

## Patterns of daily torpor and day-roost selection by male and female big brown bats (*Eptesicus fuscus*)

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Received September 20, 1993

Accepted January 26, 1994

HAMILTON, I.M., and BARCLAY, R.M.R. 1994. Patterns of daily torpor and day-roost selection by male and female big brown bats (*Eptesicus fuscus*). 1994. *Can. J. Zool.* **72**: 744–749.

Daily torpor can provide significant energy savings, but in bats may reduce rates of fetal and juvenile development and spermatogenesis. We examined the use of torpor during the day by male and female big brown bats (*Eptesicus fuscus*) in the field during the female gestation, lactation, and postlactation periods. While both sexes used torpor, males used it significantly more often and used deeper torpor than did reproductive females, indicating that the costs of torpor are higher for reproductive females. We suggest that by using shallow torpor, females may gain some of the benefits of torpor while minimizing the fitness costs. The different patterns of torpor may be responsible for observed differences in day-roost location amongst males, reproductive females, and nonreproductive females. Males should choose roosts with lower ambient temperatures than do females in order to increase the energy savings of torpor. Males and nonreproductive females roosted away from the maternity colonies more often than did reproductive females. Within one maternity colony, males roosted in the west end of the colony, while females roosted in the east end. These patterns of roosting may be related to how the roost warms during the day.

HAMILTON, I.M., et BARCLAY, R.M.R. 1994. Patterns of daily torpor and day-roost selection by male and female big brown bats (*Eptesicus fuscus*). 1994. *Can. J. Zool.* **72** : 744–749.

La torpeur durant le jour peut favoriser grandement les économies d'énergie, mais, chez les chauves-souris, elle peut réduire la vitesse de développement des fœtus et des juvéniles et inhiber la spermatogénèse. Nous avons étudié la torpeur chez des mâles et des femelles de la Sérotine brune (*Eptesicus fuscus*) en nature, au cours de la gestation des femelles, au cours de l'allaitement et après l'allaitement. Les chauves-souris des deux sexes ont des périodes de torpeur, mais ces torpeurs sont significativement plus fréquentes et plus profondes chez les mâles que chez les femelles reproductrices, et il semble donc que les coûts reliés à la torpeur soient plus élevés chez ces femelles. En se laissant aller à une torpeur moins profonde, les femelles bénéficient de certains de ses avantages tout en minimisant son influence sur le fitness. Ces utilisations différentes de la torpeur sont peut-être responsables des différences observées aux dortoirs de jour entre les mâles, les femelles reproductrices et les femelles non reproductrices. Il faut s'attendre à ce que les mâles choisissent des perchoirs à température ambiante plus basse que les femelles pour augmenter leurs économies d'énergie. En nature, les mâles et les femelles non reproductrices se perchaient loin des colonies « pouponnières » plus souvent que les femelles reproductrices. Au sein d'une pouponnière, les mâles se perchaient à l'extrémité ouest et les femelles se perchaient à l'extrémité est. Ces patterns sont probablement reliés au mode de réchauffement du dortoir durant le jour.

[Traduit par la Rédaction]

### Introduction

Temperate insectivorous bats, like many other small endotherms, have the ability to enter torpor. Daily torpor is a controlled decrease in body temperature below normothermic levels that allows for considerable energy savings over homeothermy (Wang and Wolowyk 1988). The use of torpor is widespread among small mammals and birds (Bartholomew 1971).

Although the energy saved via the use of torpor can be high (for a review see Wang and Wolowyk 1988), maintenance of body temperature below normothermic values may be costly. Rates of fetal and juvenile development depend on temperature. The use of torpor by pregnant female bats results in slowed fetal development (Racey and Swift 1981). In temperate areas, the time over which adequate food supplies are available to bats is limited to 4 or 5 months, and any delay in fledging may result in both females and juveniles not being able to store adequate amounts of fat for hibernation, resulting in lower overwinter survival (Kunz 1987; Thomas et al. 1990). The immediate energetic benefits of daily torpor may thus not be high enough to counteract the lowering of maternal fitness through lower juvenile and maternal survival. During pregnancy and lactation, females should minimize the use of torpor, as has been found in previous studies (Audet and Fenton 1988; Grinevitch et al. 1994; Kurta et al. 1987).

