

BENEFITS OF LIVING IN A BUILDING: BIG BROWN BATS (*EPTESICUS FUSCUS*) IN ROCKS VERSUS BUILDINGS

CORI L. LAUSEN AND ROBERT M. R. BARCLAY*

Department of Biological Sciences, University of Calgary, Calgary, Alberta T2N 1N4, Canada

Individuals of some species of bats roost in human-made structures despite the apparent availability of natural roosts. We compared patterns of thermoregulation in relation to microclimate and compared reproductive timing for maternity colonies of big brown bats (*Eptesicus fuscus*) roosting in natural and building roosts in the prairies of southeastern Alberta. During pregnancy, bats roosting in buildings used torpor less frequently than did rock-roosting bats, but achieved lower body temperatures when torpid. Less-frequent use of torpor leaves more active days for fetal development, and bats in building roosts gave birth earlier than those in rock roosts. We observed predators and predation in rock roosts, but not in building roosts, and suggest that bats roosting in rocks use shallower torpor to remain vigilant. Patterns of torpor use suggest that bats in buildings save more energy than rock-roosting individuals by roosting in the warmer microenvironments of buildings and by achieving lower body temperatures when ambient conditions are cold and foraging is not productive. The warmer building roosts are also conducive to juvenile growth, and young building-roosting bats fledged 1–2 weeks before rock bats. We propose that advantages for bats roosting in buildings (lower predation risk, earlier births, faster juvenile growth rates, and increased energy savings) lead to greater long-term reproductive success for building-roosting bats and make buildings preferred roosts.

Key words: bats, buildings, Chiroptera, microclimate, reproductive success, rock crevices, roost selection, thermoregulation, torpor

Bats use a variety of structures as diurnal roosts, and these are vital to the survival and successful reproduction of bats (Kunz and Lumsden 2003). Regardless of the type of structure, roosts used by reproductive female bats (maternity roosts) must provide protection from predators and adverse ambient conditions, a microclimate that promotes pre- and postnatal growth while minimizing energy expenditure by the female and juvenile, and space suitable for social interactions.

Some individuals of many species of bats use buildings as maternity roosts (Kunz 1982; Kunz and Lumsden 2003). Indeed, for some species, information regarding their ecology and behavior comes almost exclusively from studies of individuals roosting in buildings (Barclay and Cash 1985; Kunz 1982). However, if conditions differ between buildings and natural roosts, false conclusions may be drawn regarding a species's ecology, behavior, and physiology. For example, the structure of a roost influences its microclimate, which in turn can influence the energetics and reproduction of bats (Chruszcz and Barclay 2002; Lausen and Barclay 2002; Tuttle 1975;

Vaughan and O'Shea 1976; Vonhof and Barclay 1997). There is relatively little information regarding the differences between conditions in natural versus building roosts, let alone the energetic, reproductive, or fitness consequences of such differences.

It has been argued that buildings have allowed some species of bats to increase in abundance and expand their geographic range (Davis et al. 1962; Fenton 1970; Kunz 1982; Wilson 1971). Others debate whether buildings are preferred roost sites because they provide better roosting conditions for bats, or are simply a last resort when natural roosts have been destroyed (Brigham 1991; Gaisler 1963; Kunz 1982). Buildings might provide several advantages over natural roosts. For example, buildings may be subject to lower predator activity, may provide superior microclimate for reproduction, or may allow larger colonies and advantages that accompany aggregations.

Temperature has been argued to be critical in determining the quality of a maternity roost to bats because it influences the energy costs of maintaining a high body temperature (T_b) and the growth rate of embryos and young (Sedgeley 2001; Vonhof and Barclay 1996). Reproductive females of several species select roosts on the basis of temperature (Chruszcz and Barclay 2002; Hutchinson and Lacki 2001; Kerth et al. 2001; Lausen and Barclay 2003; Willis and Brigham 2005) and select different roost microclimates than do males and nonreproductive females (Hamilton and Barclay 1994). Despite roost

* Correspondent: barclay@ucalgary.ca

selection, conditions arise in which reproductive female bats in both natural and building roosts opt to enter torpor, thereby saving energy that would otherwise be spent maintaining a high T_b (Audet and Fenton 1988; Chruszcz and Barclay 2002; Hamilton and Barclay 1994; Lausen and Barclay 2003). Individuals must balance the energetic benefits of entering torpor with the costs, including decreased movement and vigilance (Choi et al. 1998; Lyman et al. 1982), prolonged gestation (Racey 1973), reduced milk production (Wilde et al. 1995), and diminished heat transfer to offspring (Cossins and Bowler 1987). If natural and building roosts differ in temperature, the trade-off between the costs and benefits of using torpor may differ, resulting in different thermoregulatory patterns of female bats and different timing of reproduction. Ultimately, the fitness of individuals occupying natural and building roosts may differ.

