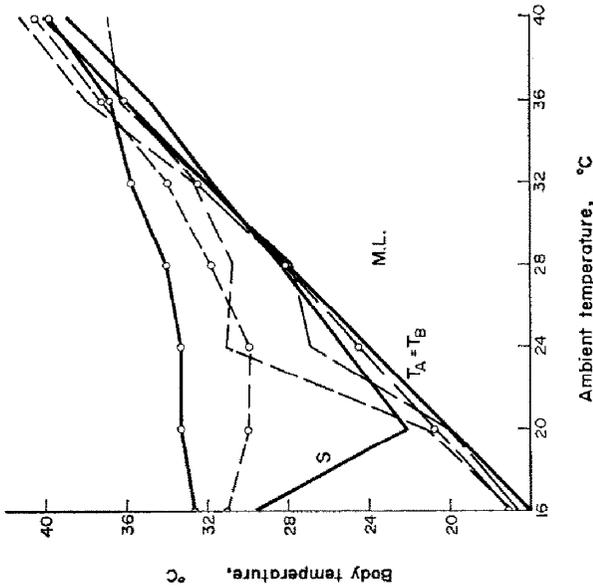


FIG. 4. Body temperatures of six pregnant *M. lucifugus* at various ambient temperatures on 13 and 21 (circles) June 1970. An individual classed as a shifter is indicated by an S.

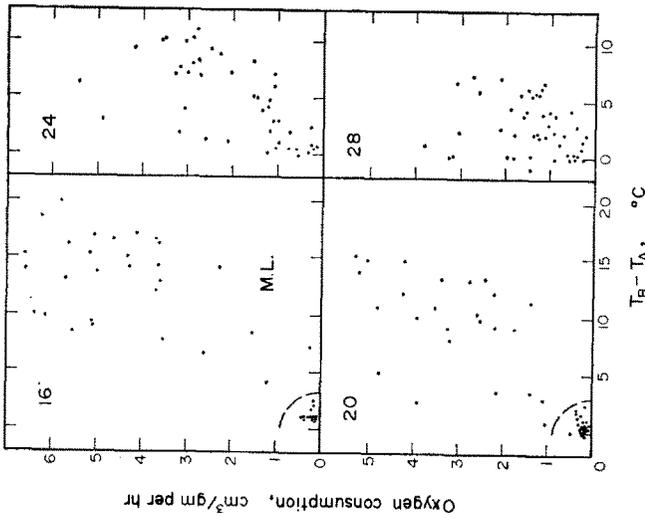


FIG. 6. Relation of oxygen consumption to body temperature ( $T_b$ )-ambient temperature ( $T_a$ ) differential in *M. lucifugus* at four different  $T_a$ 's (16, 20, 24 and 28°C). Individuals separated by the dashed semi-circles are considered to be conformers.

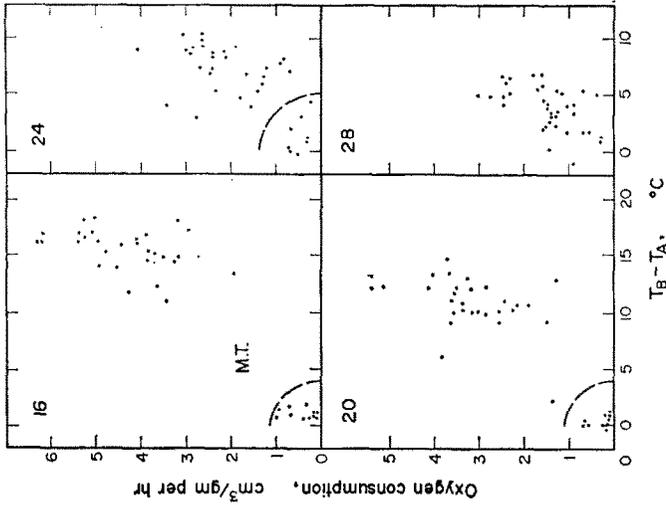


FIG. 7. Relation of oxygen consumption to body temperature ( $T_b$ )-ambient temperature ( $T_a$ ) differential in *M. thysanodes* at four different  $T_a$ 's (16, 20, 24 and 28°C). Individuals separated by the dashed semi-circles are considered to be conformers.

terms apply only to data collected for individual bats under the described experimental conditions. If the reader is accustomed to the use of other terms to describe these conditions of OC and  $T_b - T_a$ , he is free to mentally substitute those terms. Using these criteria to distinguish regulators from conformers, several analyses of raw data have been performed. Table 1 illustrates the numbers of bats studied at

TABLE 1—NUMBERS OF FEMALE *M. lucifugus* AND *M. thysanodes* IN DIFFERING REPRODUCTIVE CONDITIONS WHICH CONFORMED (C) OR REGULATED (R) AT  $T_a$ 's OF 16 AND 20°C.

Reproductive condition	<i>M. lucifugus</i>		<i>M. thysanodes</i>	
	C	R	C	R
16°C				
Pregnant	7	13	5	23
Lactating	5	4	6	6
Post-lactating	1	11	1	16
20°C				
Pregnant	13	13	6	22
Lactating	5	4	6	6
Post-lactating	3	9	4	13

specific  $T_a$ 's which were regulating or conforming to that  $T_a$  throughout the summer reproductive cycle. Chi-square tests on the data in Table 1 based on a 50 : 50 hypothesis in each reproductive phase show that significantly more adult female *M. lucifugus* regulate at 16°C than conform at that  $T_a$  ( $\chi^2 = 10.243$ ; d.f. = 3;  $P < 0.01$ ); although there is no significant tendency in this species to regulate at 20°C ( $\chi^2 = 3.11$ ; d.f. = 3;  $0.10 > P > 0.05$ ). A 50 : 50 hypothesis is used to represent no trend so that differences indicate significant tendencies within the sample to regulate or conform. Analysis within each reproductive phase in *M. lucifugus* also based on a 50 : 50 hypothesis shows that the only significant trend toward regulation occurs in post-lactating individuals at 16°C ( $\chi^2 = 8.332$ ; d.f. = 1;  $P < 0.005$ ). Similarly, the same  $\chi$ -square analyses on *M. thysanodes* show a significant tendency to regulate at both 16 and 20°C ( $\chi^2 = 24.8$ ; d.f. = 3;  $P < 0.005$ ; and,  $\chi^2 = 12.3$ ; d.f. = 3;  $P < 0.01$ , respectively). Pregnant *M. thysanodes* at both 16 and 20°C showed a significant trend toward regulation ( $\chi^2 = 11.57$ ; d.f. = 1;  $P < 0.005$ ; and,  $\chi^2 = 9.142$ ; d.f. = 1;  $P < 0.005$ , respectively). Post-lactating individuals at 16°C also showed significantly more regulators ( $\chi^2 = 13.23$ ; d.f. = 1;  $P < 0.005$ ). Fisher's exact probability analyses of the data in Table 1 show for *M. lucifugus* at 16°C that there is a significant shift toward regulation from lactating to post-lactating individuals ( $P = 0.029$ ). In *M. thysanodes* at 16°C, a significant switch away from regulation occurs from pregnant to lactating individuals ( $P = 0.047$ ), followed by a significant shift toward regulation from lactating to post-lactating females

( $P = 0.011$ ). Finally, at  $16^{\circ}\text{C}$ , *M. thysanodes* show a significantly greater tendency to regulate than *M. lucifugus* ( $P = 0.028$ ) and a nearly significant tendency at  $20^{\circ}\text{C}$  ( $P = 0.060$ ).

