1

of/de

1

National Library
of Canada

Bibliothèque nationale
du Canada

Canadian Theses Service

Services des thèses canadiennes

Ottawa, Canada
K1A 0N4

CANADIAN THESES

THÈSES CANADIENNES

NOTICE

The quality of this microfiche is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us an inferior photocopy.

Previously copyrighted materials (journal articles, published tests, etc.) are not filmed.

Reproduction in full or in part of this film is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30.

**THIS DISSERTATION
HAS BEEN MICROFILMED
EXACTLY AS RECEIVED**

AVIS

La qualité de cette microfiche dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de qualité inférieure.

Les documents qui font déjà l'objet d'un droit d'auteur (articles de revue, examens publiés, etc.) ne sont pas microfilmés.

La reproduction, même partielle, de ce microfilm est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30.

**LA THÈSE A ÉTÉ
MICROFILMÉE TELLE QUE
NOUS L'AVONS REÇUE**

HETEROTHERMY AND ACTIVITY IN THE BIG BROWN BAT, EPTESICUS

FUSCUS: A FIELD STUDY

by

© Doris Audet, B.Sc.

A thesis submitted to the Faculty of Graduate Studies
and Research in partial fulfillment of the requirements
for the degree of Master of Science.

Department of Biology, Carleton University

Ottawa, Canada

December 1986

Permission has been granted to the National Library of Canada to microfilm this thesis and to lend or sell copies of the film.

The author (copyright owner) has reserved other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without his/her written permission.

L'autorisation a été accordée à la Bibliothèque nationale du Canada de microfilmer cette thèse et de prêter ou de vendre des exemplaires du film.

L'auteur (titulaire du droit d'auteur) se réserve les autres droits de publication; ni la thèse ni de longs extraits de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation écrite.

ISBN 0-315-35846-7

The undersigned hereby recommend to the Faculty of
Graduate Studies and Research acceptance of this thesis, submitted by

Doris Audet, B.Sc., in partial fulfillment of the
requirements for the degree of Master of Science.

Chairman, Department of Biology

Supervisor

Carleton University

December 1986

ABSTRACT^G

Using radio-telemetry, I studied the importance of heterothermy for free-living Eptesicus fuscus during the warm season. The use of daily torpor by Eptesicus fuscus was influenced by ambient temperature (T_a) and varied with reproductive state. Lactating females used torpor significantly less than pregnant and non-reproductive females. The use of torpor coincided with a greater proportion of warmer nights during lactation and the tendency of lactating females to remain active more often than the others at nightly minimal ambient temperatures between 9° and 12°C . Active bats showed temperature variations that differ from strict homeothermy suggesting that they remained active at lower energetic costs. The time of parturition varied between two consecutive years as a result of a different extent in the use of torpor by pregnant females. Foraging activity of the bats was also affected differently by ambient temperature according to different reproductive states. Foraging time of females in late pregnancy did not increase under warmer ambient temperatures, but it did during lactation. Heterothermy appears to be an important factor influencing the energetic balance of free-living bats.

ACKNOWLEDGEMENTS

Firstly, I want to extend my warmest thanks to my supervisor Dr Brock Fenton. Not only did Brock provide academic, logistic, moral and financial support, but he was also the most outstanding contributor to the "improvement" of my english vocabulary. Thanks very much for giving me the opportunity to go to Africa, to which I am addicted now, and where I learned about eye-ball-collecting-trees and hyena-resistance.

I also want to thank the other members of my advisory committee, Drs H.G. Merriam and B.J.R. Philogène. I am especially grateful to Gray for innumerable, but always appreciated criticism and helpful suggestions. Thanks to G. Monette, R. Thomas and J.Fox for statistical advice.

Nils Meyer, Marc Audet and Kathy Worton kindly modified their circadian rhythms to help with the field work. Thanks Nils for climbing those high and steep roofs without complaining (I know, we don't all have the hots for heights!), and letting me "sleep in" during some of those long-cold-nights when the bats stayed in their comfortable roosts and entered torpor while laughing at us.

Thanks to the Bat Lab.: Hugh Aldridge, Jonathan Balcombe, Mark Brigham, Brian Hickey, Mike Stoneman and Virginia Wai-Ping who provided help in so many ways (including chocolate), and most importantly, for their friendship.

Thanks to Jeanne Audet for lots of "cheer up" phone calls and for making possible the acquisition of the "Doris-mobile".

Finally, I want to acknowledge the financial support of NSERC, for which I am grateful.

TABLE OF CONTENTS

	Page
Abstract	iii
Acknowledgements	iv
Table of contents	v
List of Tables	vii
List of Figures	viii
Introduction	1
Study Animal and Study Site	3
Materials and Methods	4
I- Radio-transmitters	4
II- Bat capture and data collection	5
III- Statistical analysis	6
Results	7
A- Heterothermy	7
I- Daily variations of body temperatures	7
II- Use of torpor	8
III- Roost temperatures	9
IV- Behavioural observations	10
V- Timing of parturition and growth of young	10
B- Foraging Activity	12
Discussion	13
I- Daily variations in body temperatures	13
II- Use of torpor	14

III- Foraging activity	19
IV- General discussion	21
Conclusions	23
Tables	24
Figures	31
Literature Cited	43

LIST OF TABLES

	Page
1. Sample sizes temperature recordings	24
2. Occurrence of torpor and active state	25
3. Results of χ^2 test comparing occurrence of the two thermoregulatory strategies	26
4. Results of Wilcoxon 2-sample test comparing T_b min	27
5. Results of Wilcoxon 2-sample test comparing T_r max	28
6. Sample sizes foraging data	29
7. Thermoregulatory strategy following different foraging times	30

LIST OF FIGURES

	Page
1. Photograph of the radio-transmitters	31
2. Hourly changes in body temperatures	32
3. Incidences of torpor and active state	33
4. Minimal body temperatures	34
5. Hourly changes in roost temperature	35
6. Minimal roost temperatures	36
7. Maximal roost temperatures	37
8. Temperature readings from thermistors	38
9. Hourly changes in roost temperatures and temperatures from thermistors	39
10. Changes in body mass of pregnant females	40
11. Foraging time	41
12. Factors affecting thermoregulation	42

INTRODUCTION

There is some diversity of thermoregulatory strategies in bats. The large Megachiroptera are homeothermic and smaller tropical microchiropterans include homeothermic and heterothermic species. Temperate Microchiroptera are heterotherms (Lyman 1970). The thermoregulatory pattern of a species has been related to size and feeding habits (McNab 1969, McNab 1970, Studier and Wilson 1969).