The purpose of our study was to compare some costs and benefits to reproductive female bats of using buildings and natural roosts as maternity sites. Because previous studies identified roost microclimate as important in roost selection by bats, we chose to focus on roost temperature, patterns of thermoregulation, and reproduction. We hypothesized that buildings are preferred roosts for thermoregulatory reasons. Specifically, we predicted that building roosts are more thermally stable than rock-crevice roosts and thus remain warmer at night and early in the morning, allowing females to maintain a high T_b and resort to torpor less often than individuals in natural roosts. In turn, we predicted that less frequent use of torpor results in earlier parturition and weaning. We studied these aspects in maternity colonies of big brown bats (*Eptesicus fuscus*) occupying natural sites (rock crevices) and buildings in southern Alberta.

MATERIALS AND METHODS

Study sites.—We studied 3 maternity colonies of *E. fuscus* along the South Saskatchewan River in southeastern Alberta between the city of Medicine Hat and the village of Empress (total distance approximately 100 km). Although some cottonwood trees (*Populus*) are found in the river valley, most natural roosting habitat for bats is in the eroded rock walls of the river valley. Near the town of Bindloss (50°38'N, 110°11'W; 620 m elevation), approximately 34 reproductive female *E. fuscus* roosted in rock crevices that, as one of us (CLL) has observed, differed from randomly available crevices by being more vertical in orientation, farther from level ground above and below, and having smaller opening sizes (Lausen and Barclay 2002). No buildings were within 5 km of this study area, and rock roosts used during pregnancy, lactation, and postlactation differed in physical attributes (Lausen and Barclay 2003). In the town of Empress, 37 km northeast of the Bindloss colony, the Empress Community Hall (50°57'N, 110°00'W) housed approximately 200 female *E. fuscus* and their young. It was a wooden building located 1.0 and 5.5 km from the Red Deer and South Saskatchewan rivers, respectively. The attic was not insulated and ranged in height from 0.2 to 1.5 m. Another building-roosting colony (Elm Street School, 50°02'N, 110°39'W) is 75 km south of the Bindloss site in the city of Medicine Hat. The building was 1 km from the South Saskatchewan River in a residential area on the floodplain. The surrounding valley consists of sandstone with eroded rock crevices. The attic of this early-1900s red-brick building

was not insulated, varied in height from 2 to 6 m, and housed a maternity colony of approximately 100 female *E. fuscus* each summer.

Capture and radiotelemetry.—We captured bats with mist nets or by taking bats from rafters in the attics, and distinguished adults from juveniles by examining the finger joints for ossification (Anthony 1988). We estimated age of juveniles based on either forearm length (Holroyd 1993) or epiphyseal gap (Hamilton 1996), depending on size. We made the assumption that growth rates for *E. fuscus* at the school were the same as those of other *E. fuscus* in southeastern Alberta and provided a rough estimate of juvenile development. We classified females as nonreproductive, pregnant, lactating, or post-lactating (Racey 1988), and used colored plastic split-bands (A. C. Hughes, Hampton Hill, United Kingdom) for individual identification.

We used radiotelemetry to locate rock-crevice roosts and measure skin temperature of roosting bats (see Lausen and Barclay [2003] for details). All radiotransmitters (Holohil Systems Ltd., Carp, Ontario, Canada) were <5% of each bat's body mass (Aldridge and Brigham 1988), and were attached to the dorsal fur of reproductive females using SkinBond surgical adhesive (Smith and Nephew United, Inc., Largo, Florida). All work conformed to guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998), and the legal requirements of Canada regarding conservation and animal welfare.

Microclimate comparison.—We collected roost microclimate data in rock-crevice roosts (May–August 2000 and June–August 2001), in the school (June–August 2000), and in the hall (June–August 2001). We measured ambient temperature (T_{amb}) and roost temperature using 2 types of dataloggers: Thermochron iButtons, model DS1921 (Dallas Semiconductor Corp., Dallas, Texas) and HOBO Loggers (Onset Computer Corporation, Pocasset, Massachusetts). Roost sensors were placed as far as possible into crevices where bats had roosted. Microclimate data were collected within 5 days of bats leaving the roost, thereby avoiding sensors coming in contact with bats. In the attics, we placed HOBO dataloggers within 2 m of where bats roosted or where fecal accumulations suggested they commonly roosted. We measured ambient conditions using dataloggers encased in radiation shields. All sensors recorded conditions every 10 min.

Thermoregulation.—We collected thermoregulation data for rock-crevice-roosting bats from May to August 2000. We compared these data to those collected for attic-roosting (school) bats by I. Hamilton during May–August 1991–1993 (Hamilton and Barclay 1994) and by L. Hollis during June–July 2001 (Hollis 2004).