Regulating and conforming bats of each species were segregated according to age groups as young adults (aged 1 or 1+) or old adults (aged 2-4). When the two groups were analyzed by  $\chi$ -square test of independence and Fisher's exact probability, there were no significant differences found in the proportions of young or old adults which regulated or conformed for the entire population or within any reproductive condition for either *M. lucifugus* or *M. thysanodes*. Additionally, fat indices were determined for all bats studied using the method of Ewing *et al.* (1970), and analyses were performed which showed no significant relationship between proportion of body fat and tendency to regulate in either species. Pregnant bats were then segregated into groups based on the weights of embryos: group 1 including those bats with embryos too small to weigh, group 2 including bats with embryos weighing from a few milligrams to 0.250 g, and group 3 including bats with embryos weighing in excess of 0.250 g. Results of this grouping of individuals are shown in Table 2. The  $\chi$ -square test of independence on the

TABLE 2—NUMBERS OF FEMALE *M. lucifugus* AND *M. thysanodes* IN DIFFERING STAGES OF PREGNANCY WHICH CONFORMED OR REGULATED AT  $T_a$ 's OF 16 AND  $20^{\circ}\text{C}$ .

Group	<i>M. lucifugus</i>		<i>M. thysanodes</i>	
	C	R	C	R
$16^{\circ}\text{C}$				
1	11	6	5	13
2	5	10	1	13
3	8	8	6	10
$20^{\circ}\text{C}$				
1	11	6	7	10
2	10	5	0	14
3	9	7	7	9

Group 1, embryos too small to weigh; Group 2, embryos from few milligrams to 0.250 g; Group 3, embryos larger than 0.250 g.

data in Table 2 reveals a significant departure from expected values only for *M. thysanodes* at a  $T_a$  of  $20^{\circ}\text{C}$  ( $\chi^2 = 8.45$ , d.f. = 2,  $P < 0.05$ ). Analysis by Fisher's exact probability shows that in *M. thysanodes* at a  $T_a$  of  $20^{\circ}\text{C}$ , there is a significant shift toward regulation going from bats in group 1 to bats in group 2 ( $P = 0.0074$ ) and a similar significant reversal away from regulation again in the bats of group 3 ( $P = 0.0056$ ). Similarly, nearly significant shifts also occur in both species at a  $T_a$  of  $16^{\circ}\text{C}$ . It is statistically true then that in bats of both species tested, there exists a trend within the population toward regulation in early pregnancy and away from

regulation in late pregnancy. Finally the proportion of *M. thysanodes* which regulate throughout the entire pregnancy period is significantly greater than in *M. lucifugus* at  $T_a$ 's of both 16°C ( $P = 0.0099$ ) and 20°C ( $P = 0.0013$ ).

Table 3 indicates the numbers of bats of each species which regulated at both 16 and 20°C, which conformed at both  $T_a$ 's and which shifted from conforming to

TABLE 3—NUMBERS OF FEMALE *M. lucifugus* AND *M. thysanodes* IN DIFFERING REPRODUCTIVE CONDITIONS WHICH CONFORMED, REGULATED OR SHIFTED IN THE  $T_a$  RANGE OF 16–20°C

Reproductive condition	Conformers	Shifters	Regulators
	<i>M. lucifugus</i>		
Pregnant	14	18	16
Lactating	4	2	3
Post-lactating	2	1	13
	<i>M. thysanodes</i>		
Pregnant	10	7	26
Lactating	4	3	5
Post-lactating	2	6	25

regulating or vice versa at 16 and 20°C (shifters). The  $\chi$ -square test of independence on the data in Table 3 shows a significant departure from generated expected values in *M. lucifugus* ( $\chi^2 = 13.45$ ; d.f. = 4;  $P < 0.01$ ), but not in *M. thysanodes*. The significance of  $\chi$ -square in *M. lucifugus* data in Table 3 results from a decrease throughout the reproductive cycle in the numbers of bats which shift leading to greater numbers of regulators later in the reproductive cycle.

To summarize the preceding data, summer maternity populations of both species show a tendency to regulate their  $T_b$ 's at moderately low  $T_a$ 's with a more pronounced tendency evident in *M. thysanodes*. Additionally, although again more pronounced in *M. thysanodes*, the greater proportion of both populations oscillates away from regulation after pregnancy during lactation and toward regulation after lactation during the post-lactation period. In both species, some individuals shift between conforming and regulating at moderately low  $T_a$ 's. There exists a significant drop in the numbers of *M. lucifugus* which shift as the summer progresses, although during the same time span there is no significant change in the numbers of *M. thysanodes* which exhibit this shifting characteristic.

Neglecting the conforming individuals, mean  $T_b$ 's at various  $T_a$ 's of the regulating individuals for both species are depicted in Figs. 8 and 9 with reduced numerical data shown in Table 4. Polynomial regression lines for the data shown in Figs. 8 and 9 are given in Table 5. In *M. thysanodes* and *M. lucifugus* the Y-intercept of lactating individuals is significantly lower than the Y-intercept of pregnant and post-lactating individuals ( $t = 23.8$ ,  $N = 38$ ,  $P < 0.001$ ; and,  $t = 23.0$ ,  $N = 27$ ,  $P < 0.001$ , respectively, for *M. thysanodes*; and,  $t = 39.3$ ,  $N = 33$ ,

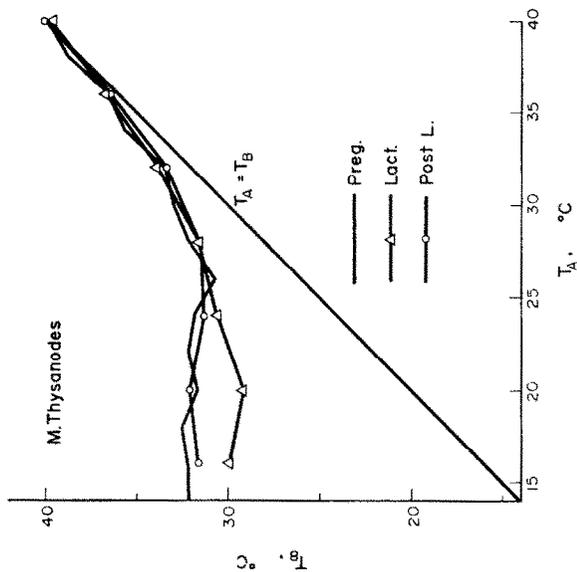


FIG. 9. Mean body temperatures of regulating *M. thysanodes* at various ambient temperatures in bats of differing reproductive condition. See Table 4 for sample size, arithmetic means and S.E. of the means.

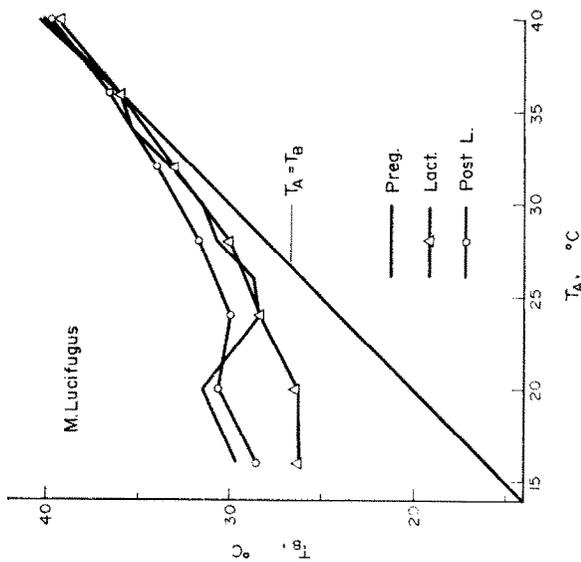


FIG. 8. Mean body temperatures of regulating *M. lucifugus* at various ambient temperatures in bats of differing reproductive condition. See Table 4 for sample size, arithmetic means and S.E. of the means.