Heterothermy was considered to be a primitive characteristic of bats (Hock 1951). Studier and Wilson (1969) suggested that the variation in thermoregulatory abilities of individuals of the same species could reflect different physiological states or the non-adaptive value of thermoregulation. McNab (1969) suggested that torpor evolved in the tropics in response to the high cost of thermoregulation for animals of small body mass. The inability of some insectivorous species to enter torpor may be the major factor limiting their distribution. All temperate bat species are insectivorous and therefore exposed to a discontinuous food supply. One of the most important factors influencing energy expenditure is the thermal regime in the environment (McNab 1982). So heterothermy, which allows daily torpor as well as seasonal hibernation, is important in reducing the energetic constraints of some bats. Most of the studies about temperature regulation in heterothermic bats were conducted in the laboratory. They include studies concerning the response in body temperature to ambient temperatures for different bat species (eg. Davis and Reite 1967, Reite and Davis 1966). Other studies related rate of metabolism to body temperatures for different species (Hock 1951,

O'Farrell and Studier 1970, Stones and Wiebers 1967). So far, little information is available on the occurrence of daily torpor in free-living bats (Kunz 1980).

Foraging flights also involve great energetic cost. Continuous flight under laboratory conditions showed that a bat weighing 70 to 110 grams may increase its metabolic rate more than 34 times over the resting state (Thomas and Suthers 1972). There are variations in flight cost related to different foraging strategies (Bell et al. 1986).

The purpose of this study was to test two hypotheses:

I- That heterothermic bats should make differential use of daily torpor, according to the different energetic constraints associated with their reproductive state.

II- That heterothermy would allow bats to adjust their foraging activity according to climatic conditions, to minimize the cost/gain ratio of foraging.

Radio-telemetry allowed me to gather information on variations of body temperature and foraging activity of Eptesicus fuscus, a temperate insectivorous bat. Using radio-transmitters to monitor body temperatures, I followed the hourly changes not observable otherwise. Radio-telemetry also allowed me to collect information about the roost microclimate.

STUDY ANIMAL AND STUDY SITE

Eptesicus fuscus was well suited for this study because it is abundant, widely distributed and has been studied extensively (eg. Barbour and Davis 1969, Brigham 1985, Kunz 1974, Philips 1966). Eptesicus fuscus weighs between 12.1 and 23.6 grams (van Zyll de Jong 1985) and is quite robust.

I conducted the field work in southeastern Ontario (Manotick and Stittsville) between May and October 1985 and May and August 1986. In that area, females form nursery colonies in buildings during the summer months, while adult males are seldom found in those buildings; they are thought to roost singly or in small groups in other roosts. After a two month gestation period the females usually give birth to twins, and lactation lasts about six weeks. The young start flying around their fourth week and have attained adult size by the fall (Kunz 1974).

MATERIALS AND METHODS

I- Radio-transmitters

In this study I used temperature-sensitive radio-transmitters (Holohill Systems Ltd, Woodlawn, Ont.) to collect temperature and activity data. For each transmitter, a calibration curve (pulse rate versus temperature) was plotted prior to use in the field. The temperature sensor on the surface of the 1985 transmitters (0.9 g) measured skin temperature and their temperature sensitivity generally ranged from 15 to 40 °C. The 1986 transmitters included some transmitters similar to the 1985 model and some with the temperature sensors away from the unit (1.0 g) permitting recording of roost temperature (Fig. 1). All the 1986 transmitters had improved and more consistent sensitivity (0 to approx. 40 °C) and better calibration curves which allowed me to estimate the temperatures to $\pm 0.5^{\circ}\text{C}$ between 10° and 35° C. The accuracy of the calibration decreases above 40° ($\pm 1^{\circ}\text{C}$) because of the exponential shape of the curve at the extremes of temperature. I measured pulse rates by timing 10 pulses 3 times. The 1985 transmitters were used to determine if the bats were active or torpid. I used the 1986 transmitters to estimate the actual temperatures. Surface skin temperature in the interscapular region was used to infer body temperature. The estimation of body temperature by this method is possible because of the small size of the bats and their high thermal conductances.

I attached the transmitters using Skin Bond Cement (Canadian Howmedica, Guelph, Ont.). The radio signals (173.800 to 174.075 MHz) were read by a Merlin 12 receiver (Custom Electronics, Urbana, Illinois)

and 5-element Yagi antenna.

II- Bat capture and data collection

I collected information on bats from six maternity colonies. Emerging bats were caught at or near roost entrances in Tuttle traps (Tuttle 1974), mist nets or hand nets. Inside the main building used by one of the colonies, the bats often were accessible and could be caught by hand. I caught three males in a Tuttle trap at the entrance of a night roost. Captured bats were banded (National Band and Tag. Co., Newport, Kentucky), sexed, weighed and their forearms measured. Reproductive state of the females was determined directly during late pregnancy, lactation and post-lactation. For the females captured in May, pregnancy was assessed by subsequent captures. Females with body masses >18.8 g were considered to be in late stage of pregnancy because 18.8 g corresponded to the maximum weight of females after parturition. Only one of the 14 females radio-tagged in May and for whom pregnancy could not be determined by palpation was not recaptured.

No data were collected on the night the transmitters were attached. The next day I started to monitor foraging activity and to collect temperature data. From the time foraging bats returned to their roost, I took temperature readings from the radio-tags (body and roost temperatures) every half hour, every third day. Outside ambient temperature (T_a) was noted for each reading from the transmitters. Foraging activity was monitored every night until the transmitters were shed.