Male bats do not assist in raising offspring, so the use of torpor by males should not affect juvenile development or survival. However, males undergo spermatogenesis during the summer (Racey 1982). Inhibition of or delays in spermatogenesis and testicular development have been suggested as a possible cost of torpor to male fitness (Kurta and Kunz 1988). Low temperatures reduce rates of spermatogenesis in mice (Meistrich et al. 1973), and spermatogenesis is inhibited by winter hibernation in ground squirrels (Michener 1992). However, spermatogenesis is initiated in some heterotherms during hibernation (Wimsatt 1969). Inhibition of spermatogenesis in bats using daily torpor during the summer has not been demonstrated. In male rat-tailed bats, *Rhinopoma kinnearyi*, spermatogenesis coincides with the use of torpor during the winter (Kumar 1965).

Roost choice by male and female bats may be influenced by their thermoregulatory strategies. Female bats should select warm microclimates as roosts, thereby reducing the energetic costs of maintaining a high body temperature and high rates of juvenile development (McNab 1982). Maternity colonies tend to be located in warm sites (e.g., Tuttle and Heaney 1974; Kunz 1982). If males use torpor frequently, they should roost in cooler microclimates to maximize the difference between ambient and normothermic temperatures and thus energy savings. The presumed lower fitness costs of

torpor to males have been related by several authors to differences in habitat use between males and females (Thomas 1988; Barclay 1991).

Although maternity colonies of temperate-zone bats are typically composed almost exclusively of females and their young, at our study site in Medicine Hat and in some other colonies (e.g., Kurta and Kunz 1988) small numbers of males also occur. There are two possible explanations for the use of these colonies by males. If males do not normally use torpor except in periods of limited food availability, as suggested by Kurta and Kunz (1988), maternity colonies would offer the same advantage to males as to reproductive females, namely high ambient temperature, allowing them to maintain normothermic temperature at a low energetic cost. Alternatively, males may select microclimates within the colony that are more suitable for torpor.

The purpose of this study was thus to examine day-roost selection and the use of torpor during the day by big brown bats (*Eptesicus fuscus*). We predicted that if the costs to fitness of using torpor are higher for females than for males, as is indicated by the greater use of nocturnal torpor by males (Grinevitch et al. 1994), then males should use torpor during the day more often than do reproductive females, and this should be related to differences in roosting behaviour.

### Methods and materials

We studied the roosting and thermoregulatory behaviour of *E. fuscus* in the summers of 1991 through 1993 in Medicine Hat, Alberta (50°N, 111°W). *Eptesicus fuscus* (Vespertilionidae) is widespread in North America and commonly roosts in old buildings (Kunz 1982). Adult mass is 15–20 g and is thus appropriate for thermoregulatory and telemetry studies, as individuals are large enough to carry radio transmitters (Aldridge and Brigham 1988).

We studied two maternity colonies located in the attics of red-brick schoolhouses: Elm Street School and Montreal Street School. Both maternity colonies contain over 100 adult bats, mostly females, but with a small number of resident males. The two schools are located within the city on the floodplain of the South Saskatchewan River. The natural vegetation of the Medicine Hat region, most of which has been converted to agriculture or urban development, is shortgrass prairie with some cottonwood (*Populus* spp.) forest along the South Saskatchewan River and its tributaries. The climate is characterized by hot summers and low precipitation. Over the course of the study, daily maximum temperatures were usually between 20 and 30°C; minimum temperatures rarely fell below 10°C.