TABLE 4—BODY TEMPERATURES OF FEMALE *M. thysanodes* AND *M. lucifugus* AT VARYING AMBIENT TEMPERATURES

R.C.*	Ambient temperature (°C)						
	16	20	24	28	32	36	40
<i>M. thysanodes</i>							
PR	32.2†	31.7	31.9	32.1	33.5	36.7	39.9
	19	19	18	24	24	24	16
	0.37	0.35	0.39	0.42	0.26	0.28	0.32
LA	29.9	29.2	30.2	31.7	33.8	36.7	39.7
	6	7	8	9	9	12	12
	0.63	1.40	0.90	0.62	0.23	0.22	0.46
PL	31.6	32.1	31.7	31.6	33.4	36.6	39.9
	15	12	13	17	17	17	15
	0.60	0.62	0.47	0.49	0.33	0.31	0.22
<i>M. lucifugus</i>							
PR	29.6	31.5	28.4	30.7	33.3	36.0	39.5
	14	10	23	23	23	23	20
	1.24	1.22	0.83	0.57	0.28	0.23	0.32
LA	26.2	26.3	28.3	30.1	33.2	36.1	39.8
	4	4	9	9	9	9	9
	1.66	1.91	1.18	0.46	0.21	0.39	0.31
PL	28.4	30.6	29.9	31.7	34.1	36.6	39.7
	11	9	11	11	10	10	10
	1.27	0.85	0.81	0.64	0.28	0.53	0.34

\* Reproductive condition with PR, pregnant; LA, lactating; PL, post-lactating.  
 † Numbers from top to bottom are mean, sample size and S.E. of the mean.

TABLE 5—POLYNOMIAL REGRESSION EQUATIONS OF BODY TEMPERATURES AT VARIOUS AMBIENT TEMPERATURES IN REGULATING *M. lucifugus* AND *M. thysanodes* IN DIFFERING REPRODUCTIVE CONDITIONS

Reproductive condition	N	Regression equation for $T_b$ vs. $T_a$ (S.E. $\bar{x}$ of Y-intercept, $T_b$ )
<i>M. thysanodes</i>		
Pregnant	28	$T_b = 0.0263(T_a)^2 - 1.16T_a + 44.1$ (0.119)
Lactating	12	$T_b = 0.0201(T_a)^2 - 0.664T_a + 34.8$ (0.372)
Post-lactating	17	$T_b = 0.0270(T_a)^2 - 1.19T_a + 44.2$ (0.167)
<i>M. lucifugus</i>		
Pregnant	26	$T_b = 0.0277(T_a)^2 - 1.16T_a + 41.7$ (0.236)
Lactating	9	$T_b = 0.0184(T_a)^2 - 0.447T_a + 28.3$ (0.247)
Post-lactating	11	$T_b = 0.0148(T_a)^2 - 0.386T_a + 31.3$ (0.300)

$P < 0.001$ ; and,  $t = 7.75$ ,  $N = 18$ ,  $P < 0.001$ , respectively, for *M. lucifugus*). Since regulators could be distinguished from conformers in *M. thysanodes* up to a  $T_a$  of  $24^\circ\text{C}$ , straight line regression equations of  $T_b$  vs.  $T_a$  in this species were determined in small  $T_a$  intervals (Table 6) to establish where the deviation of lactating individuals from pregnant and post-lactating individuals occurred. Within any of the

TABLE 6—REGRESSION EQUATIONS RELATING BODY TEMPERATURE TO AMBIENT TEMPERATURE IN THREE AMBIENT TEMPERATURE RANGES IN REGULATING *M. thysanodes* IN DIFFERING REPRODUCTIVE CONDITIONS

Reproductive condition	N	Regression equation (S.E. $\bar{x}$ of slope and intercept)
<i>M. thysanodes</i>		
14–24°C		
Pregnant	22	$T_b = -0.029T_a + 32.5$ (0.123) (0.185)
Lactating	8	$T_b = 0.0453T_a + 28.9$ (0.238) (0.624)
Post-lactating	13	$T_b = 0.0105T_a + 31.6$ (0.159) (0.321)
24–32°C		
Pregnant	26	$T_b = 0.222T_a + 26.2$ (0.108) (0.194)
Lactating	9	$T_b = 0.454T_a + 19.2$ (0.160) (0.362)
Post-lactating	17	$T_b = 0.225T_a + 25.9$ (0.135) (0.250)
32–40°C		
Pregnant	27	$T_b = 0.797T_a + 8.06$ (0.054) (0.149)
Lactating	12	$T_b = 0.713T_a + 11.7$ (0.145) (0.583)
Post-lactating	17	$T_b = 0.813T_a + 7.36$ (0.0578) (0.166)

three  $T_a$  ranges analyzed, there are no significant differences in the regression coefficients irrespective of reproductive condition, although the mean slope of lactating individuals in the  $T_a$  ranges of 14–24°C and 24–32°C is higher than in pregnant or post-lactating bats. The Y-intercepts of lactating *M. thysanodes* in the  $T_a$  ranges of 14–24 and 24–32°C are both significantly lower than in pregnant and post-lactating individuals ( $t = 5.53$ ,  $N = 28$ ,  $P < 0.001$ ; and,  $t = 3.85$ ,  $N = 19$ ,  $P < 0.01$ , respectively, for the 14–24°C interval; and,  $t = 17.1$ ,  $N = 33$ ,  $P < 0.001$ ; and,  $t = 15.2$ ,  $N = 24$ ,  $P < 0.001$ , respectively, for the 24–32°C interval). Since in *M. lucifugus* it is not possible to distinguish regulators from conformers at  $24^\circ\text{C}$ , a similar analysis was not performed on the  $T_b$  to  $T_a$  relations in this species.

Although there is no difference in the Y-intercept of pregnant and post-lactating *M. thysanodes*, this value for pregnant *M. lucifugus* is significantly higher than for post-lactating individuals ( $t = 27.2$ ,  $N = 35$ ,  $P < 0.001$ ). Comparing the intercepts of *M. thysanodes* with those of *M. lucifugus* in different reproductive conditions, we find that values for *M. thysanodes* are each significantly higher than in *M. lucifugus* in similar reproductive condition ( $t = 9.09$ ,  $N = 52$ ,  $P < 0.001$  for pregnant bats;  $t = 14.5$ ,  $N = 19$ ,  $P < 0.001$  for lactating bats; and,  $t = 37.6$ ,  $N = 26$ ,  $P < 0.001$  for post-lactating individuals).

Since we have previously shown that embryo weight significantly affects the tendency to regulate in these species, an analysis was performed to determine if embryo weight affects the absolute  $T_b$  of regulators, with non-significant results. It appears, therefore, that the level of regulated  $T_b$  does not change with increasing embryo weight.

Summarizing this section of data, at low  $T_a$ 's, lactating regulators of both species maintain significant lower controlled  $T_b$ 's than bats in other reproductive conditions. Although not true of *M. thysanodes*, post-lactating *M. lucifugus* maintain a lower  $T_b$  than pregnant individuals. Finally, irrespective of reproductive condition, controlled  $T_b$ 's of *M. thysanodes* at low  $T_a$ 's are significantly higher than those of *M. lucifugus*.

Judging from Fig. 9, *M. thysanodes* appear to become hyperthermic at  $T_a$ 's above 24°C. From the interval regression lines calculated for Table 6, we find that the regression coefficients for the 24–32°C interval are significantly greater than zero in pregnant bats ( $F = 11.9$ , d.f. = 1 and 25,  $P < 0.005$ ), lactating bats ( $F = 17.3$ , d.f. = 1 and 8,  $P < 0.005$ ) and in post-lactating bats ( $F = 7.83$ , d.f. = 1 and 16,  $P < 0.025$ ). Since  $T_b$  is no longer independent of  $T_a$ , we conclude that irrespective of reproductive condition, *M. thysanodes* become hyperthermic at  $T_a$ 's in excess of 24°C. Although similar calculations could not be made on the *M. lucifugus* data, it appears from Fig. 8 that *M. lucifugus* also become hyperthermic at  $T_a$ 's above 24°C and possibly at  $T_a$ 's above 20°C.