I used two receivers to monitor the foraging activity of the bats. A

receiver at the roost was used to record exit and return time of the bats (± 1 min) as well as to monitor the activity of the bats within range of the roost. The second receiver was used to follow one bat every night during its entire foraging period.

Hourly temperature readings were made from thermistors in attics of buildings used by two of the bat colonies from May to August 1985. In mid-May 1986, a temperature transmitter was placed in the position in attic where the bats sometime roosted. Later (late June to the end of July) thermistors were set at three locations known to be used as roosts.

III- Statistical analysis

I used the Kruskal-Wallis non-parametric one way analysis of variance (Siegel 1956) to test for significant differences in the temperature data from radio-tracking. When overall significant differences were detected, I made multiple comparisons using the Wilcoxon two-sample test (Sokal and Rohlf 1981) and adjusted the levels of significance according to the Bonferroni procedure (Miller 1966).

I used a SAS computer program (Allen Ray 1982) to compare the daily means and ranges ($T^{\circ}\text{max}-T^{\circ}\text{min}$) of temperatures recorded at the three locations in the attic. The analysis of variance of the means and ranges included a test for autocorrelation between consecutive days, the Durbin-Watson procedure (Harvey 1981).

RESULTS

A-HETEROTHERMY

I collected temperature data for 143 bat-days from 59 Eptesicus fuscus (Table 1). Most of my data are from adult females but three of the adult males were caught and observed at nursery colonies, the other one roosted by himself. Only two juveniles (one male, one female) were radio-tagged in late July and September when their size allowed them to carry a transmitter.

I-Daily variations of body temperatures

The body temperatures (Tb) of roosting Eptesicus fuscus recorded in 1986 varied from 9.7° to 41°C . The daily changes in body temperature showed two patterns: 1) remaining active i.e. maintaining Tb between 27.6° and 41°C during the entire day. 2) entering torpor i.e. allowing Tb to follow ambient (Fig. 3). Active bats show fluctuations in their body temperatures and the differences between the maximum (Tb max) and minimum (Tb min) within a day varied from 2 to 10°C .

When the bats entered torpor, however, their Tb's dropped as much as 15.8°C within 30 minutes. The slope of the cooling curve depended on the initial difference between Tb and Ta. Before entering torpor, the bats remained active for different time intervals after entering the roost. Although the sample size precluded statistical analysis, pregnant females remained active longer than the others before entering torpor when Tb varied passively with Ta. The time of arousal from torpor also varied. One lactating female actively increased her body temperature from 23° to 31.3°C ($0.28^{\circ}/\text{min}$) as soon as 08:30h, and at the other extreme,

some bats started to arouse only 20 minutes before they left the roost (maximum warming rate $0.81^{\circ}\text{C}/\text{min}$). When the bats actively increased their body temperatures, they remained active until emergence, with the exception of a juvenile male who increased his T_b from 27° to 34° within 15 minutes at 15:30h and entered torpor again 30 minutes later. He then started to rewarm 30 minutes before leaving the roost at 19:05h.

II- Use of torpor

Male and female bats, both adults and juveniles stayed active or entered torpor. Females in all reproductive states also used both strategies (Table 2). Two bats in the same reproductive state sometimes used a different strategy on a given day (Fig. 2). However, the occurrence of each strategy (quantified as numbers of bat-days) was influenced by the T_a 's and varied according to sex and reproductive state. T_a influenced the occurrence of each strategy within reproductive states, for example, in 1986 females observed during late pregnancy did not enter torpor while those in 1985 did (Table 2). The minimal T_a 's encountered by females in late pregnancy in 1985 were significantly lower than those in 1986 (Wilcoxon 2 sample test, $C=125$ $p<0.001$ $N=16$). The response of the females to a given range of minimum ambient temperatures varied according to their reproductive state (Fig. 3). During cold nights ($T_a \text{ min} < 9^{\circ}\text{C}$) most bats entered torpor but on warm nights ($T_a \text{ min} > 12^{\circ}\text{C}$), most females remained active. Between T_a 's of 9 and 12°C most lactating females stayed active significantly more often than the non reproductive and pregnant females (Table 3). Males, observed in most instances at $T_a \text{ min}$ of 9° to 12°C , usually entered torpor but the sample size precludes

statistical analysis.

For the bats tagged in 1986 I also used the T_b min recorded every night as an indication of the thermoregulatory strategy (Fig. 4) and the same two patterns can be observed (i.e. torpor or activity). A Kruskal-Wallis one way analysis of variance indicates a significant difference in T_b min between early pregnancy, late pregnancy and lactation ($H=10.66$, $df=2$, $p<0.01$ $N=26$). Multiple comparisons show a significant difference between lactating and early pregnant females (Table 4) which can be attributed to the lower range of T_a 's encountered by the early pregnant females (Fig. 3). The other categories (male, juvenile female, non reproductive females) were not included in this analysis because of the sample size.

III- Roost temperatures

The daily changes of roost temperature (T_r) over time (Fig. 5) resemble the daily curves of body temperature. Large variations between subsequent recordings could be accounted for by the movements of an active bat within the roost. High T_r 's (Fig. 5a) are often due to clustering behaviour of the roosting bats. A Kruskal-Wallis analysis of variance indicates no significant difference in the T_r min (Fig. 6) between pregnant, lactating and post-lactating females ($H=3.26$, $df=2$, $N=23$, $p>0.1$) but significant difference between T_r max (Fig. 7) at these three reproductive states ($H=6.6$, $df=2$, $N=24$, $p<.05$). Multiple comparisons show a significant difference between the lactating and post-lactating females (Table 5) attributable to the higher T_a 's encountered by the post-lactating females.

Daily temperature profiles from three locations where the bats occasionally roosted differ (Fig. 8), but there are no significant differences between the daily mean temperatures at those three locations ($F=2.937$ $p=.0957$ $N=35$). The ranges of daily temperatures at p1 are, however, significantly different from those at the other two locations ($F=205.2$ $N=35$ $p<0.001$). The daily changes in T_r also always differ from the temperature profiles from fixed locations in the building (Fig. 9).