We recorded T_b of the rock-roosting bats every 10 min using a Lotek SRX 400 scanning receiver (Lotek Engineering Inc., Newmarket, Ontario, Canada) according to transmitter-specific calibration curves (provided by Holohil Systems Ltd.). Skin temperature measured using these methods accurately reflects T_b (Audet and Thomas 1996; Barclay et al. 1996; but see Willis and Brigham 2003).

Reproductive condition and timing.—We captured bats from all 3 maternity colonies periodically over the course of 4 years: school captures occurred 8 May–17 August 2000 (7 capture day–night periods), 26 May–2 August 2001 (13), 7 June–14 July 2002 (19), and 2 July 2004; hall captures occurred 25 June–13 August 2001 (7), 30 May–21 August 2002 (4), and 7–8 July 2004 (2); Bindloss captures occurred 27 May–20 August 2000 (24), 22 May–19 August 2001 (37), 24 May–28 August 2002 (22), and 5–7 July 2004 (3). We measured forearm length (mm) and mass (g), determined degree of toothwear (tooth classes 1–7, with 1 being reserved for individuals less than 1 year old, and 7 representing teeth more than one-third worn down—Holroyd 1993), and assessed reproductive condition for each captured bat.

Statistical analyses and definition of terms.—We transformed non-normal data (e.g., \log_{10}) to meet assumptions of normality. We used an

alpha value of 0.05 and present means \pm SE. Chi-square (Yates correction factor applied when $df. = 1$ —Zar 1984) and Fisher's exact test (when expected sample sizes were <5) were performed using Statistix 4.1 (Analytical Software, Tallahassee, Florida). We conducted t -tests and analyses of covariance (ANCOVAs) using SYSTAT 7.0.1 (SPSS Inc. 1997). T_{amb} was a covariate in all ANCOVA models to account for site and year differences.

Microclimate was compared between rock roosts and the school in 2000 and rock roosts and the hall in 2001. We described roost microclimate using several measures of temperature: time to reach maximum temperature is the number of minutes after sunrise the roost took to reach maximum temperature for the day, range of roost temperature (the maximum minus the minimum temperature for a particular day), and the number of degrees the minimum roost temperature was above minimum T_{amb} . For statistical analyses, we used 4 daily readings of T_{amb} and roost temperatures: minimum night temperature (usually near civil-morning twilight, when the sun is 6° below the horizon); minimum day temperature (near sunrise); maximum day temperature (at some point during the day); maximum night temperature (usually near civil-evening twilight). Maximum day temperature was measured in 2 ways for the school attic, using the warmest sensor, and using the coolest sensor. In Bindloss in 2000, we measured microclimate in 37 rock-crevice roosts, and in 2001 we measured microclimate in an additional 8. Temperatures of rock-crevice and building roosts were compared for the same days. Paired-sample t -tests were used to compare the hall with rock roosts, and ANCOVA, using T_{amb} as a covariate, was used to compare the school with rock roosts.

We defined torpor, shallow torpor, and deep torpor as described by Grinevitch et al. (1995) and Hamilton and Barclay (1994). An individual was torpid when its T_b dropped below its active temperature (T_{act}). T_{act} was determined by recording T_b within 10 min before a bat's emergence each night to forage, then selecting the lowest of these temperatures. A drop in a bat's temperature $\leq 10^\circ\text{C}$ below T_{act} was termed shallow torpor. A drop in a bat's temperature $> 10^\circ\text{C}$ below T_{act} was termed deep torpor.

We defined a "day" as from civil-morning twilight (or when the bat returned to the roost for the last time) until the bat emerged to forage that night. A torpor-day was any day on which a bat entered at least 1 bout of torpor. This definition also applied to deep-torpor days. For a bat-day (1 bat monitored for 1 day by telemetry) to be used in all other measures of torpor, T_b had to be recorded for a minimum of 10 h beginning no later than 0900 h. If no bouts of torpor were observed, the day was deemed a nontorpor day. For all analyses, each individual was used in 1 reproductive stage only.

Hamilton and Barclay (1994) reported patterns of torpor use by pregnant and lactating females in terms of frequency (percentage of bat-days). They also presented both morning and afternoon data, but because torpor-days always involve morning torpor (Lausen 2001), we used only data from the morning period in comparisons with our data.

To analyze the proportion of bats in torpor (and in deep torpor), we used generalized linear models, which tested for significant effects with likelihood-ratio (G) tests (McCullagh and Nelder 1989). These analyses considered binomial error distribution and a logit transformation of the observed proportions, and considered location (attic versus rocks) and reproductive stages (pregnancy versus lactation) as crossed, categorical, independent variables. Minimum T_{amb} was a continuous covariate, and we used generalized estimating equations (Liang and Zeger 1986) to account for the repeated measurement of individual bats on different days. We compared the minimum T_b of rock-roosting bats during torpor to those of torpid *E. fuscus* in the school for 1991–1993 (I. Hamilton, in litt.) using ANCOVA.