Bats were captured in mist nets as they emerged from or returned to the maternity colonies. Bats were banded with numbered, coloured split plastic rings (Barclay and Bell 1988) and weighed to within 0.05 g. Only adults were used in this study; subadults were determined by examination of the cartilaginous gap between the diaphyses of the metacarpal and proximal phalanges (Anthony 1988). Reproductive status of females was classified as pregnant, lactating, postlactating, or nonpregnant (captured during the pregnancy period). Pregnancy was determined by palpation of the abdomen to detect the fetus and lactation by expression of milk (Racey 1988). The reproductive status of females caught during the pregnancy period, but which were not obviously pregnant, was assessed by their condition upon recapture. Males were assigned to the reproductive class of the females caught at the same time, so that we compared the behaviour of bats experiencing the same environmental and prey conditions. For some analyses, female reproductive classes were combined into "reproductive" (pregnant and lactating) and "non-reproductive" (nonpregnant and postlactating).

The skin temperature and location of known individual *E. fuscus* were obtained by attaching temperature-sensitive radio transmitters (Holohil Systems Limited, R.R. 2, Woodlawn, ON K0A 3M0,

Canada) to 18 adult females and 9 adult males in 1991, 10 females and 8 males in 1992, and 5 females and 3 males in 1993. The transmitters (0.8–0.9 g) were attached to the skin between the shoulder blades with Skinbond™ surgical adhesive. No bats were tagged if the radio exceeded 5% of their body mass, generally considered an allowable load (Aldridge and Brigham 1988). Bats were monitored from when they returned to the roost after foraging until 11:00 the following morning by means of five-element antennae and Merlin 12 receivers (Custom Electronics, Urbana, Ill.). Exit and return times were recorded  $\pm 10$  min.

Skin temperatures of roosting bats were determined by measuring the time required for the transmitters to emit 10 pulses, averaged over three trials, and comparing the mean with calibration curves for each transmitter. The mean time of return to the roost from the final foraging bout in the early morning was approximately 135 min before sunrise. From this time until 11:00 was operationally defined as the morning period, during which the skin temperature of each bat was taken every 30 min. The period from 11:00 to 20:00 was defined as the afternoon period. During the afternoon, a single temperature reading was taken, and the location of each tagged bat within the maternity colony was determined. After 20:00, bats began to become active and move in the roost in preparation for foraging. At each reading, the ambient temperature outside the colonies was measured to within 0.5°C.

We used the same definition of torpor as Grinevitch et al. (1994): the skin temperature of the bat is below the "active temperature." The active temperature was defined for each bat as its lowest skin temperature recorded within 15 min prior to exit or movement within the attic. "Deep torpor" was defined as the occurrence of a skin temperature more than 10°C below the active temperature.

The day-roost location of radio-tagged bats was determined in two ways. First, we noted whether the bats roosted within or away from the two maternity colonies. Second, we determined the location of bats within the Elm Street School colony. We recognized three roost areas: the east and west wings of the attic, and roosts clustered around the northfacing wall from where the bats entered and exited the building. We did not determine the location of bats within Montreal Street School because of the difficulty in locating roost sites at that colony.

The use of torpor by males and females and the frequency of roost use were compared using contingency tables, with Yates' correction when necessary (Zar 1984). Mean differences between active and minimum skin temperature were compared for males and females using a mixed-model analysis of variance. Sex and female reproductive class were tested for significant effects. Individuals within the sex by reproductive stage interaction were treated as a random variable. Proportions of the morning spent in torpor were compared using analysis of covariance with the General Linear Models procedure (SAS Institute Inc. 1985). We tested for a significant effect of sex and reproductive period, with ambient temperature at emergence as a covariate. For all tests, a Type I error rate of 0.05 was used.