IV- Behavioural observations

At least five of the six maternity colonies used roost sites in more than one building. Within a building the bats used different sites as roosts. In the building where I put the temperature sensors I noticed that the site used as a roost varied with the weather conditions. On four occasions when the weather was cool and cloudy, 30 to 40 bats roosted in a cluster at the location of the temperature probe recording the highest daytime temperatures (p3 in Fig.8). On four sunny days, no bats roosted at this site, but I could however hear them squeaking and scratching in interstices of the stone wall (p1 in Fig. 8). In July, these bats started to roost in the overhanging part of the roof, which was inaccessible to us. The members of this colony moved to another building in mid-June, after I mist netted near the roost entrance on four consecutive nights and began to move back about 10 days later.

V- Timing of parturition and growth of young

The timing of parturition was different in 1985 and 1986. In 1986, most of the bats gave birth between 30 May and 4 June when 28 of 30 bats in the roost already had their pups. The exact time of parturition

is not known for 1985 but none of 20 females captured between 3 and 5 June was lactating. The increase in weight of pregnant females was also faster in 1986 than 1985 (Fig. 10).

The first volant young were caught on the 27 June in 1986 and on 10 July 1985. I caught juveniles on 18 July of 1985 and 1986. There was no significant differences in the masses of either juvenile males or juvenile females between the two years (One way ANOVA, $F=1.021$ $p>0.1$ $N=10$ for females; $F=1.29$ $p>0.25$ $N=8$ for males).

B- FORAGING ACTIVITY

I observed foraging activity for 134 bat-nights (Table 6). Only the lactating females made more than one foraging trip per night; they made one to six foraging trips a night. I considered time away from the roost equivalent to foraging time because for all the time I was in contact with the bats away from the roost (1986), they used night roosts on only 6 of 134 bat nights (4.6% of the nights).

The time spent foraging and the response to ambient temperature varied seasonally (Fig. 11). In May, foraging time appears to have been independent of T_a 's at dusk. The increased variability in foraging time in June coincides with the beginning of lactation. Both lactating and post-lactating females often foraged for longer times at high T_a 's. Later in the season, foraging time decreased. On 4 of 10 bat-days in September, the bats went out for a short time (less than 50 min), coinciding with a high proportion of cold nights.

On 15 occasions bats did not forage (8 days) and on 14 of them the T_a at dusk was below 14°C . Bats that did not forage were either active or torpid when others emerged. In every case, however, they eventually entered torpor (Table 7). This table also shows the variability in thermoregulation following different foraging times.

DISCUSSION

I- Daily variations in body temperatures.

I observed two patterns in the daily variations of Tb for free-living Eptesicus fuscus: entering torpor or maintaining a relatively high body temperature. Even when the bats remained active I observed variations up to 10 C° within a day.

These two patterns of daily variation of Tb for roosting Eptesicus fuscus correspond to the patterns found in laboratory studies. Herreid and Schmidt-Nielsen (1966) observed that captive E. fuscus either maintained an active Tb (over 30°C) or followed ambient temperature within 1 or 2 C° with a relative absence of intermediates. In my study, the absence of intermediates is shown by the body temperatures of different bats on the same day; Tb min of torpid individuals are within 2 C° of one another.

At one time bats were considered to be poor thermoregulators and even recently it was thought that resting bats had no choice but to enter torpor (Hock 1951). Menaker (1962) demonstrated that the ability of Myotis lucifugus to arouse at low Ta's differed during hibernation and summer daily torpor. During deep hibernation, bats arouse spontaneously or in response to very low temperatures. Moreover during daily torpor, the minimum Ta at which different bat species will arouse seems to be related to their roosting habits. Lasiurus borealis, a tree roosting bat, arouses at higher ambient temperatures than E. fuscus (Davis and Reite 1967). Roosting bats also can thermoregulate against a large temperature gradient, depending on their nutritional state (Mc Nab 1982).

Hock (1951) presented the first study of metabolic rate according to

different body temperatures for Myotis lucifugus. He found that heterothermy allows these bats to have a ratio between highest and lowest resting metabolic rates of 138:1 within the range of ambient temperatures they encounter in nature. Little information is available so far about the energetics of E. fuscus but we can expect that it will show a hyperbolic variation of metabolic rate with increasing body temperature.

Some insectivorous bats are active at relatively low Tb (O'Farrell and Bradley 1977, Studier et al. 1977), and O'Farrell and Bradley (1977) found that E. fuscus could initiate flight at rectal Tb's of 26.3° to 30.4° C. Moreover these bats maintained a temperature gradient of a few C° between different tissues that varied according to the activity level (Hirshfeld and O'Farrell 1976). The threshold between "torpor" and "activity" is not always obvious for $\min Ta > 14^{\circ}$ C (Fig. 14). The daily variations in body temperatures that I observed for active E. fuscus suggest that they use heterothermy to a certain extent even when they remain active. Tropical insectivorous bats that are not capable of torpor also show variations in their Tb's rather than maintaining high temperatures within narrow limits (Bell 1986, Howell 1975).

II- Use of torpor.

In the field I observed that in E. fuscus thermoregulation strategy is affected by Ta. Torpor is mainly related to the nightly minimum Ta's for all of the reproductive states and both sexes. The differences in the use of torpor by the different reproductive classes is paralleled by different incidences of colder and warmer nights. Moreover, the timing of parturition is related to the extent of use of torpor during pregnancy. The

most important finding of my study is, however, that for T_a minima of 9° to 12°C lactating females remained active significantly more often than pregnant and non reproductive females despite the high energetic cost of lactation.

The energy requirements of bats, like other mammals, vary with their reproductive state, increases through pregnancy and reaches a maximum during lactation (Bronson 1985). By several methods, it has been demonstrated that the energetic cost of lactation is greater than that of pregnancy (Kunz 1980, Studier et al. 1973).