Of all bats tested of both species, very few attempted to regulate  $T_b$  at  $T_a$ 's of 36 and 40°C. In *M. lucifugus*, twelve of thirty-nine individuals tested (30.8 per cent) maintained  $T_b$ 's of 1°C or more below a  $T_a$  of 40°C and even less, two of thirty-nine (5.1 per cent), held  $T_b$ 's 2°C or more below a  $T_a$  of 40°C. Similarly, in *M. thysanodes*, four of forty-three (9.3 per cent) and two of forty-three (4.7 per cent) maintained  $T_b$ 's of more than 1 and 2°C, respectively, below a  $T_a$  of 40°C. In nearly all of the situations just described, the great majority of the regulating bats were pregnant, with a total for both species at a  $T_a$  of 40°C of eleven of seventy-two pregnant bats (15.3 per cent) and three of ninety-two lactating or post-lactating bats (3.3 per cent) which maintained  $T_b$ 's of 1°C or more below ambient.

Table 7 shows reduced data of  $T_b$ 's of conforming bats of both species studied throughout their summer reproductive stages. Although numbers tested are too small to be statistically analyzed, it appears that throughout the summer, from pregnancy to lactation to post-lactation, conforming bats of both species exhibit continually higher  $T_b$ 's at the same  $T_a$ .

TABLE 7—AVERAGE BODY TEMPERATURES ( $T_b$ ) OF CONFORMING *M. thysanodes* AND *M. lucifugus* DURING PREGNANCY (PR), LACTATION (LA) AND POST-LACTATION (PL) AT VARIOUS AMBIENT TEMPERATURES ( $T_a$ ).

$T_a$ (°C)	$T_b$ (°C)		
	PR	LA	PL
<i>M. thysanodes</i>			
16	16.7 (5)	17.3 (6)	17.0 (1)
20	20.2 (5)	20.5 (5)	23.3 (5)
24	24.8 (6)	26.0 (1)	25.3 (3)
<i>M. lucifugus</i>			
16	16.8 (4)	17.2 (5)	18.1 (1)
20	20.6 (13)	20.3 (5)	21.6 (3)

Sample sizes indicated in parentheses.

Although very little data were collected on thermal relations of adult male *M. thysanodes* and *M. lucifugus*, tested individuals yielded data very similar to that found for females. Both species are capable of regulating, although conformers and shifters were also found. One adult male *M. lucifugus* provided the following interesting observation. Recorded  $T_b$ 's at  $T_a$ 's of 14, 18 and 22°C indicate that this individual was a simple conformer; however, while the  $T_a$  was being raised from 18 to 22°C, the  $T_b$  of this bat rose from 18°C to 30°C and fell back to 22.5°C within a time span of less than 5 min.

Individuals of both species were tested to determine the minimum  $T_b$  required for flight. Of seven *M. lucifugus* studied, mean minimum  $T_b$  necessary for flight was 30.3°C (S.E.  $\bar{x}$  = 0.328, range 28.6–31.2°C), while for eight *M. thysanodes*, mean minimum  $T_b$  for flight was 24.3°C (S.E.  $\bar{x}$  = 0.830, range 20.0–26.6°C). The difference in these means is significant ( $t$  = 6.73,  $N$  = 13,  $P$  < 0.001), indicating that *M. thysanodes* can attain flight at a lower  $T_b$  than is required for *M. lucifugus*. Mean  $T_b$  of eight *M. lucifugus* taken immediately upon their capture by mist net was 36.7°C (S.E.  $\bar{x}$  = 0.272, range 35.4–37.4°C). The  $T_b$  required for initiation of flight is significantly lower than  $T_b$  during prolonged flight in *M. lucifugus* ( $t$  = 15.0,  $N$  = 13,  $P$  < 0.001).

Existing equipment was too large to use on neonates to determine  $T_b$  at tested  $T_a$ 's. We have, therefore, relied on oxygen consumption as a parameter to indicate controlled  $T_b$ . As seen in Figs. 6 and 7, there is a wide discrepancy in OC of regulators as opposed to conformers at  $T_a$ 's of 16 and 20°C. We have consequently used an OC of greater than 1 cm<sup>3</sup>/g per hr as indicating regulation of  $T_b$  at  $T_a$ 's of 16 and 20°C. Since it is impossible to distinguish regulators from conformers in adult *M. lucifugus* above a  $T_a$  of 20°C and in adult *M. thysanodes* above 24°C, no attempt has been made to segregate neonatal regulators from conformers above these  $T_a$ 's. From the general pattern of data for both species, neonates do not

TABLE 8—MEAN MINIMUM BODY TEMPERATURE REQUIRED FOR INITIATION OF FLIGHT IN SOME BATS

Species	$T_b$ (°C)	Reference
<i>Rhinolophus</i> sp.	30	Burbank & Young (1934)
<i>Tadarida brasiliensis</i>	31	Herreid (1963)
<i>Tadarida brasiliensis</i>	32	O'Farrell & Bradley (1968)
<i>Tadarida loriae</i>	31	Kulzer <i>et al.</i> (1970)
<i>Myotis lucifugus</i>	30.3	Present study
<i>Myotis lucifugus</i>	29	Stones & Wiebers (1967)
<i>Myotis yumanensis</i>	33	Reeder & Cowles (1951)
<i>Myotis yumanensis</i>	31	Present study
<i>Myotis thysanodes</i>	24.3	Present study
<i>Myotis californicus</i>	26	O'Farrell & Bradley (1968)
<i>Myotis velifer</i>	21.6*	Humphrey†
<i>Myotis sodalis</i>	21.3*	Humphrey†
<i>Myotis keeni</i>	25*	Humphrey†
<i>Myotis adversus</i>	27	Kulzer <i>et al.</i> (1970)
<i>Pipistrellus subflavus</i>	26*	Humphrey†
<i>Pipistrellus hesperus</i>	24.8	Bradley & O'Farrell (1969)
<i>Plecotus townsendi</i>	24.3	Reeder & Cowles (1951)
<i>Plecotus townsendi</i>	24	O'Farrell & Bradley (1968)
<i>Antrozous pallidus</i>	25.5	O'Farrell & Bradley (1968)
<i>Eptesicus fuscus</i>	28	O'Farrell & Bradley (1968)
<i>Lasiurus cinereus</i>	23‡	O'Farrell & Bradley (1968)
<i>Miniopterus schreibersi</i>	31	Morrison (1959)
<i>Nyctalus noctula</i>	30–33	Burbank & Young (1934)

\*  $T_b$  of bats arousing from hibernation in hibernacula.

† Personal communication.

‡  $T_b$  rises rapidly upon initiation of flight.

develop a uniform capacity for regulation but, rather, become shifters, and then later become full regulators. In *M. lucifugus*, the youngest bat tested which exhibited increased OC at  $T_a$ 's of 16 or 20°C was a male individual whose age we estimated (O'Farrell and Studier, unpublished data) at 9.6 days. Several younger bats of this species did not yield any evidence of regulation. In *M. thysanodes*, the youngest bats which were tested, both aged 4.6 days, yielded evidence of ability to regulate, as shifters in the  $T_a$  range of 16–24°C. Among adult-sized young of both species, most would be classed as shifters; however, since "shifting" is also an adult characteristic, these youngest neonates which showed some ability to regulate can be considered to exhibit adult regulatory ability. Although we do not have sufficient data for statistical analysis, it certainly appears that *M. thysanodes* sucklings are capable of regulating at a younger age than *M. lucifugus*.

Data of  $T_b$  and  $T_a$  were collected sporadically in the field. This field-collected data was as variable as the laboratory data collected in similar  $T_a$ 's; and we feel that the field data further reinforces the indication that the laboratory obtained data is a

true representation of naturally occurring phenomena. The thermal relations of roosting bats of both species are extremely variable in  $T_b$ 's obtained from roosting bats. One example only will be cited. On 25 September 1970, five female *M. thysanodes* were taken from a single crack between two rafters in the attic of Montezuma Seminary at about 14.00 hr. These bats were quite closely packed and touching each other. At a  $T_a$  of 16°C, the  $T_b$ 's of these bats as removed in order from the crack were 22.5, 26.3, 19.1, 24.3 and 17.0°C. Other field data will be included in later discussion.