### Results

Radiotelemetry observations were made on a total of 27 bats in 1991, 18 in 1992, and 8 in 1993. Two ( $n = 9$  bat-nights) nonpregnant females captured during the pregnancy period, 19 ( $n = 75$  bat-nights) pregnant females, 13 ( $n = 69$  bat-nights) lactating females, 3 ( $n = 14$  bat-nights) postlactating females, and 17 ( $n = 100$  bat-nights) adult males were monitored over the three seasons. Pregnant bats and males carried radios at the same time from 7 May to 27 June in 1991 and from 24 May to 19 June in 1993. Lactating females and males carried radios at the same time, from 30 June to 26 July in 1991 and from 26 June to 2 August in 1992. Nonpregnant females and males carried radios at the same time from 31 May to 18 June in 1992. Postlactating

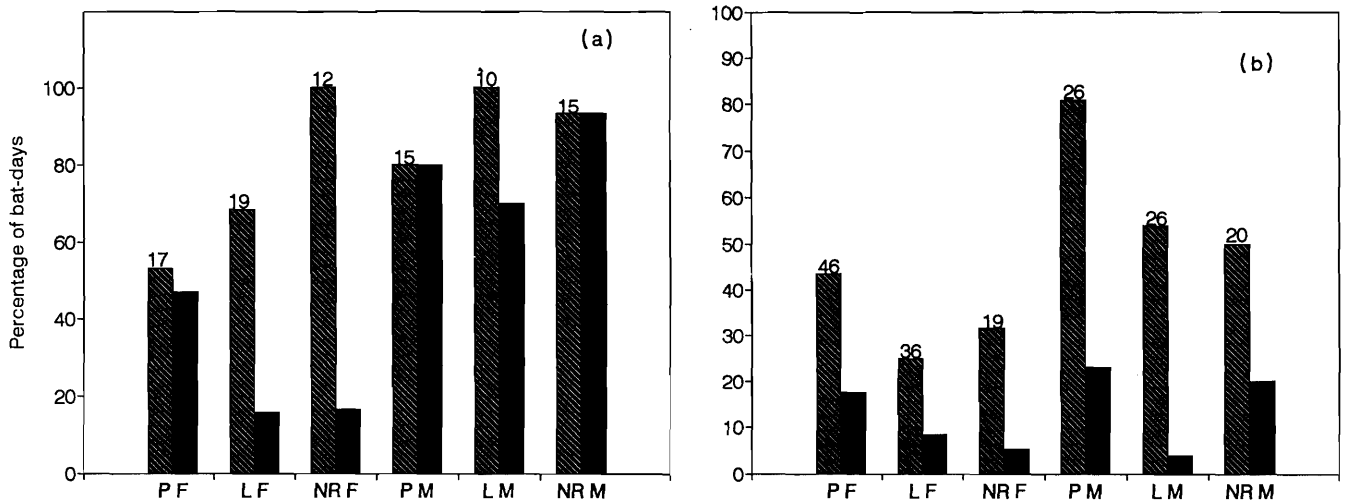


FIG. 1. Use of torpor during the morning (a) and afternoon (b) periods by male (M) and female (F) *Eptesicus fuscus* as a percentage of total bat-days. Hatched bars indicate use of torpor; solid bars indicate use of deep torpor. P, pregnant females and males at the same time; L, lactating females and males at the same time; NR, nonreproductive females (nonpregnant and postlactating) and males at the same time. Sample sizes (bat-days) are indicated above the bars.

females and males carried radios at the same time from 31 July to 16 August in 1991 and from 26 July to 10 August in 1992. The proportion of the morning period spent in torpor and the minimum body temperature while in torpor were measured for males and females during the nonpregnancy, lactating, and postlactating periods in 1992 and during the pregnancy period in 1993.