Studier and O'Farrell (1972) found that the thermoregulatory patterns of Myotis thysanodes and M. lucifugus varied with the stage of reproduction of adult females. Pregnant and post-lactating bats thermoregulated but lactating ones did not when maintained at T_a of 16°C in a metabolism chamber. Studier and O'Farrell observed a greater proportion of thermoregulating bats during mid-pregnancy, and Kurta (1986) obtained similar results by exposing M. lucifugus to two different temperature regimes (12° to 22°C and 12° to 32°C). The mean T_b 's of lactating females were lower than those of pregnant or post-lactating females.

These laboratory results contrast with my field observations for E. fuscus where thermoregulation is affected by T_a . During pregnancy, the effect of T_a 's is especially important and seems to be responsible for variation in the timing of parturition. The differences in the use of torpor between early and late pregnant females coincides with a different occurrence of colder and warmer nights (Fig. 4). Similarly, the

contradictory results for the use of torpor during late pregnancy between 1985 and 1986 are related to a greater proportion of warmer nights in 1986. Assuming that fertilization occurred at approximately the same time for the two years, the more frequent use of torpor by the pregnant females in 1985 (Table 3) accounts for the later parturition that year, agreeing with the findings of Racey (1973) who demonstrated that the growth of embryos of Pipistrellus pipistrellus was stopped for the time interval the mothers were torpid. Racey and Swift (1981) also demonstrated that the gestation period in a free-living colony of P. pipistrellus varied as a consequence of different weather conditions between years.

The bats used in the laboratory studies (Studier and O'Farrell 1972, Kurta 1986) were captured and tested after foraging, so the animals may have been in a good nutritional state when the experiments were conducted. Racey (1973) showed that the effect of low ambient temperature on gestation length was attenuated when the bats were well fed because they would thermoregulate. He later suggested that in well nourished animals the high progesterone levels could account for a better thermoregulatory ability during pregnancy (Racey and Swift 1981). In the field, T_a 's also affect food availability directly, so the thermoregulatory ability of free-living pregnant bats can be decreased by a poor nutritional state during cold nights.

I found that lactating females made the least use of torpor. This might be a direct consequence of more warmer nights (Fig. 3 and 4), but for minimum T_a 's of 9° to 12°C , lactating females remained active

significantly more often than pregnant and non reproductive females.

Because thermoregulation is energetically expensive, some authors suggested that lactating bats could not afford it (Ransome 1973, Studier and O'Farrell 1972, Studier et al. 1973). Several factors could explain the apparent contradictions between what I observed and the laboratory studies. The stress of captivity can affect thermoregulation (Mc Nab 1982, Studier and Wilson 1979). Lactating Big Brown Bats that I captured were much calmer and did not attempt to bite when handled, while pregnant females were always more aggressive. In captivity, bats in different reproductive states may respond differently to the stress of the experiment, especially females isolated from their pups. Finally, the Ta's recorded in my study are temperatures outside the roost. There are different temperature regimes inside a building and roosting behaviour of E. fuscus could contribute to the ability of lactating females to maintain higher Tb's.

By selecting appropriate roost sites, bats can minimize the energy cost of roosting (Kunz 1980). Several bat species select roosts within very narrow limits of temperature (Cross 1965, Vaughan and O'Shea 1976). The use of geothermally-heated roosts and a "frugal" foraging strategy allows Macrotus californicus, an insectivorous species non capable of torpor to live in a temperate area (Bell et al. 1986). During cold nights, pregnant M. lucifugus use night roosts that are warmer than their day roost (Barclay 1982, and some bat species (eg. Macrotus californicus and Antrozous pallius) roost in thermal environments close to their thermoneutral zone (Bell 1986, Trune and Slobodchikoff 1976). The variations in Tb I observed

in active E. fuscus (up to 10°C) when T_a was low suggest that these T_b can in part be accounted for by the roost environment. The thermoneutral point for this species was estimated at 35°C by Herreid and Schmidt-Neilsen (1966). However, E. fuscus can be expected to be under thermoneutrality within a wider range of temperatures, like other bat species (Bell 1986, Genoud and Bonaccorso 1986) and the maximal T_r 's encountered by E. fuscus (Fig.7) suggest a thermoneutral zone between 30° and 36°C .

Clustering is another important adaptation for minimizing energy expenditure during roosting by reducing heat and water losses and it allows bats to attain a higher T_b at all reproductive states (Kurta 1986). Trune and Slobodchikoff (1976) demonstrated that A. pallidus roosting individually at any ambient temperature, consume more oxygen and lose more weight daily than bats in a cluster. The position of a bat in a cluster does not affect significantly the T_b of that bat (Howell 1976, Kurta 1985). Clustering behaviour and roost selection are important to the maintenance of a high T_b at a lower metabolic cost especially during lactation.

The non reproductive, including post-lactating females, appear to chose a thermoregulatory pattern related to T_a 's. Energy is metabolized more efficiently when the bats are torpid and this may contribute to a quicker accumulation of fat reserves (Kunz 1980, Pagels and Blem 1973). Entering torpor is therefore a good strategy for non reproductive females, males and fully grown juveniles.

During the "active" season, heterothermic bats must produce offspring that will have time to attain adult size and accumulate adequate fat

reserves to survive winter. It could be advantageous for the bats to maintain high body temperatures during gestation and give birth early, but my results suggest that delayed parturition can be compensated by a faster growth rate of the young after birth.

III-Foraging activity

I observed seasonal changes in foraging times of E. fuscus. The response to T_a 's varied throughout the summer and coincided with different reproductive states. Only during lactation did the bats make more than one foraging trip per night.

Anthony and Kunz (1977) found that lactating Myotis lucifugus consumed more insects every night than pregnant females and juveniles. They related variability in foraging success of pregnant females to food availability. Anthony et al. (1981) also observed that for the same species, the proportion of time spent foraging varied seasonally and daily in relation to reproductive state, insect availability and temperature.