## DISCUSSION

### *Thermoregulatory patterns*

At the onset of discussion of the observed thermal responses shown by the *Myotis* in this study, we feel that it is of critical importance to mention that there is a point of distinction in these species between the thermoregulatory capabilities of individual bats and the truly natural thermoregulatory patterns. Most physiological studies of thermoregulation measure the thermoregulatory capabilities of organisms exposed to various controlled, usually stressful conditions. The observation that a bat does or does not control its  $T_b$  in laboratory tests is important to the biology of the species only if the test conditions reflect conditions of the roost which might exist at the time of testing and, further, if the laboratory response agrees with field observations. Hock (1951), for example, showed that *M. lucifugus* is capable of conforming while in a state of summer lethargy, while, contrariwise, Stones & Wiebers (1967) have published that *M. lucifugus* is capable of regulating their  $T_b$  throughout most of the summer period. Our observations both in the field and laboratory indicate that while both *M. lucifugus* and *M. thysanodes* can always, or nearly always, regulate their  $T_b$  during the summer, these bats do also become lethargic at various times throughout the summer. It becomes important, therefore, to illustrate the natural proportions of *M. lucifugus* and *M. thysanodes* which regulate or conform and to attempt to elucidate those parameters which are responsible for causing the individuals tested and, therefore, the significant proportion of the population to "option" for or against regulation.

In *M. lucifugus* at a  $T_a$  of 16°C, a significant tendency exists within the population to regulate  $T_b$ , while at a  $T_a$  of 20°C, no such tendency exists. In *M. thysanodes*, females regulate at both 16 and 20°C. Although it is quite obvious that in several species of bats various proportions of tested bats either regulate or conform (e.g. in *Tadarida brasiliensis* and *Eptesicus fuscus*, Herreid & Schmidt-Nielsen, 1966; *Myotis myotis* and others, Kulzer, 1965a; *Myotis lucifugus*, Stones & Wiebers, 1967; *Carollia perspicillata* and others, Studier & Wilson, 1970; etc.), we have been unable to locate comparative data on the relative proportions of regulators and conformers within any species. At relatively low  $T_a$ 's, *M. thysanodes* as a population exhibit a greater proportion of regulators than *M. lucifugus*. Stones & Wiebers (1967) have segregated the *M. lucifugus* they studied into relative proportions of measurements in which  $T_b$  was greater than or less than 29°C. Within the population of *M. lucifugus* they studied, there are 70.4 per cent of the individuals which maintained a

$T_b$  in excess of 29°C and 29.6 per cent which either conformed or maintained  $T_b$ 's less than 29°C. Although not statistically comparable to our data, it appears that *M. lucifugus* in New Mexico (61.4 per cent regulators: 38.6 per cent conformers at  $T_a$ 's of 16 and 20°C) do not regulate in as great proportions as in Michigan or Indiana. Whether this represents physiological or ecological differences in the populations will be discussed later. At  $T_a$ 's of 16 and 20°C, 75.4 per cent of the *M. thysanodes* tested regulated.

Throughout the summer, significant proportions of both *M. lucifugus* and *M. thysanodes* exhibit trends toward regulation during the pregnancy and post-lactation periods of the reproductive cycle, with lactating individuals exhibiting no significant "preference" toward regulation. This oscillation is more pronounced in *M. thysanodes* than in *M. lucifugus* but does occur in both species. This lack of thermoregulation during lactation disagrees with data on some other chiropterans (e.g. *Miniopterus schreibersi*, Dwyer, 1964; *Myotis lucifugus*, Stones & Wiebers, 1967; etc.) and with the generalization of Stones & Wiebers (1965b) that in the summer, bats exhibit daily rhythmic homeothermy. Present data regarding thermoregulatory patterns in *M. lucifugus* and *M. thysanodes* during the reproductive cycle can best be compared with the data of Stones & Wiebers (1967) for *M. lucifugus*. During pregnancy, bats we studied showed a significant or nearly significant tendency to regulate, with 65 per cent of the *M. lucifugus* regulating at 16°C, 50 per cent regulating at 20°C, with 82 per cent of *M. thysanodes* regulating at 16°C and 79 per cent regulating at 20°C. Stones & Wiebers (1967), however, state that pregnant *M. lucifugus* were never found to be torpid although 10 per cent of their pregnant (their winter-spring group) bats maintained  $T_b$ 's below 29°C in  $T_a$ 's below 29°C. As judged from their data, few, if any, lactating individuals were conformers whereas approximately one-half of the *M. lucifugus* and *M. thysanodes* we tested conformed. Post-lactating bats tested by the previous authors yielded quite variable results with bats exhibiting frequent bouts of hypothermia. A significant proportion of the *M. lucifugus* and *M. thysanodes* we studied were regulators during post-lactation; although in previous studies (O'Farrell & Studier, 1970), we have reported some post-lactating individuals of both species as exhibiting non-homeothermic metabolism. Our data from two successive years (1969 and 1970), therefore, disagrees with itself. It has been proven or assumed that most species of *Myotis* spend the winter in hibernation. In our 1969 study (O'Farrell & Studier, 1970) we found that some *M. lucifugus* and *M. thysanodes* were apparently metabolically capable of hibernation at the time of emigration from the maternity roost; however, none or very few had deposited sufficient fat reserves to withstand a long period of hibernation at the time of exodus from the summer roost (Ewing *et al.*, 1970). In the present study, it is apparent that a significant proportion of the population of adult females were not, based on patterns of thermoregulation, prepared to enter hibernation at the time of exodus from the maternity colony. Similarly, most of the individuals were calculated to not have enough fat reserves to withstand a long period of hibernation in the 1970 sampling. It would seem, therefore, that neither *M. lucifugus* nor *M. thysanodes* begin the period of hiber-

nation, if they indeed hibernate, at the time of emigration from the summer roost. The bats studied by Stones & Wiebers (1967), however, behaved as hibernators during at least part of the post-lactation period. Although subsequently discussed more thoroughly, Menaker (1962) found that *M. lucifugus* undergo rapid changes in thermoregulatory patterns upon arrival and departure from the summer colonies. Based on this observation, there is no real disagreement between our data for successive years or between our data and that of Stones & Wiebers (1967), with thermoregulatory patterns late in the summer being a simple indication of the preparedness of the bats for over-wintering.

Analysis of thermoregulatory data during pregnancy (see Table 2) shows no tendency on the part of pregnant *M. lucifugus* or *M. thysanodes* to regulate during very early and late pregnancy, with a significant tendency to regulate sandwiched between these times. Menaker (1962) and Dwyer (1964) have shown that the thermoregulatory patterns of pregnant bats, particularly in early pregnancy, are strongly affected by the immediate prior thermal environment. There exists then a transition in the thermoregulatory abilities of pregnant bats in hibernals and pregnant bats in maternity colonies, with the former tending to conform and the latter tending to regulate at moderate  $T_a$ 's. This may account for the discrepancy between our data and that of Stones & Wiebers (1967) since their bats were kept in captivity at room temperature or higher for an indefinite period of time prior to testing. It also appears that the individuals carrying intermediate-sized embryos probably all occupied the maternity roost for some considerable period of time prior to testing. These tendencies to regulate while carrying intermediate-sized embryos are much more pronounced in *M. thysanodes* than in *M. lucifugus*. A second related observation is that *M. lucifugus* exhibit a nearly continual influx into the maternity colonies (Cope & Humphrey, 1970; our observations) while the population of *M. thysanodes* levels off after the initial spring influx. Since these bats apparently develop a tendency to regulate only after spending some unknown period of time after returning to their summer roosts and since *M. lucifugus* "trickle" into the maternity colonies while *M. thysanodes* return as a much more coherent population, this may partially account for the prolonged period of time of parturition in *M. lucifugus* (4–10 weeks) and the more concentrated period of parturition in *M. thysanodes* (2–3 weeks). We have found, in addition, that there is no significant tendency in either species to regulate while carrying large embryos. Although disagreeing with the studies of Stones & Wiebers (1967), other investigators have found term-pregnant bats to be torpid, particularly in cool environments (Twente, 1955; Dwyer, 1964). It seems to us that females carrying large embryos may be at a selective disadvantage energetically should they regulate at low (below 16°C) or even moderate (16–20 or 24°C)  $T_a$ 's. This would be particularly true in the bats presently under study since  $T_a$ 's in the maternity roost at that time of year seldom drop below 20°C, and if they do, such low  $T_a$ 's rise rapidly above 20°C shortly after sunrise. Since above a  $T_a$  of 20°C for *M. lucifugus* and 24°C for *M. thysanodes* there is no measurable means of segregating regulators from conformers based on differences in metabolism or  $T_b$ - $T_a$  differential (see Figs. 6 and 7), there