#### Use of torpor

During the day-roosting period, both males and females used torpor frequently. There was no difference in the frequency of torpor in the morning between males and females in either the female pregnancy or lactating periods (pregnancy:  $\chi^2 = 1.53$ ,  $df = 1$ ,  $P > 0.05$ ; lactation:  $\chi^2 = 2.29$ ,  $df = 1$ ,  $P > 0.05$ ; Fig. 1a). However, in both periods there was a trend for males to use torpor more frequently than females, and when pregnancy and lactation are combined into the "reproductive" status, males used torpor significantly more often than did reproductive females at the same time ( $\chi^2 = 4.05$ ,  $df = 1$ ,  $P < 0.05$ ). In the afternoon, males used torpor more frequently than did females in either the females' pregnancy or lactation periods (pregnancy:  $\chi^2 = 7.96$ ,  $df = 1$ ,  $P < 0.005$ ; lactation:  $\chi^2 = 4.22$ ,  $df = 1$ ,  $P < 0.05$ ; Fig. 1b). There was no difference in the frequency of torpor between nonreproductive females and males at the same time (morning:  $\chi^2 = 0.83$ ,  $df = 1$ ,  $P > 0.05$ ; Fig. 1a; afternoon:  $\chi^2 = 1.37$ ,  $df = 1$ ,  $P > 0.05$ ; Fig. 1b). Although pregnant and lactating females used torpor less often than did nonreproductive females in the morning period ( $\chi^2 = 7.63$ ,  $df = 2$ ,  $P < 0.025$ ; Fig. 1a), there was no difference in its use in the afternoon period ( $\chi^2 = 3.14$ ,  $df = 2$ ,  $P > 0.05$ ; Fig. 1b). Males used torpor equally often during the females' pregnancy, lactation, and nonreproductive periods in both the morning and afternoon (morning:  $\chi^2 = 2.96$ ,  $df = 2$ ,  $P > 0.05$ ; Fig. 1a; afternoon:  $\chi^2 = 5.87$ ,  $df = 2$ ,  $P > 0.05$ ; Fig. 1b).

Males used deep torpor in the morning significantly more frequently than did lactating ( $\chi^2 = 6.29$ ,  $df = 1$ ,  $P < 0.025$ ; Fig. 1a) or nonreproductive females at the same time ( $\chi^2 = 13.21$ ,  $df = 1$ ,  $P < 0.001$ ; Fig. 1a). There was no significant difference in the frequency of deep torpor between

pregnant females and males at the same time ( $\chi^2 = 2.42$ ,  $df = 1$ ,  $P > 0.05$ ). However, when the pregnancy and lactation periods are combined into the reproductive period, males used deep torpor significantly more frequently than did females in this period ( $\chi^2 = 10.44$ ,  $df = 1$ ,  $P < 0.0025$ ). There was no significant difference in the use of deep torpor in the morning between reproductive and nonreproductive females ( $\chi^2 = 0.32$ ,  $df = 1$ ,  $P > 0.05$ ; Fig. 1a) or between males in the females' reproductive period and males in the females' nonreproductive period ( $\chi^2 = 0.94$ ,  $df = 1$ ,  $P > 0.05$ ; Fig. 1a). In the afternoon period, few bats used deep torpor and there was no significant difference between the sexes in its use over the two reproductive periods ( $\chi^2 = 1.85$ ,  $df = 3$ ,  $P > 0.05$ ; Fig. 1b).

When bats did use torpor, the body temperature of males fell further from their active temperature than did that of females ( $F = 8.09$ ,  $df = 1$ ,  $9.84$ ,  $P < 0.025$ ; Table 1). Individuals differed ( $F = 2.47$ ,  $df = 10$ ,  $48$ ,  $P < 0.025$ ), but reproductive period and the interaction between sex and reproductive period were not significant (reproductive period:  $F = 2.02$ ,  $df = 3$ ,  $8.61$ ,  $P > 0.05$ ; interaction:  $F = 1.43$ ,  $df = 3$ ,  $8.52$ ,  $P > 0.05$ ).

The proportion of the morning spent in torpor was also not significantly affected by sex ( $F = 1.46$ ,  $df = 1$ ,  $45.85$ ,  $P > 0.05$ ; Table 2) or reproductive period ( $F = 0.23$ ,  $df = 3$ ,  $45.28$ ,  $P > 0.05$ ). Individuals differed in the proportion of the morning spent in torpor, and the ambient temperature at emergence the night before significantly influenced that proportion (individuals:  $F = 8.24$ ,  $df = 8$ ,  $38$ ,  $P < 0.001$ ; ambient temperature:  $F = 6.72$ ,  $df = 1$ ,  $38$ ,  $P < 0.025$ ). Although the results were not significant, there was a trend for males to be torpid over a greater proportion of the morning than were females.