In my study, females during early pregnancy encountered low nightly T_a 's and the limited foraging time for these bats could be the result of a reduced food supply at these temperatures; insect abundance in temperate areas being dependant on T_a (Anthony and Kunz 1977). Females during late pregnancy were exposed to a wider range of nightly temperatures but did not show increased foraging time at higher T_a 's. In this case the increased cost of foraging due to the weight of the embryo might exceed the gain from feeding. At high T_a 's lactating females foraged for longer times. The energy requirements of these bats are the highest coinciding with a time of high insect availability. Therefore, assuming that energy intake by the

bats increases with foraging time, the ability of lactating E. fuscus to maintain higher body temperatures can be facilitated by the longer foraging times I observed. The post-lactating females observed during warm nights in July show variable foraging times. Anthony and Kunz (1977) found that lactating M. lucifugus filled their stomach more rapidly than the pregnant ones and may either stop foraging or continue to feed, passing food quickly while foraging. Post-lactating females foraged under prey availability conditions similar to the lactating ones, so the variability in foraging time could reflect both these alternatives.

In September, the bats showed a greater tendency not to go foraging. Rosenzweig (1974) predicted that increased foraging time may result from a reduction in prey density or T_a as long as there is a net profit to foraging. With no net profit, inactivity is preferable. Because of the high cost of foraging for some bats and because they have variable daily energy requirements from their ability to enter torpor, Anthony et al. (1981) suggested that inactivity in response to low temperatures and food availability is more advantageous to heterothermic bats. At low T_a 's E. fuscus does not necessarily remain inactive but may enter torpor after foraging. The variability in thermoregulatory strategy shown by bats after foraging trips of given length (Table 11) is the result of the combined action of reproductive state and T_a 's for both affect the cost of foraging. Energy requirements vary with reproductive state and affect the energy intake necessary to maintain a high body temperature. During late pregnancy, for example, a bat can remain active all day after foraging only 17 minutes. Finally the energy intake for a given foraging time is

likely to be related to T_a because of the variable insect densities according to T_a .

IV- General discussion

From my study, it appears that heterothermy is an important factor influencing the energetic balance in bats. For free living bats, heterothermy interacts with and is affected by other factors as summarized in Fig. 12. I directly tested the effect of ambient temperature and reproductive state on heterothermy and used behavioural observations to show the effect of ambient temperature on roost selection. This study does not allow me to assess directly the effect of reproductive state on roost selection. I documented the effect of reproductive state and T_a 's on foraging activity.

This study also allowed me to observe the effect of heterothermy on the length of the gestation period in the bats. The timing of insect emergence is dependant on T_a 's, and may act as a regulatory mechanism in the timing of parturition. Insect ~~availability~~ is reflected in the nutritional state of the bats, which in turn affects their use of daily torpor. The timing of parturition can therefore be synchronized to occur at a time where insect abundance will support the high energy cost of lactation. My results suggest that in addition to the time of parturition, other factors are important in insuring that the young will be able to survive their first winter. Tuttle (1975) found that the post-natal growth rate of Myotis grisescens was related with roost temperature, and Kunz (1974) showed that during lactation, E. fuscus allocated additional energy to the offspring through maternal fat reserves. Assuming that a greater use of torpor is

indeed responsible for delayed parturition, it is unlikely that the young born later are bigger. One could therefore test the hypothesis that to increase the chances of surviving their first winter, juvenile heterothermic bats born later should have faster post-partum growth rate. In the context of Fig. 12, a faster growth rate could result from high body temperatures maintained by the lactating females by affecting milk production and contributing to a warmer and more stable environment for the juveniles. For the females this energy input to the young can be reflected through their energy intake and fat depletion.

CONCLUSIONS

1- Free-living Eptesicus fuscus show two trends of daily variations in Tb: maintaining a relatively high temperature or entering torpor.

2- The use of torpor is influenced by outside ambient temperature (Ta) for both sexes and all reproductive states in the females.

3- Lactating females enter torpor at lower Ta's than pregnant and non reproductive females.

4- Tb of active bats varied between 27.6° and 40°C , suggesting that they remained active at lower energetic costs than required for strict endothermy.

5- The daily changes in Tr were different from the temperature profiles of sites available as roosts, suggesting roost selection and clustering behaviour.

6- Gestation length varied between the two consecutive years of the study and appears to be related to the extent of use of torpor by the pregnant females.

7- Foraging activity and the effect of Ta on foraging time varied with reproductive state.

Table 1. Sample sizes for temperature recordings from transmitters indicating body temperature (Tb) and from transmitters indicating roost temperature (Tr).

		Adult					Juv.	Total	
		Male	Female						
			Preg.		Lact.	Non-reproductive			
			Early	Late		Post-lact.	Other		
Tb	# Indiv.	4	5	9	14	6	6	2	46
	Bat-days	9	7	16	44	13	21	6	116
Tr	# Indiv.	-	1	6	4	2	-	-	13
	Bat-days	-	2	7	12	6	-	-	27

TABLE 2. Occurrence of torpor and active state recorded as the number of bat-days in 1985 and 1986 for adult and juveniles, males and females at different reproductive states.

	Male	Adult		Female		Juv.	
		Preg.		Lact.	Non- reprod.		
		Early	Late		Post-lact.	Other	
<hr/>							
1985							
torpid	5	2	8	10	9	12	2
active	2	0	1	20	2	5	0
1986							
torpid	1	3	0	3	1	0	2
active		2	7	11	1	2	2

TABLE 3. Results of the X^2 test for differences in occurrence of the two thermoregulatory strategies (number of bat-days) between pregnant (PR), lactating (LA), and non reproductive (NR) females. The expected frequencies () were calculated using the marginal totals.

	PR	LA	NR	Total
Active	7 (6.875)	5 (9.375)	13 (8.75)	25
Torpid	4 (4.125)	10 (5.625)	1 (5.25)	15
Total	11	15	14	40

$$X^2=10.95 \quad df=2 \quad p<0.01$$

Table 4. Results of the Wilcoxon 2-sample test. Multiple comparisons between T_b min of females during early pregnancy, late pregnancy and lactation.

	Pregnant Early Late	Lactating
Early pregnant	C = 28 p > 0.2	C = 60 * p = 0.05
Late pregnant		C = 54 p > 0.2

Table 5. Results of the Wilcoxon 2-sample test, multiple comparison between T_{max} of females during pregnancy, lactation and post-lactation.