would appear to be no selective advantage to regulation at this time and a selective disadvantage energetically. Similarly, during the period of lactation,  $T_a$ 's in the maternity colony are nearly always above 20°C, therefore, imposing little thermal stress at a time of great energy demand for the synthesis of milk (Davis *et al.*, 1962; Huijbregtse, 1966; Jenness *et al.*, 1971). Again, there would appear to be no selective advantage to regulation during lactation for the same reasons that no such selective pressure apparently exists in late pregnancy. These data refute to some extent the hypothesis that regulation, particularly during all of pregnancy and lactation, is directly hormonally controlled as has been suggested (Kolb, 1950). Although physiological control of thermoregulation, particularly in conjunction with pregnancy and the remaining reproductive cycle, may be causal in the determination of the tendency to regulate, behavioral thermoregulation in the sense of habitat selection is a stronger factor in the determination of thermal patterns. Differences in behavioral and physiological thermoregulation may also account for the discrepancies between our data and that of Stones & Wiebers (1967) and for much of the contradictory thermoregulatory data present in the literature. Being unaware of the environment from which the bats studied by Stones & Wiebers (1967) were taken plus the fact that their bats were acclimated to laboratory conditions, it is impossible to estimate whether or not there might exist selective pressure for regulation within the population of *M. lucifugus* they studied. The selection of a non-stressful thermal environment by *M. lucifugus* and *M. thysanodes* during late pregnancy and lactation presents an energetically favorable situation in which an ability to or the execution of regulation of body temperature is insufficiently advantageous to occur.

Other factors may also exert control on the tendency to regulate. One such factor is food availability or the state of nutrition of test subjects (Herreid, 1963; Stones & Wiebers, 1967; McNab, 1969). These authors have shown that captive bats frequently exhibit different thermal patterns than freshly tested individuals. For these reasons, we have studied bats only on the day of capture to establish natural thermal patterns. It well may be that bats during late pregnancy are not agile enough to feed properly and that the amount of food eaten the previous night may affect the existence of regulation during the next roosting period, which would, of course, also yield results similar to our observations. We feel, however, that even bats in late pregnancy are capable of nearly normal feeding, as judged primarily by the amount of guano produced during late pregnancy which does not appear to differ in quantity from amounts produced at other times of the summer. Other factors which may affect regulation include age, weight, body fat, clustering, etc. We have found no significant relation between age of bats and their tendency to regulate. Stones & Wiebers (1966) found that heavy male *M. lucifugus* were more active in raising their body temperatures than light males, while no such correlation was found in females. The relative fat reserves of *M. lucifugus* or *M. thysanodes* do not significantly affect thermoregulatory patterns. We have frequently observed in both *M. lucifugus* and *M. thysanodes* that among roosting bats, grouped bats tend to be uniformly active or lethargic, while no such uniformity

exists in those bats roosting individually. Similar observations have been recorded by Twente (1955), Kolb (1950), Dwyer (1964) and others.

We wish to discuss lastly the existence of shifters within both species. This sort of thermoregulatory pattern has apparently not been previously described for bats although Stones & Wiebers (1967) have presented data indicative of shifters. We feel that this shifting thermoregulation is evidence of a "sampling" procedure in the bats in which the energy cost of regulation is tested. Theoretically, regulation would be adopted, then, if the energy demand is sufficiently low, or if sufficient fat reserves are present to supply the extra energy concomitant with regulation of body temperature. Conversely, regulation may be abandoned if energy cost is too great. This shifting thermoregulation is primarily a characteristic of *M. lucifugus* and the relative proportion of shifters within the population decreases throughout the summer. Ecologically, this indicates that shifting is eliminated when the roost temperatures are sufficiently high that regulation is not significantly selected for within the population or when there is no selective advantage in thermoregulation.

#### *Levels of controlled body temperatures*

Averaging controlled  $T_b$ 's at combined  $T_a$ 's of 16 and 20°C for the entire summer, we find a  $T_b$  of 31.5°C for *M. thysanodes* (seventy-eight determinations, forty-two individuals) and 29.4°C for *M. lucifugus* (fifty-two determinations, thirty-one individuals). These mean controlled  $T_b$ 's are very low in comparison to most bats (see Kulzer, 1965a; McNab, 1969) and are approximated only by the  $T_b$ 's of some molossids (Herreid, 1963; Leitner, 1966; Morrison & McNab, 1967; McNab, 1969; Studier & Wilson, 1970) and a small vespertilionid, *Histiotus velotus* (McNab, 1969). Stones & Wiebers (1967) found a mean  $T_b$  of 35.3°C for laboratory acclimated *M. lucifugus*. Control of  $T_b$  at lower levels would, of course, lower  $T_b - T_a$  differentials and, consequently, require expenditure of less energy. It would appear that in smaller bats with their greater surface : weight ratio that lower controlled  $T_b$ 's would be a mechanism for energy conservation. McNab (1969) has found that smaller bats tend to maintain lower  $T_b$ 's.

In both *M. thysanodes* and *M. lucifugus* controlled  $T_b$ 's during lactation are significantly lower than during pregnancy and post-lactation. Stones & Wiebers (1967) found a similar drop in regulated  $T_b$ 's in *M. lucifugus* from their winter-spring group to their early summer group. Again, the maintenance of lowered  $T_b$  would seem particularly advantageous from an energetics viewpoint during the period of lactation. The further probable importance of energy demand in control of  $T_b$  is reinforced by the previous observation that there is no significant tendency on the part of either species to regulate during lactation. The maintenance of regulated  $T_b$ 's during post-lactation which occurs in both species seems to be energetically wasteful. Furthermore, we cannot present a hypothesis to explain the observation that regulated  $T_b$ 's during post-lactation are lower than during pregnancy in *M. lucifugus*; however, this would act in the conservation of energy.

The relationship of regulated  $T_b$  to  $T_a$  is curvilinear in both species which, of course, is similar to the theoretical relation of  $T_b$  to  $T_a$  in homeotherms (see, for

example, McNab & Morrison, 1963). In most homeotherms, the  $T_b$ - $T_a$  relationship is depicted by two straight lines, one representing controlled  $T_b$  at low  $T_a$ 's and one representing  $T_b$ 's in relation to  $T_a$ 's during hyperthermia. In *M. thysanodes*,  $T_b$  is controlled at  $T_a$ 's of 14–24°C; there is then a region of partial hyperthermia in a  $T_a$  range of 24–32°C and, finally, a region of true hyperthermia in  $T_a$ 's from 32–40°C (see Table 6). To rephrase, *M. thysanodes* maintains a controlled  $T_b$  at low  $T_a$ 's, maintains a semi-controlled  $T_b$  which approaches  $T_a$  in  $T_a$ 's of 24–32°C and  $T_b$  approximates  $T_a$  during true hyperthermia, in  $T_a$ 's greater than 32°C. This relation is also true in *M. lucifugus* although partial hyperthermia is initiated at  $T_a$ 's above 20°C. The prime difference in  $T_b$ - $T_a$  relations in these regulating bats and the relation in other homeotherms is the  $T_a$  range of transition between  $T_a$ 's in which  $T_b$  is accurately controlled and  $T_a$ 's which will induce hyperthermia. Hyperthermia begins then at  $T_a$ 's between 24 and 28°C in *M. thysanodes* and between 20 and 24°C in *M. lucifugus*. The  $T_a$ 's in which most bats enter hyperthermia are much higher than reported here (see Leitner, 1966; Carpenter & Graham, 1967; Morrison & McNab, 1967; McNab, 1969). Furthermore,  $T_a$ 's which induce partial hyperthermia are below the zone of thermoneutrality for these species (Stones & Wiebers, 1967; O'Farrell & Studier, 1970; Studier & O'Farrell, unpublished data). The observation that  $T_b$  begins to rise at  $T_a$ 's below the thermoneutral zone in these species is not surprising in view of the low regulated  $T_b$ 's exhibited by them, and also, because of the loss of distinction between regulators and conformers at low  $T_a$ 's. Again, the thermolability in the  $T_a$  range of partial hyperthermia does not place thermal stress on the bats and, in fact, is also an energetically favorable situation.