#### Location

Male bats roosted during the day away from the maternity colonies more often than did females (males: 37.4%,  $n = 123$ ; females: 6.8%,  $n = 192$ ;  $\chi^2 = 44.21$ ,  $df = 1$ ,  $P < 0.001$ ; Fig. 2). The location of the other day roosts varied and included cliffs along the South Saskatchewan River, houses

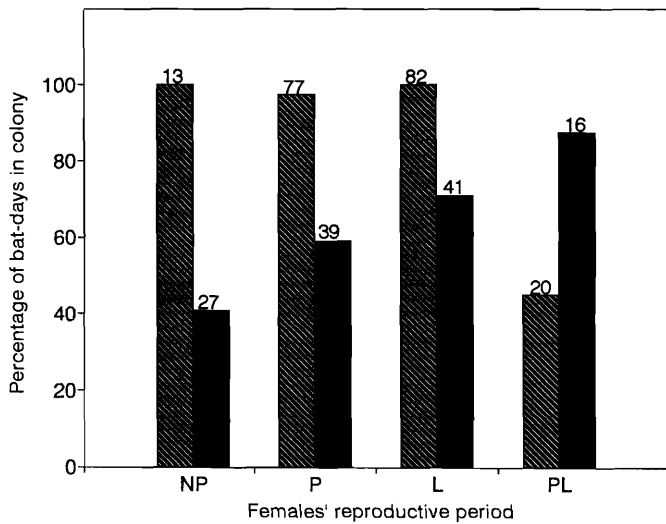


FIG. 2. Percentage of bat-days on which individuals roosted in or away from the maternity colonies, according to sex and female reproductive period. NP, nonpregnant; P, pregnant; L, lactating; PL, postlactating. Hatched bars represent females; solid bars represent males. Sample sizes (bat-days) are indicated above the bars.

TABLE 1. Active and minimum skin temperatures during torpor in male and female big brown bats (*Eptesicus fuscus*)

Females' reproductive period	Active temp. (°C)		Minimum temp. (°C)		n
	Mean	SE	Mean	SE	
<b>Nonpregnancy</b>					
Males	31.5	5.26	15.3	2.63	5
Females	32.8	0.27	27.9	2.84	7
<b>Pregnancy</b>					
Males	32.3	0.06	18.9	1.08	7
Females	32.5	0.64	14.9	1.97	9
<b>Lactating</b>					
Males	32.2	0.30	20.1	1.09	10
Females	31.8	0.70	25.8	1.50	13
<b>Postlactating</b>					
Males	33.0	0.00	15.1	0.87	9
Females	34.7	0.00	26.0	0.97	5

in the residential area surrounding the maternity colonies, and nearby industrial buildings. Postlactating females roosted away from the maternity colonies more frequently than did females in other reproductive periods ( $\chi^2 = 82.72$ ,  $df = 3$ ,  $P < 0.001$ ; Fig. 2). Males captured during the postlactating period roosted away from the maternity colonies less frequently than did males in the females' other reproductive periods ( $\chi^2 = 11.12$ ,  $df = 3$ ,  $P < 0.025$ ; Fig. 2).

In the maternity colony at Elm Street School, males and reproductive females chose day roosts located in different areas of the attic ( $\chi^2 = 36.23$ ,  $df = 2$ ,  $P < 0.001$ ; Fig. 3). Males roosted primarily in the west wing of the attic, while females roosted in the east wing or near the exits.