Masses in spring were compared (using ANCOVA) whenever bats at different colonies could be captured within 6 days of each other (school versus rocks in 2000 and 2001, and hall versus rocks 2002). The proportion of nonreproductive females in each colony was compared using data collected after 5 June, when pregnancy is more easily detected (chi-square; school versus rocks in 2000 and 2001, and hall versus rocks in 2001 and 2002). Timing of reproduction (parturition and weaning) was monitored via captures of adults and juveniles, and compared for school versus rocks in 2000 and all 3 maternity colonies in 2001 and 2004. Average age of individuals also was compared for all 3 colonies using toothwear measurements (analysis of variance [ANOVA]).

RESULTS

Microclimate.—The school roost cooled less at night than did rock-crevice roosts (minimum night temperature, adjusted least squares means, rocks = $19.5^\circ\text{C} \pm 0.5^\circ\text{C}$, attic = $24.0^\circ\text{C} \pm 0.5^\circ\text{C}$; minimum day temperature, rocks = $18.8^\circ\text{C} \pm 0.5^\circ\text{C}$, attic = $23.1^\circ\text{C} \pm 0.4^\circ\text{C}$; Table 1). The attic also warmed more slowly during the day (time to reach maximum temperature, rocks = 608 ± 19 min, attic = 700 ± 18 min). Some areas of the attic reached warmer day temperatures (maximum day temperature, rocks = $28.4^\circ\text{C} \pm 0.6^\circ\text{C}$, maximum day temperature at warmest sensors, attic = $30.8^\circ\text{C} \pm 0.6^\circ\text{C}$), whereas other areas provided maximum day temperatures similar to those available in the rock crevices (maximum day temperature at coolest sensors, attic = $28.6^\circ\text{C} \pm 0.6^\circ\text{C}$). The attic also remained warmer relative to minimum T_{amb} than did rock-crevice roosts (temperature elevation above minimum T_{amb} , rocks = $5.2^\circ\text{C} \pm 0.5^\circ\text{C}$ above minimum T_{amb} , attic = $9.6^\circ\text{C} \pm 0.5^\circ\text{C}$). Overall, temperature in the attic fluctuated less with T_{amb} than did that in rock crevices (Fig. 1).

Because *E. fuscus* in Bindloss moved to deeper rock crevices with more stable temperature regimes at the onset of lactation (Lausen and Barclay 2003), we tested whether differences in temperature between rock-crevice and building roosts still existed when only the lactation period was considered. We thus performed ANCOVA on each microclimate attribute during the lactation period only and found that the same microclimatic differences existed. In summary, throughout June, July, and August, the school attic was warmer at night, offered warmer temperatures during the day, and temperature was more stable than in rock crevices.

In 2001, temperatures in all 3 sensor locations in the hall were higher than in rock-crevice roosts during the day (maximum day temperature) and at the beginning of the night (maximum night temperature; Table 2). The warmest location in the hall attic at the end of the night (minimum night temperature) was warmer than in rock crevices, but the coolest locations did not differ from the rock-crevice roosts. In the morning (minimum day temperature), at the coldest time of the day, some parts of the attic were cooler than the rock crevices, whereas other parts of the attic were no different from the rock crevices. The hall attic had a larger range in daily temperatures (mean daily temperature fluctuation, rocks = $4.5^\circ\text{C} \pm 0.4^\circ\text{C}$, hall = $11.9^\circ\text{C} \pm 0.8^\circ\text{C}$, paired t -test, $t = 9.6$, $df. = 41$, $P < 0.001$).

TABLE 1.—Results of analyses of covariance describing microclimates in 2 types of roosts of *Eptesicus fuscus* (locations: Elm Street School attic versus rock-crevice roosts). Models describe number of minutes after sunrise the roost took to reach maximum temperature for the day, minimum night and minimum and maximum day temperatures, range in day temperature, and temperature elevation above minimum ambient. Maximum day temperatures selected from the warmest and coolest attic sensors were analyzed. Reproductive stage was included as a main effect for all temperature comparisons, and the covariate was ambient temperature (T_{amb}). Asterisks (*) indicate models in which microclimate differed significantly between the 2 locations.