Lack of controlled  $T_b$  at high  $T_a$ 's in the species we studied agrees with previously published papers which show such hyperthermia to be a common feature in small bats (see Licht & Leitner, 1967b). Henshaw & Folk (1966) have reported that *M. lucifugus* can maintain  $T_b$ 's significantly lower (3°C or more) than  $T_a$  at  $T_a$ 's of 35°C or more. Hock (1951), however, has found this species to always become hyperthermic at similar  $T_a$ 's. Although our data agree in great part with that of Hock (1951), we have found that some pregnant *M. lucifugus* do maintain  $T_b$  to  $T_a$  differentials. Attempted regulation at high  $T_a$ 's in pregnant bats does have some obvious survival advantages for the species; however, we must agree with Licht & Leitner (1967b) in their statement that the energy requirement and water loss requirements necessary to maintain significant differentials at high  $T_a$ 's are simply prohibitive.

Additionally, at high  $T_a$ 's, most *M. thysanodes* and a few *M. lucifugus* periodically exhibited unusual behavior worthy of mention. Often throughout the summer during the hottest parts of the day, bats became unresponsive; i.e. they did not respond to our presence in the roost, did not respond to light and exhibited a general lethargy until the bats were individually touched. When an individual was picked up in these conditions, its immediate response was that of a normally active bat. Although analyses of oxygen consumption are not as yet complete and will be reported in detail in a later publication, some bats studied in the laboratory

exhibited abnormally low metabolic rates at high temperatures and we, therefore, suggest that during the hottest parts of the day, during the summer, most *M. thysanodes* and a few *M. lucifugus* do aestivate.

#### *Other aspects of thermoregulation*

Since male *Myotis* are rarely collected in temperate regions during the summer, relatively little data concerning thermoregulation are available. Similarly, we have studied thermal patterns in few adult males. It generally appears that there is little, if any, difference in the thermoregulatory patterns of adult male and female *M. thysanodes*, *M. lucifugus* or *M. yumanensis*. Bradley & O'Farrell (1969) found no difference between the sexes in thermoregulation in *Pipistrellus hesperus*. Herreid & Schmidt-Nielsen (1966) mention no differences in thermoregulation in male or female *Tadarida brasiliensis* or *Eptesicus fuscus*, nor do Lyman & Wimsatt (1966) for *Desmodus rotundus*. Although not specifically stated, several authors studying *Myotis* (Stones & Wiebers, 1965a, 1967; Fenton, 1970) give the indication that in the summer, males choose cooler microclimates in which to roost and do not "choose" to regulate  $T_b$  in as high proportions as do females. We judge that the majority of both very early and very late summer *M. lucifugus* males we observed were torpid. Menaker (1962) showed differences in thermal patterns of summer and winter females and stated that winter males exhibited thermal patterns similar to winter females and that summer females exhibited abnormal arousal patterns from even moderately low  $T_a$ 's (7–11°C). Summer females in our studies are quite capable of "normal" arousal from a  $T_a$  of 16°C; and, based on the single example mentioned previously, so are males. Stones & Oldenburg (1968) observed normal and rapid arousal of a summer male *M. lucifugus* from a  $T_a$  of 5.5°C, while summer female *M. lucifugus* were incapable of such rapid arousal. There appear, therefore, to be some subtle or simply poorly understood differences both in thermoregulatory capabilities and natural thermal patterns of male and female *Myotis*.

Minimum  $T_b$  necessary for flight in the *Myotis* we studied and other values from the literature are shown in Table 8. There are no significant differences in minimum  $T_b$  required for flight in winter or summer in *P. hesperus*, *Antrozous pallidus* and *Myotis californicus* (O'Farrell & Bradley, 1968), nor in males or females of these three species (O'Farrell and Bradley, 1968) or *M. lucifugus* or *M. thysanodes*. In *Plecotus townsendi*, females may be able to initiate flight at lower  $T_b$ 's than males (O'Farrell & Bradley, 1968). Judging from the data in Table 8, bats may be roughly divisible into two groups based on minimum  $T_b$  required for flight. One group would include those bats in which average  $T_b$ 's of 29–33°C are prerequisite to flight, and the other group includes species capable of flight at average  $T_b$ 's between 20 and 28°C. *M. lucifugus* falls into the first group while *M. thysanodes* falls into the second. Comparison of minimum  $T_b$  required for flight with regulated  $T_b$  throughout the year provides an interesting paradox in these two species. While *M. thysanodes* can initiate flight at a mean minimum  $T_b$  of 24.3°C, the mean controlled  $T_b$  is 31.5°C throughout the summer, and controlled  $T_b$  in each reproductive state is greater than 24.3°C. In *M. lucifugus*, however, minimum  $T_b$

required for flight is 30.3°C while mean regulated  $T_b$  in the summer population is 29.4°C. Additionally, mean controlled  $T_b$  during lactation in *M. lucifugus* is 26.3°C, a  $T_b$  which is too low to initiate flight.

Bartholomew *et al.* (1964) discuss the ontogeny of thermoregulation in *Pteropus poliocephalus*, a flying fox, which is apparently the only published study dealing with the development of thermoregulation in bats. Their study shows that at an age of 2 days, neonates already possess some physiological thermoregulatory capabilities. As these young bats grow, they are capable of maintaining higher and higher controlled  $T_b$  until at 1 month, they were able to maintain  $T_b$  constant at adult levels at a  $T_a$  of 10°C. This pattern of ontogeny of thermoregulation is similar to that of other small mammals (Hissa, 1968). In general, development of thermoregulation involves both an increasing ability to regulate  $T_b$  at successively lower  $T_a$ 's and an ability to maintain higher and higher  $T_b$ 's at specific  $T_a$ 's. Since adult *M. lucifugus* and *M. thysanodes* frequently show no significant tendency to regulate, because regulated  $T_b$ 's vary greatly, and since adults show "shifting" as a part of their thermal patterns, it is difficult to discuss ontogeny of thermoregulation in neonates of these species. We have found metabolic patterns similar to those of adults in *M. thysanodes* at 4.6 days and in *M. lucifugus* at 9.6 days. *M. thysanodes* may be able to regulate at ages younger than 4.6 days since we did not test any younger bats of this species. Some older bats of each of these species exhibited no tendency to regulate, indicating again that in young bats, as well as adults, the ability to regulate may not be evident in laboratory or field situations and the expression of thermoregulation in young may be profoundly affected by state of nutrition, thermal stress, behavior, etc. The development of some thermoregulatory capabilities in *P. poliocephalus* at 2 days of age may be indicative of earlier development of regulatory capabilities in megachiropterans or in those species which are categorized as good homeotherms. It would not be surprising to find delayed ontogeny of thermoregulation in *M. lucifugus* and *M. thysanodes* since adults frequently do not regulate. In connection with this, regulation might become evident in neonatal *M. thysanodes* sooner than in *M. lucifugus* since adult *M. thysanodes* regulated in significantly greater proportions than adult *M. lucifugus*. Also, the energetic cost of regulation in these very small mammals would be excessive. Finally, thermal patterns of volant, immature males and females of both species are identical to those of adult females.