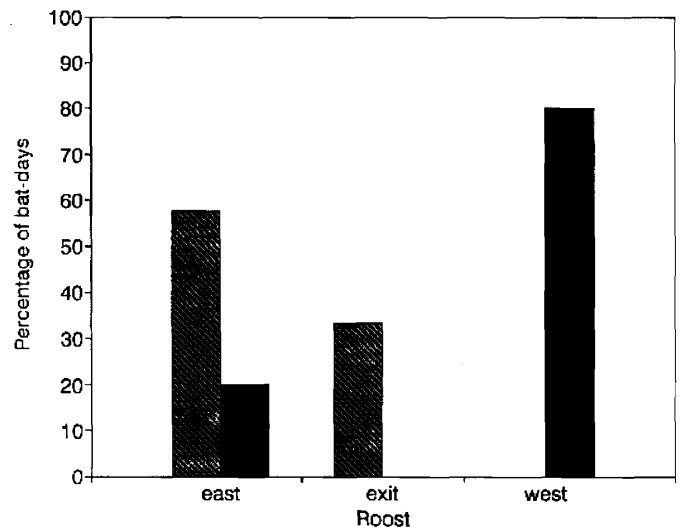


FIG. 3. Percentage of bat-days that individuals spent at different locations in the maternity colony at Elm Street School. Hatched bars represent reproductive females ( $n = 30$ ); solid bars represent males ( $n = 20$ ).

TABLE 2. Proportion (%) of the morning period spent in torpor by adult male and female big brown bats (*Eptesicus fuscus*)

Females' reproductive period	Males			Females		
	Mean	SE	n	Mean	SE	n
Nonpregnancy	99	1.0	5	33	6.9	7
Pregnancy	88	10.6	7	90	7.2	9
Lactating	93	2.9	10	49	10.4	13
Postlactating	93	3.2	9	83	6.5	5

## Discussion

This study and other field studies (e.g., Audet and Fenton 1988; Grinevitch et al. 1994) indicate that energetically non-stressed individual *E. fuscus* frequently use torpor in the field. In laboratory studies of little brown bats (*Myotis lucifugus*), regular use of torpor was found only under conditions of severe energetic stress (Kurta et al. 1987; Kurta and Kunz 1988). A reduced frequency of daily torpor may be an artifact of laboratory studies. White-footed mice, *Peromyscus leucopus*, also use torpor more frequently in the field than in laboratory studies, even with abundant food (Lynch et al. 1978). The low frequency of torpor in captive *M. lucifugus* may be a result of the disturbance due to capture and temperature recording with a rectal thermometer. Less invasive techniques, such as temperature-sensitive radio transmitters, should provide a better estimate of the importance of torpor in the daily energy strategies of small endotherms.

In the morning, reproductive female *E. fuscus* used torpor less often than did males or nonreproductive females. Males also used deep torpor more often than did females. Although the benefits, in terms of energy savings per degree Celsius decrease in body temperature per gram of body mass, should be equal for males and females, the observed patterns suggest that costs to fitness are higher for females than for males. The use of torpor does not appear to prevent spermatogenesis, though possible effects of torpor on the timing of male fertility

are unknown (Grinevitch et al. 1994). By extending the period of spermatogenesis over several months, as opposed to several weeks as in most mammals, male bats may be able to complete spermatogenesis during periods of activity.

Nonreproductive females used torpor as frequently as did males. This is consistent with the hypothesis that the cost of torpor to females is in terms of slowed fetal (Racey and Swift 1981) and neonatal development. Because the costs to fitness of torpor would therefore be lower for nonreproductive and postlactating females than for reproductive females, greater net benefits can be obtained through the use of daily torpor by nonreproductive females.

Reproductive females did use torpor during more than 50% of the mornings on which they were observed, and it is thus an important part of their energetic strategy. The fitness costs of torpor to females may be mitigated somewhat by the body temperature not dropping as low as in males. Females used deep torpor less frequently than did males, and on average the minimum body temperature of females was higher than that of males. The costs in terms of slowed juvenile development increase linearly as the body temperature decreases (McNab 1982). On the other hand, the energy saved via torpor follows a nonlinear function as temperature decreases. For *M. lucifugus*, the energy saved through a drop in body temperature from 37 to 33°C was 46.86 J·g<sup>-1</sup>·h<sup>-1</sup>, whereas subsequent reduction in body temperature from 33 to 29°C resulted in an energy savings of only 34.3 J·g<sup>-1</sup>·h<sup>-1</sup> (Studier 1981). Substantial energy savings are thus gained from slight drops in body temperature (Webb et al. 1993), whereas subsequent energy savings are lower as body temperature approaches ambient. For reproductive females, the nonenergetic costs of reduced body temperature (i.e., the costs associated with delays in fetal and neonatal growth rates) may outweigh the additional energetic benefits of deeper torpor.