	Pregnant	Lactating	Post-lactating
Pregnant	-	C = 25 p > 0.3	C = 15 p > 0.3
Lactating,	-	-	C = 64.5 p < 0.003 **

TABLE 6. Sample size for foraging time of male and females of different reproductive states.

Reproductive state	Bat-nights	Time out of roost (min)	Time in contact (min)	Complete trips monitored
Pregnant				
early	31	1064	419	7
late	36	1436	660	9
Lactating	29	3499	1273	23
Post-lact.	19	1362	411	5
Non-reprod.	9	920	151	1
Juvenile	9	408	39	0
Male	1	115	111	1
Total	134	8804	3064	46

TABLE 7. Thermoregulation state (Active (A) or Torpid (T)) after foraging periods of different durations for females in different reproductive states and for juveniles of both sexes.

Foraging time in minutes									
		Pregnant		Lactating		Non-reprod.		Juv.	
Early		Late							
A	T	A	T	A	T	A	T	A	T
	27	17	—		36		0		0
55		23			46		0		0
	60	32		47		5			63
	70	38		67		30			81
89		41		133		38	98		
		45		137		41	109		
		46		150		50			
		46		157		60			
		48		162		75			
				178		105			
				181					
				198					
				201					

Figure 1.

Photograph of the radio-transmitters used to monitor body temperature (a), and roost temperature (b).

Figure 2.

Example of hourly changes in body temperature of two females during early pregnancy (07/05/86) chosen to illustrate the two thermoregulatory patterns: Staying active (Tb 1) and entering torpor (Tb 2). Ta=outside ambient temperature.

Figure 3.

Incidence of use of torpor and active state (number of bat-days)
for different ranges of minimal nightly ambient temperatures.

ep= early pregnant females

lp= late pregnant females

la= lactating females

nr= non-reproductive females (including post-lactating)

j= juveniles

Figure 4.

Minimal body temperatures (T_b min) of the bats as a function of minimal nightly ambient temperatures (T_a min).

▽ = early pregnancy

▼ = late pregnancy

● = lactation

○ = post-lactation

◇ = juvenile

□ = ♂

Figure 5.

Hourly changes in roost temperature recorded by the transmitters carried by two females during early pregnancy (07/05/86).

Ta=outside ambient temperature.

Tra and Trb=temperature readings from the transmitters.

Figure 6.

Minimal nightly roost temperatures (T_r min) as a function of minimal nightly ambient temperatures (T_a min).

T_r 's are recorded by transmitters.

▽ = early pregnancy

▼ = late pregnancy

● = lactation

○ = post-lactation

Figure 7.

Maximal daily roost temperatures (T_r max) as a function of maximal daily ambient temperatures (T_a max). Roost temperatures are recorded by transmitters.

▽=early pregnancy

▼=late pregnancy

●=lactation

○=post-lactation

Figure 8.

Representative example of hourly temperature readings from thermistors at three sites in attic (21-22/07/86), showing the different temperature regimes of sites used as roost.

Figure 9.

Example of hourly changes in temperature from two thermistors (T1 & T2) in attic and from a transmitter carried by a lactating female (Tr), showing the differences existing between the actual roost site and available sites in attic. T1 and T2 are located at sites occasionally used by the bats as roost. The interrupted line for Tr indicates that the bat was out foraging.

Figure 10.

Changes in body mass ($\bar{x} \pm s.d.$) of pregnant females.

● = females captured in 1985

○ = females captured in 1986

n = number of individuals

Figure 11.

Nightly foraging time of E. fuscus as a function of ambient temperature at dusk ($\bar{x} \pm \text{s.d.}$ for all individuals observed on a given night).

- a) May
- b) June, July
- c) August, September

Figure 12.

Summary of the factors influencing temperature regulation in heterothermic bats. Solid lines represent relationships demonstrated in this study. Broken lines represent suggested relationships not shown in this study. The aspects of life history affected by heterothermy are represented in shaded boxes.

LITERATURE CITED

- Allen Ray A. 1982. SAS User's Guide: Basics, SAS Institute Inc, Cary, N.C.
- Anthony E.L.P., T.H. Kunz. 1977. Feeding strategies of the Little Brown Bat, Myotis lucifugus, in southern New Hampshire. Ecology, 58:775-786.
- Anthony E.L.P., M.H. Stack, T.H. Kunz. 1981. Night roosting and the nocturnal time budget of the Little Brown Bat, Myotis lucifugus: Effects of reproductive status, prey density, and environmental conditions. Oecologia 51:151-156.
- Bell G.P., G.A. Bartholomew, K.A. Nagy. 1986. The roles of energetics, water economy, foraging behavior, and geothermal refugia in the distribution of the bat, Macrotus californicus. J.Comp.Physiol B 156:441-450.
- Barbour R.W., W.H. Davis 1969. Bats of America. University Press of Kentucky, Lexington, KY.
- Barclay R.M.R. 1982. Night roosting behavior of the little brown bat, Myotis lucifugus. J.Mammal. 63:464-474.
- Brigham R.M.B. 1985. The functional significance of communal roosting by the Big Brown Bat, Eptesicus fuscus. M.Sc. Thesis, Carleton University, Ottawa.
- Bronson F.H. 1985. Mammalian Reproduction: An Ecological Perspective. Biology of Reproduction. 32:1-26.
- Cross S.P. 1965. Roosting habits of Pipistrellus hesperus. J.Mammal. 46:270-279.
- Davis W.H., O.B. Reite. 1967. Response of bats from temperate regions to changes in ambient temperature. Biol.Bull. 132:320-328.
- Genoud M., F.J. Bonnaccorso 1986. Temperature regulation, rate of metabolism and roost temperature in the greater white-lined bat Saccopteryx bilineata (Emballonuridae). Physiol.Zool. 59:49-54.
- Harvey A.C. 1981. The Econometric Analysis of Time Series. Philip Allan Publishers Ltd. Oxford.
- Herreid C.F., K. Schmidt-Neilson. 1966. Oxygen consumption, temperature and water loss in bats from different environments. Am.J.Physiol. 211:1108-1112.
- Hirshfeld J.R., M.J. O'Farrell. 1976. Comparisons of differential warming rates and tissue temperature in some species of desert bats. Comp.Biochem.Physiol. 55A:83-87.
- Hock R.J. 1951. The metabolic rates and body temperatures of bats. Biol.Bull.