Source	F-ratio	P
Time to reach maximum temperature		
Location	$F = 12.0, df = 1, 69$	<0.001*
Stage	$F = 6.56, df = 2, 69$	<0.001
T_{amb}	$F = 11.5, df = 1, 69$	0.001
Minimum night temperature		
Location	$F = 39.3, df = 1, 69$	<0.001*
Stage	$F = 7.65, df = 2, 69$	<0.001
T_{amb}	$F = 15.2, df = 1, 69$	<0.001
Minimum day temperature		
Location	$F = 45.0, df = 1, 69$	<0.001*
Stage	$F = 5.87, df = 2, 69$	0.004
T_{amb}	$F = 31.7, df = 1, 69$	<0.001
Maximum day temperature—warmest sensors		
Location	$F = 7.04, df = 1, 69$	0.009*
Stage	$F = 2.34, df = 2, 69$	0.104
T_{amb}	$F = 2.26, df = 1, 69$	<0.001
Maximum day temperature—coolest sensors		
Location	$F = 0.16, df = 1, 69$	0.692
Stage	$F = 0.96, df = 2, 69$	0.388
T_{amb}	$F = 24.0, df = 1, 69$	<0.001
Range in day temperature		
Location	$F = 4.47, df = 2, 69$	0.094
Stage	$F = 1.55, df = 2, 69$	0.219
T_{amb}	$F = 5.59, df = 2, 69$	0.021
Temperature elevation above minimum ambient		
Location	$F = 45.9, df = 1, 69$	<0.001*
Stage	$F = 5.73, df = 2, 69$	0.005
T_{amb}	$F = 7.05, df = 1, 69$	0.010

Thermoregulation.—In 2000 in Bindloss, we banded a group of 34 adult female *E. fuscus*. Because no unbanded individuals were captured at the end of the season, this likely represented most if not all of the adult females comprising this maternity colony. Transmitters were placed on 11 pregnant, 11 lactating, and 11 postlactating females. We tested the effect of colony location and reproductive state on frequency of torpor (Table 3). More frequent use of torpor occurred in the rock colony compared with the school attic colony ($\chi^2 = 4.81, df = 1, P = 0.028$). There was also an interaction between reproductive stage and minimum T_{amb} ($\chi^2 = 4.37, df = 1, P = 0.037$; see below for explanation of interaction). When frequency of deep torpor was analyzed, we found no difference between locations ($\chi^2 = 0.91, df = 1, P = 0.34$), and a difference between reproductive stages that neared significance ($\chi^2 = 3.17, df = 1, P = 0.075$).

The minimum T_b of torpid bats roosting in rock crevices was higher than minimum T_b of torpid bats in the school (ANCOVA, school: $n = 8$ individuals, 27 bat-days, adjusted least squares mean = $23^\circ\text{C} \pm 2^\circ\text{C}$; rocks: $n = 22$ individuals, 131 bat-days, adjusted least squares mean = $29^\circ\text{C} \pm 1^\circ\text{C}$; $F = 8.06, df = 1, 124, P = 0.005$). Variation in the model also was explained by reproductive stage (pregnancy, lactation, or postlactation, $F = 10.4, df = 1, 124, P < 0.001$), minimum T_{amb} ($F = 33.6, df = 1, 124, P < 0.001$), individual ($F = 5.10, df = 27, 124, P < 0.001$), and the interaction between reproductive stage and minimum T_{amb} ($F = 5.62, df = 2, 124, P = 0.005$). This interaction reflects the fact that T_b s of pregnant and postlactating bats decreased with T_{amb} , whereas T_b of lactating bats did not, corroborating previous findings (Lausen and Barclay 2003).

Reproductive timing and condition.—The maternity colony roosting in rocks consisted of more nonreproductive females than either of the building colonies (years 2000 and 2001, school, 3 nonreproductive of 98 total captures versus rocks, 19 of 66, $\chi^2 = 14.8, df = 1, P < 0.05$; years 2001 and 2002, hall, 8 of 93 versus rocks, 14 of 47, $\chi^2 = 6.1, df = 1, P < 0.05$), despite being composed of individuals of similar age as determined by toothwear (school mean toothclass 4.7 ± 0.15 , hall 5.1 ± 0.16 , rocks 4.7 ± 0.27 ; ANOVA, $F = 2.04, df = 2, 222, P > 0.1$).

Females in the buildings gave birth and weaned their young earlier than those in rock crevices. In 2000, we captured 6 neonates in the school on 3 July, the oldest being 10 days old (estimated from forearm length—Holroyd 1993). Despite constant monitoring, the 1st neonates in the Bindloss rock roosts were not heard (isolation calls—Kurta and Baker 1990) until 1 July, and the 1st was captured on 6 July. On 26 July, 5 volant juveniles were captured in the school and epiphyseal gaps of the 4th metacarpals ranged from 1.5–2.7 mm (L. Hollis, in litt.), indicating that the oldest juvenile was 33–38 days old (age-predictive equation for the school—Hamilton 1996). On 28 July, 4 volant juveniles were captured in the Bindloss area, and epiphyseal gaps ranged from 3.0 to 4.0 mm, indicating that juveniles were younger than in the school, with the oldest estimated to be 25–28 days old. Therefore, young in the Bindloss area fledged at least 1 week later than those from the school colony.