There was a general trend for males to use torpor over a greater proportion of the morning than did females, although the results were not significant, possibly due to the small sample size. The high proportion of the morning period spent in torpor by pregnant females may be a result of the unusually cold and wet summer of 1993.

The observed differences in roost selection, and different energy strategies in terms of the use and depth of torpor, underline the importance of microclimate selection in the energy strategies of bats. By selecting warm microclimates, female bats are able to increase the growth rate of juveniles (McNab 1982). High roost temperatures also allow females to reduce the energy expended in maintaining an elevated body temperature (Kurta 1990). Males, on the other hand, use a strategy of frequent deep torpor. This would not be facilitated by warm roost areas, and males would therefore be expected to select cooler roosts.

Passive rewarming may be an important part of the energy strategies of both male and female bats. The most energetically costly phase of torpor is rewarming (Prothero and Jurgens 1986). If bats can passively rewarm as their roost warms, this cost could be reduced (Vaughan and O'Shea 1976). If passive rewarming is important, males should roost in areas that warm slowly or later in the day, to maximize the difference between normothermic and ambient temperatures for a longer time. In the attic of Elm Street School, we found that males roosted in the west end of the school and females in the east end and around the exits. One explanation for this

distribution is that the east end may heat earlier in the morning as the sun rises, whereas the west end remains relatively cool until the afternoon, thereby facilitating deeper torpor for a longer time. Females roosting near the north-facing exits may choose these roosts to provide protection for young from disturbance and from being injured in falls, as these roosts are difficult to access and are close to the ground.

Male and nonreproductive female bats have no offspring to care for, therefore they can and do choose roosts away from the maternity colonies. Reproductive females are more restricted to the maternity colonies because the young are there and cannot be easily moved. Also, the maternity colony provides microclimates that are suitable for the energy strategies of reproductive females. By choosing appropriate microclimates for deep torpor, males can also roost in the maternity colony without high energy costs. However, the benefits of roosting there are unclear. Individuals fly for up to 12 km from the maternity colonies to foraging areas along the South Saskatchewan River (L. Wilkinson, personal communication), a distance that could be reduced by choosing roosting sites closer to the foraging areas. The maternity colonies, however, may provide a microclimate that allows males to use passive rewarming during the afternoon. During cool periods, male bats roosting in cliffs along the river often remained torpid for several days without becoming active, even at night. In 1993, males roosted away from the colonies less often than in previous years. This may be due to the unusually low temperatures that year which may have prevented the maternity colonies from becoming too hot, or may have resulted in alternative roosts not rewarming during the day. Finally, males captured at one maternity colony were never observed to roost during the day at the other maternity colony, and many of the males were originally captured as juveniles at the colony where they roosted as adults (R.M.R. Barclay, unpublished data). The males in each maternity colony thus appear to have been born in that colony. With conditions in the maternity colonies still allowing for the use of torpor, even if the maternity colonies are suboptimal for males and nonreproductive females, the energy costs of searching for a new roost may outweigh any benefits gained.

### Acknowledgements

We acknowledge Darrell MacKinnon and the Medicine Hat Board of Education for logistical support and access to the roosts. We thank Lisa Wilkinson, Patrick Garcia, Susan Holroyd, Lara Grinevitch, Cori Lausen, and Ania Wojciechowski for field assistance. We also thank John Post, Susan Holroyd, Maarten Vonhof, Lisa Wilkinson, and two anonymous reviewers for comments regarding this paper. This research was funded in part by a Natural Sciences and Engineering Research Council of Canada (NSERC) Undergraduate Summer Studentship to I.M.H. and an NSERC operating grant to R.M.R.B.

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