### *Behavior and final comments*

The great bulk of the previous discussion has dealt with physiological thermoregulation. Habitat selection of appropriate summer roosting sites by these species totally eliminates a general requirement for thermoregulation during late pregnancy and throughout lactation in the situation presently under study, particularly when combined with diurnal and seasonal thermoregulatory movements.

Diurnal thermoregulatory movements have been described in several microchiropterans (Licht & Leitner, 1967b). The intraroost daily movements described

by these authors appeared to represent a "compromise between avoidance of extremely high  $T_a$ 's and a predilection for protected roosting sites". Similar thermoregulatory movements were evidenced by both *M. lucifugus* and *M. thysanodes*. Preferred temperatures for several *Myotis* are generally lower (Harmata, 1969) than those encountered by the bats studied by Licht & Leitner (1967b). The roost we have studied offered a much greater range of temperatures and might, therefore, be considered a more desirable site for a maternity colony. Movements of *M. lucifugus* in the present study were essentially identical to those described by Licht & Leitner (1967b) except that these bats almost invariably avoided all temperatures in excess of 39°C and movements vertically were much more extensive than those previously described. Downward movements of 4-7 ft were a daily occurrence. In the case of *M. thysanodes*, a slightly different thermoregulatory activity occurred. Prior to noon, *M. thysanodes* roosted in closely packed clumps on the west side of the attic roof. After noon, when the sun directly heated the west side, these bats flew to the east facing part of the attic roof where they positioned themselves farther down a beam. As the afternoon progressed the group continued to move as a whole farther down the beam leaving only several stragglers. It should be stressed that they remained in a coherent group and did not spread out from one another. Additionally, whereas only a very small percentage of *M. lucifugus* ever exhibited in roost "cooling off" flights, a moderate percentage of *M. thysanodes* exhibited this behavior during the hottest part of the day during certain times of the summer. This statement introduces the final aspect of behavioral thermoregulation—seasonal in-roost movements.

The roost presently under study is a very large, compartmentalized, complex attic which has been briefly described (Studier *et al.*, 1970) and will be described in more detail in a later paper. Throughout it there exists a wide variety of thermal conditions. Of importance to the present discussion, however, is only that the southernmost room in the attic is invariably much cooler than any of the others. Particularly in the case of *M. thysanodes*, the *Myotis* studied show a marked tendency to roost in this southernmost room prior to leaving the summer roost, with the interim spent in the other hotter rooms. This observation would seem to be explained previously in connection with Menaker's (1962) observation that the thermoregulatory performances of *Myotis* are directly dependent on their prior thermal history.

All of these features should be classified under behavioral thermoregulation. Behavioral thermoregulation, therefore, appears to be extremely important in the life cycle of these bats and, perhaps, is as important as physiological thermoregulation. Saint Girons *et al.* (1969) discuss the extreme importance of behavioral thermoregulation in *Rhinolophus ferrumequinum*. Regulation may be partially under hormonal control during part of the pregnancy period; however, the prime factor which appears to determine whether or not these bats regulate is the energy demand required for maintenance of a controlled  $T_b$  at the environmental  $T_a$ .

Winter roosts of *M. lucifugus* and *M. thysanodes* are unknown in New Mexico. It has been generally assumed that both species over-winter by hibernating. It is

obvious that at the time of departure from the summer roost, neither species is thermally capable of hibernation and neither species has deposited sufficient fat to over-winter in hibernation. The previous discussion, however, and data published earlier (O'Farrell & Studier, 1970) indicate that *M. lucifugus* is better prepared for hibernation than *M. thysanodes*. Furthermore, several bats which are capable of initiating flight at low  $T_b$ 's have been shown to be active throughout the entire year (O'Farrell & Bradley, 1968; Bradley & O'Farrell, 1969). Whereas bats such as *M. lucifugus* which require relatively high  $T_b$ 's to initiate flight show a significant rise in  $T_b$  after prolonged flights, bats such as *P. hesperus* and *Myotis californicus* which are capable of initiating flight at low  $T_b$ 's and are active throughout the year do not exhibit a rise in  $T_b$  after prolonged flight (Bradley & O'Farrell, 1969; O'Farrell & Bradley, 1970). We have also collected *M. thysanodes* in the vicinity of Las Vegas, New Mexico, as late as 9 November after several heavy snowfalls. In view of this information we feel compelled to conclude not only that *M. lucifugus* after emigration from this summer roost does enter hibernation after deposition of sufficient fat reserves but also that *M. thysanodes* probably migrates southward from this summer roost, or at least moves to lower elevations, where members of this species are periodically active throughout the winter.

#### SUMMARY

Thermal patterns and levels of thermoregulation in *M. thysanodes* and *M. lucifugus* throughout their tenure in summer colonies (April–September), although quite variable, have shown that:

1. Summer populations of the two species show a tendency to regulate their body temperature ( $T_b$ ) at moderately low ambient temperatures ( $T_a$ ) with a more pronounced tendency in *M. thysanodes*.

2. Although more pronounced in *M. thysanodes*, these bats regulate during pregnancy and post-lactation but not during lactation.

3. Individuals of both species are found to "shift" from regulation to conforming and vice versa at relatively low  $T_a$ 's. This tendency to shift decreases significantly throughout the summer in *M. lucifugus*.

4. The proportions of regulators during pregnancy is significantly greater in mid-pregnancy than in early or late pregnancy but bears no significant relationship to the age or amount of fat deposited by adult females.

5. Bats of both species apparently regulate if the energy demand required for regulation is not excessive.

6. The relation between  $T_a$  and  $T_b$  of regulators is curvilinear in both species.

7. Regulating, lactating bats maintain their  $T_b$  significantly lower than pregnant or post-lactating regulators. In *M. lucifugus*,  $T_b$  during post-lactation is significantly lower than during pregnancy. Regulated  $T_b$  in *M. thysanodes* as a population and during pregnancy, lactation and post-lactation are always significantly higher than in *M. lucifugus*. Weight of embryos does not relate to the level of controlled  $T_b$  in regulators.

8. It is possible to distinguish regulators from conformers in *M. thysanodes* only at  $T_a$ 's of 24°C or less and in *M. lucifugus* only at  $T_a$ 's of 20°C or less.  $T_b$ 's of conforming bats appear to increase as summer progresses.

9. *M. thysanodes* become partially hyperthermic in  $T_a$ 's exceeding 24°C, while *M. lucifugus* become partially hyperthermic in  $T_a$ 's greater than 20°C. Essentially all bats become fully hyperthermic in  $T_a$ 's greater than 32°C with only a very few which attempt to regulate at high  $T_a$ 's.

10. At high  $T_a$ 's, some bats of both species appear to aestivate.

11. Based on relatively little data, there are not gross differences in the thermal patterns of males and females of these species.

12. Minimum  $T_b$  required for flight averages 30.3°C for *M. lucifugus* and 24.3°C for *M. thysanodes*.

13. Neonatal *M. thysanodes* show metabolic patterns similar to those of adults no later than 4-6 days after birth. In *M. lucifugus*, metabolic rates indicative of regulation are not evidenced until neonates are 9-6 days old.

14. Behavioral thermoregulatory features such as habitat selection together with daily and seasonal movements may be of greater survival value to these species than physiological thermoregulation.

15. *M. lucifugus* probably over-winters from this summer roost by hibernating while *M. thysanodes*, after an initial migration, is probably active periodically throughout the winter.

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*Key Word Index*—Thermoregulation; bats; Chiroptera; Vespertilionidae; *Myotis thysanodes*; ontogeny of thermoregulation; reproductive condition on thermoregulation; behavioral thermoregulation; fat, age, season on thermoregulation; thermoregulatory patterns; *Myotis lucifugus*.