In 2001, we compared parturition dates and juvenile ages among all 3 colonies. Neonates were 1st observed in the school on 20 June (L. Hollis, pers. comm.). On 25 June, 6 neonates were captured at the hall, with the oldest estimated to be 4 days old, based on forearm length. Despite constant monitoring, no young had been detected in the rock-crevice roosts by 5 July. On 10 July, we captured 4 neonates in rock crevices, with the oldest estimated to be 3 days old. The 1st volant juveniles were captured at the school on 13 July (L. Hollis, pers. comm.), and in the rock crevices on 27 July. Postlactating females were captured at the school starting 15 July, and bats began leaving the attic colony on 8 August (L. Hollis, pers. comm.). We captured 6 postlactating females at the hall on 24 July, but none in the rock-crevice area until 9 August.

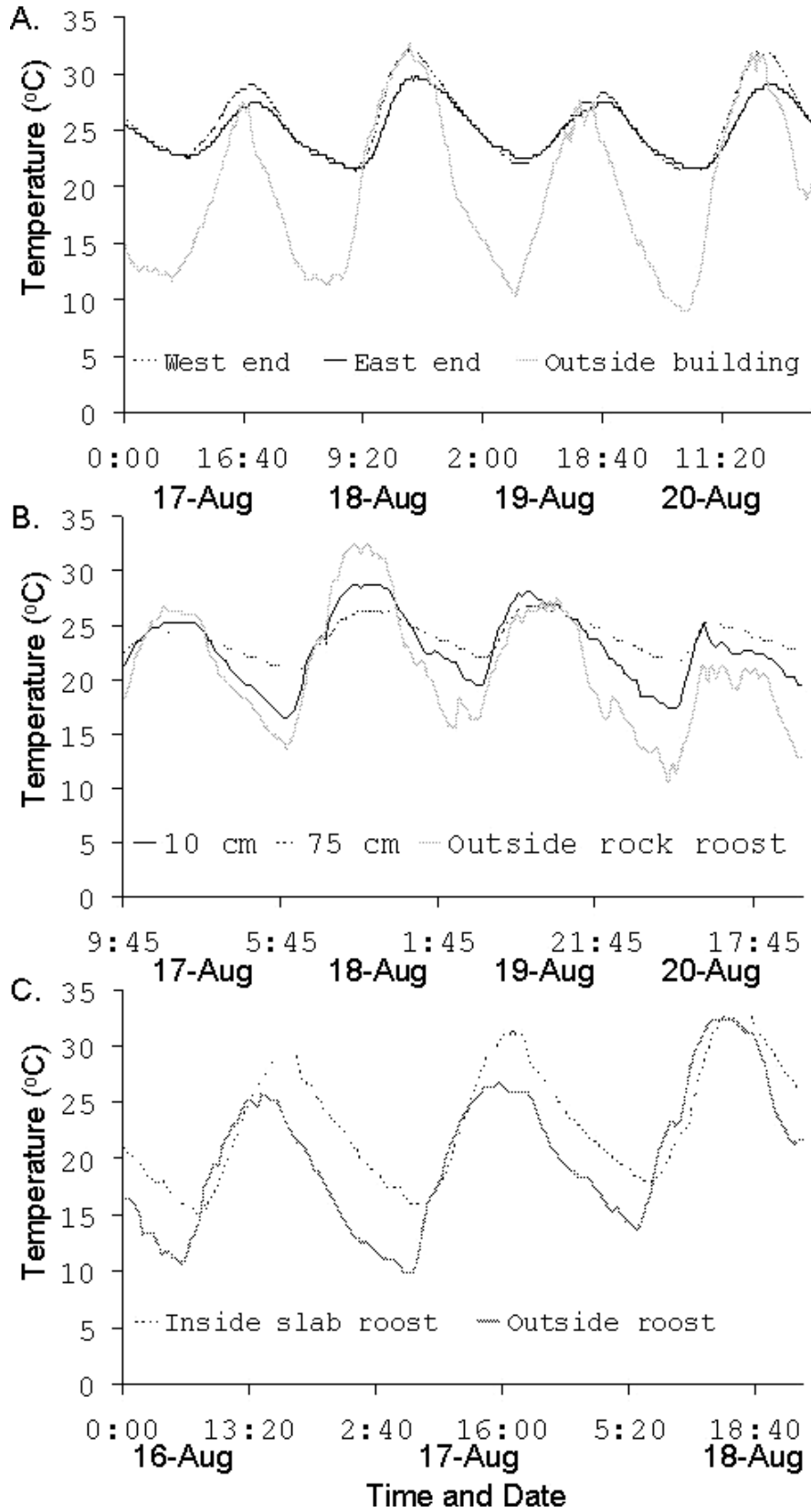


FIG. 1.—Temperature over several days in roosts of *Eptesicus fuscus* and outside the roost: A) the attic of Elm Street School and B and C) rock-crevice roosts. B shows temperature at 2 depths in a deep (125-cm), water-eroded tube in soft sandstone (lactation roost). C is temperature in a shallow (32-cm) fracture in a boulder (postlactation roost).