101:289-299.

- Howell D.J. 1976. Weight loss and temperature regulation in clustered versus individual Glossophaga soricina. *Comp.Biochem.Physiol.* 53A:197-199.
- Kunz T.H. 1974. Reproduction, growth and mortality of the vespertilionid bat, Eptesicus fuscus in Kansas. *J.Mammal.* 53:1-13.
- Kunz T.H. 1980. Daily energy budgets of tree-living bats. *Proc.Fifth International Bat Research Conference*. Texas Tech.Press, Lubbock. pp. 369-392.
- Kurta A. 1986. Factors affecting the resting and postflight body temperature of little brown bats, Myotis lucifugus. *Physiol.Zool.* 59:429-438.
- Kurta A. 1985. External insulation available to a non-nesting mammal, the little brown bat (Myotis lucifugus). *Comp.Biochem.Physiol.* 82A:413-420.
- Lyman C.P. 1970. Thermoregulation and Metabolism in Bats. In *Biology of bats* (W.A. Wimsatt Ed.), pp.301-330.
- McNab B.K. 1969. The economics of temperature regulation in Neotropical bats. *Comp.Biochem.Physiol.* 31:227-268.
- McNab B.K. 1970. Body weight and the energetics of temperature regulation. *J.Exp.Biol.* 53:329-348.
- McNab B.K. 1980. Evolutionary Alternatives in the Physiological Ecology of Bats. In *Ecology of Bats* (T.H. Kunz Ed.). pp.151-200.
- Menaker M. 1962. Hibernation-Hypothermia: An annual cycle of response to low temperature in the bat - Myotis lucifugus. *J.Cell.Comp.Physiol.* 59:163-174.
- Miller R.G. 1966. Simultaneous statistical inference. McGraw-Hill, New York.
- O'Farrell M.J., W.G. Bradley. 1977. Comparative thermal relationships of flight for some bats in the south-western United States. *Comp.Biochem.Physiol.* 58A:223-227.
- O'Farrell M.J., E.H. Studier. 1970. Fall metabolism in relation to ambient temperatures in three species of Myotis. *Comp.Biochem.Physiol.* 35:697-703.
- O'Shea T.J., T.A. Vaughan. 1977. Nocturnal and seasonal activities of the pallid bat, Antrozous pallidus. *J.Mammal.* 58:269-284.
- Pagels J.F., C.R. Blem. 1973. Metabolized energy of the big brown bat Eptesicus fuscus (Chiroptera). *Comp.Biochem.Physiol.* 45A:497-501.
- Phillips G.L. 1966. Ecology of the Big Brown Bat (Chiroptera:Vespertilionidae) in

- Northeastern Kansas. Amer.Midl.Natur. 75:168-198.
- Racey P.A. 1973. Environmental factors affecting the length of gestation in heterothermic bats. J.Reprod.Fert.Suppl. 19:175-189.
- Racey P.A., S.M. Swift. 1981. Variations in gestation length in a colony of pipistrelle bat (Pipistrellus pipistrellus) from year to year. J.Reprod.Fert. 61:123-129.
- Ransome R.D. 1973. Factors affecting the timing of births of the greater horseshoe bat (Rhinolophus ferrumequinum). Period.Biol. 75:169-175.
- Reite O.B., W.H. Davis. 1966. Thermoregulation in bats exposed to low ambient temperatures. Proc.Soc.Exp.Biol.Med. 121:1212-1215.
- Rosenzweig M.L. 1974. On the optimal aboveground activity of bannertail kangaroo rats. J.Mammal. 55:193-199.
- Siegel S. 1956. Nonparametric Statistics for the behavioral sciences. McGraw-Hill New York.
- Sokal R.R., F.J. Rohlf. 1981. Biometry. W.H. Freeman and Co. New York.
- Stones R.C., J.E. Weibers. 1966. Body temperature regulation of Myotis lucifugus at a low temperature of 10 C. J.Mammal. 47:520-521.
- Studier E.H., V.L. Lysengen, M.J. O'Farrell. 1973. Biology of Myotis thysanodes and M. lucifugus (Chiroptera: Vespertilionidae). II-Bioenergetics of pregnancy and lactation. Comp.Biochem.Physiol. 44A:467-471.
- Studier E.H., M.J. O'Farrell. 1972. Biology of Myotis thysanodes and M. lucifugus (Chiroptera: Vespertilionidae). I-Thermoregulation. Comp.Biochem.Physiol. 41A:567-595.
- Studier E.H., D.E. Wilson. 1969. Thermoregulation in some neotropical bats. Comp.Biochem.Physiol. 34:251-262.
- Studier E.H., D.E. Wilson. 1979. Effects of captivity on thermoregulation and metabolism in Artibeus jamaicensis (Chiroptera: Phyllostomatidae). Comp.Biochem.Physiol. 62A:347-350.
- Thomas S.P., R.A. Suthers. 1972. The physiology and energetics of bat flight. J.Exp.Biol. 57:317-335.
- Trune D.R., C.N. Slobodchikoff. 1976. Social effects of roosting on the metabolism of the pallid bat (Antrozous pallidus). J.Mammal. 57:656-663.
- Tuttle M.D. 1974. An improved trap for bats. J.Mammal. 55:475-477.
- Tuttle M.D. 1975. Population ecology of the gray bat (Myotis grisescens);

factors influencing early growth and development. Occas. Papers
Mus.Nat.Hist., Univ. Kansas, 36:1-24.

van Zyll de Jong C.G. 1985. Handbook of Canadian Mammals. Vol.2. Bats. National
Museums of Canada. 212pp.

END

109-03-88

FIN