TABLE 2.—Roost temperatures ($^{\circ}\text{C}$, given as mean \pm SE; measured 28 June–8 August 2001) and paired-sample *t*-test results for the rock-crevice roosts versus the Empress Community Hall attic. Maximum and minimum day temperatures, and maximum and minimum night temperatures are compared (*df.* = 41).

Sensor location	Maximum day temperature	Maximum night temperature	Minimum night temperature	Minimum day temperature
Rock crevice	26.7 \pm 0.4	25.1 \pm 0.3	23.1 \pm 0.3	22.2 \pm 0.3
Warmest attic sensor	33.2 \pm 0.8	27.9 \pm 0.5	24.0 \pm 0.4	22.2 \pm 0.4
Coollest attic sensor	28.0 \pm 0.5	26.8 \pm 0.5	23.1 \pm 0.5	21.3 \pm 0.4
Warmest, <i>t</i>	9.8	8.8	2.9	0.2
<i>P</i>	<0.001	<0.001	<0.01	0.84
Coollest, <i>t</i>	3.2	4.9	0.2	3.1
<i>P</i>	<0.010	<0.001	0.88	<0.01

In 2004, we captured 7 females (approximately 18% of colony) at Bindloss on 5–7 July. None were lactating and we did not hear any neonate vocalizations outside the roost. At the school on 2 July, we captured 11 females (approximately 11% of colony). All 11 were lactating, and were captured with a total of 7 juveniles, the oldest of which was estimated to be 6.5 days based on forearm measurements. Finally, at the hall on 7–8 July, we captured 39 females (approximately 19.5% of colony), 7 of which were lactating, and neonates could be heard in the attic roost.

In spring, rock-roosting females weighed less than building-roosting individuals (27 May–9 June 2001: school, $n = 19$, 20.2 \pm 0.2 g versus rocks, $n = 25$, 16.9 \pm 0.3 g, ANCOVA, $F = 69.1$, *df.* = 1, 41, $P < 0.001$; 25–31 May 2001: hall, $n = 8$, 17.3 \pm 0.3 g versus rocks, $n = 14$, 16.4 \pm 0.4 g, ANCOVA, $F = 5.41$, *df.* = 1, 19, $P < 0.05$). Forearm length (school 47.5 \pm 0.1 mm, hall 47.7 \pm 0.22, rocks 47.6 \pm 0.45) was used as a covariate in these analyses.

DISCUSSION

Examination of our data supports the hypothesis that buildings are preferred sites for maternity roosts of bats because they provide thermoregulatory benefits compared to natural roosts. Examination of our data further indicates that the thermoregulatory benefits promote rapid growth of young, which may result in increased fitness. However, our results were not completely consistent with our predictions. We suggest that other benefits of roosting in buildings combine with thermoregulatory advantages to produce the unexpected results.

Natural roosts in rock crevices, caves, and tree hollows typically are insulated against extreme temperatures, resulting in warmer than ambient temperatures at night, but cooler than ambient conditions during the day (Betts 1997; Brown and Bernard 1994; Lausen and Barclay 2002; Sedgely 2001). These characteristics were true of rock crevices in our study. However, both buildings offered warmer day and night temperatures than did rock crevices. Similar warm roost temperatures have been found in other studies of buildings used by bats (Lourenço and Palmeirim 2004; Williams and Brittingham 1997).

TABLE 3.—Frequency of torpor use and deep torpor use by *Eptesicus fuscus* in Elm Street School and rock crevices in 2000 in southeastern Alberta.

Colony location	Reproductive stage	Torpor (bat-days)	Total observations (bat-days)	Use (%)
All torpor				
Elm Street School	Pregnancy	9	17	53
	Lactation	62	87	71
Rock Crevices	Pregnancy	43	56	77
	Lactation	44	50	88
Deep torpor				
Elm Street School	Pregnancy	8	9	89
	Lactation	4	62	6
Rock Crevices	Pregnancy	13	43	30
	Lactation	4	44	9

Warm roosts are advantageous to reproductive female bats for several reasons (Hoying and Kunz 1998; Humphrey et al. 1977; McNab 1982; Racey and Entwistle 2000; Sedgely 2001; Tuttle and Stevenson 1982; Zahn 1999). Higher roost temperatures reduce the energetic cost of maintaining a high T_b for females during the day, and for young at night while the females are foraging. Lower thermoregulatory costs for females mean that they do not have to resort to torpor as often as rock-crevice-roosting individuals do, as examination of our data showed. This in turn promotes more rapid gestation (Racey 1973; Racey and Swift 1981) and greater milk production (Wilde et al. 1995). Furthermore, for the 1st few days after birth, young bats are unable to maintain a high T_b (Hollis 2004). Warm roost temperatures therefore result in young maintaining warmer T_b at night while the females are away foraging. When combined with lower thermoregulatory costs once juveniles can regulate their T_b , warm temperatures will increase their growth rate. Faster growth in warmer roosts has been found in other species of bats (Tuttle 1975; Zahn 1999).

As we predicted, the warmer roost microclimate in the buildings and less frequent use of torpor by reproductive females were associated with advanced reproduction. In spring, females in both buildings weighed more than rock-roosting females, suggesting that they were in a more advanced stage of gestation. This was confirmed by earlier births and weanings. Earlier reproduction allows both adults and juveniles more time to prepare for hibernation and should thus increase overwinter survival (Kunz et al. 1998; Ransome 1990). This effect should be particularly important at higher latitudes where the reproductive season is short. At such latitudes, females sometimes forego reproduction in years when cool or wet weather slows gestation (Barclay et al. 2004; Grindal et al. 1992). We suggest that there was a lower proportion of nonreproductive females in the building colonies because the thermoregulatory advantages of those roosts partially compensate for poor ambient conditions and reduce gestation delays.

Contrary to our predictions, when bats in the buildings did enter torpor, they reached lower T_b s relative to T_{amb} than did females in the rock crevices. We propose that a reduced risk of predation in buildings allowed deeper torpor.

In the vicinity of rock-crevice roosts, we observed a number of predators that could potentially gain access to roosting bats, including rattlesnakes (*Crotalus viridis*) and bull snakes (*Pituophis melanoleucus*). A bull snake ate a lactating female and her young (Lausen 2001). In 14 years that one of us (RMRB) has engaged in research at the school, no predators have been observed in the attic. Although the hall has not been monitored as closely, it is unlikely that predators can gain access to it either.

The ability of a bat to avoid terrestrial predators is compromised by using torpor (Choi et al. 1998; Lyman et al. 1982), and the deeper the torpor, the less able the bat is to move (Schmidt-Nielsen 1990). Rock-roosting *E. fuscus* may maintain a higher T_b when torpid than building-roosting individuals to remain vigilant and more mobile. Females roosting in buildings where predation risk is lower can go deeper into torpor and save more energy when conditions make foraging unprofitable.

There may be other benefits of roosting in a building. For example, roost switching is a common feature of female bats in maternity groups of many species (Brigham et al. 1997; Fenton 1983; Kerth and König 1999; Lewis 1996), including *E. fuscus* (Lausen and Barclay 2002; Willis and Brigham 2004). As one of us (CLL) has observed, individuals in both buildings in our study switched locations within each attic (Hamilton and Barclay 1994), perhaps to match microclimatic conditions with their thermoregulatory needs (Audet and Fenton 1988; Watkins and Shump 1981). Likewise, bats frequently switched rock-crevice roosts within a small section (<1.5 km) of the river valley. Females tended to roost as 1 large group during lactation but several small groups of varying membership during pregnancy, although females often roosted alone on days when they used deep torpor (Lausen 2001). This fission-fusion type of colony structure (Kerth and König 1999; O'Donnell 2000; Willis and Brigham 2004) requires communication and coordination and may be facilitated in buildings that provide individuals requiring different thermoregulatory regimes with suitable safe roosting microenvironments.

Young bats make practice flights as they learn to fly and these may be accomplished in the relative safety of an attic or other building if it is large enough. At natural roosts such as tree hollows and rock crevices, practice flights must take place outside the roost, potentially exposing young to predators.

Finally, ectoparasite loads differ between natural and building roosts. Ticks are more common on rock-roosting bats compared to building-roosting bats throughout southeastern Alberta (Lausen 2005).

Our results highlight the importance of studying populations in the conditions under which they evolved. Much of our current understanding regarding bat thermoregulatory behavior and life-history traits has come from studies of bats roosting in buildings or other artificial structures, because of their accessibility (Audet and Fenton 1988; Fenton 1970; Gaisler et al. 1979; Grinevitch et al. 1995; Hamilton and Barclay 1994; Rodrigues et al. 2003; Schowalter and Gunson 1979; Schowalter et al. 1979; Whitaker 1998; Zahn 1999). If torpor and reproductive patterns differ between individuals roosting in buildings and those in natural roosts, thermoregulatory behavior and life-history traits described on the basis of

building-roosting populations may not accurately reflect the natural patterns for the species. The effect of differences between buildings and natural roosts on bat population dynamics remains to be determined.

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