

Roosting behaviour and roost selection of female big brown bats (*Eptesicus fuscus*) roosting in rock crevices in southeastern Alberta

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Abstract: We studied big brown bats (*Eptesicus fuscus*) roosting in rock crevices along the South Saskatchewan River in southeastern Alberta. We documented roosting behaviour and roost selection. During pregnancy and lactation, individuals aggregated as several small groups or one large group (maternity colony). Postlactating females roosted alone more frequently. During postlactation, individuals periodically returned to roost with a group dominated by pups, between periods of roosting alone. We identified 72 roosts used by members of the colony. Adult females switched roosts frequently and few roosts (24%) were reused. During pregnancy and lactation, the colony roosted in a 1.25-km length of the river valley on the northwest side of the river. With the onset of postlactation, females began roosting on both sides of the river and within a longer section of the river valley, and roosts faced in a more southerly direction. Crevices selected as roosts were more vertical in orientation, were farther from level ground above, and had openings that were smaller than those randomly available. Roosts used during pregnancy, lactation, and postlactation differed in physical attributes; lactation roosts were deeper and had larger openings. Selection of crevices with particular attributes suggested that selection was based on microclimate and avoidance of predation.

Résumé : Nous avons étudié la perchée et le choix des perchoirs chez des sérotines brunes (*Eptesicus fuscus*) qui habitent dans des crevasses rocheuses le long de la rivière Saskatchewan Sud dans le sud-est de l'Alberta. Durant la grossesse et l'allaitement, les chauves-souris se rassemblaient en petits groupes ou formaient un seul grand groupe (maternité). Après l'allaitement, les femelles se perchaient le plus souvent seules, mais certaines retournaient périodiquement se percher avec un groupe dominé par les petits entre les périodes de perchées isolées. Nous avons identifié 72 perchoirs utilisés par les membres de la colonie. Les femelles adultes se déplaçaient souvent et peu de perchoirs étaient utilisés plus d'une fois (24 %). Au cours des périodes de grossesse et d'allaitement, la colonie a utilisé une zone de 1,25 km de longueur dans la vallée, du côté nord-ouest de la rivière. Après l'allaitement, les femelles se sont mises à se percher des deux côtés de la rivière, dans une section plus étendue de la vallée et leurs perchoirs étaient davantage orientés vers le sud. Les crevasses utilisées comme perchoirs étaient orientées plus verticalement, elles étaient plus éloignées du sol et elles avaient des ouvertures plus petites que l'ensemble des crevasses disponibles. Les perchoirs utilisés au cours de la grossesse, au cours de l'allaitement et après l'allaitement différaient par leurs caractéristiques physiques; en période d'allaitement, les perchoirs étaient des crevasses plus profondes, à ouvertures plus larges. Le choix de crevasses à caractères particuliers indique probablement qu'elles sont choisies en fonction de leur microclimat et de la protection qu'elles assurent contre les prédateurs.

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Introduction

Energetic demands and avoidance of predation can largely dictate how an animal behaves and the "decisions" it makes regarding use of resources (Alcock 1998). Bats have high surface area to volume ratios (McNab 1982; Schmidt-Nielsen 1990), and this, together with flight costs, can result in large energy expenditure (McNab 1982; Kurta et al. 1989a). Reproductive females have the added energy demands of preg-

nancy and lactation (Gittleman and Thompson 1988). Like some other small mammals and some birds, bats are able to conserve energy by lowering their body temperature in daily torpor (Wang and Wolowyk 1988). However, for temperate-zone bats with a relatively short reproductive season, costs associated with the use of torpor, such as prolonged gestation (Racey 1973; Lewis 1993) and decreased milk production (Tuttle 1976; Wilde et al. 1995, 1999), tend to limit use of torpor, and individuals use alternative energy-saving strategies (McNab 1982; Hill and Smith 1984). Such strategies include clustering with other individuals (Kunz 1982; McNab 1982; Tuttle and Stevenson 1982; Roverud and Chappell 1991) and roosting in temperatures within the thermal neutral zone (Vaughan and O'Shea 1976; Churchill et al. 1997). Predation risk also likely moulds roosting behaviour and roost selection (Altringham 1996).

Because bats spend most of the day in a roost, roost conditions likely influence fitness. As refugia, roosts should be

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selected to minimize the risk of predation and of being parasitized (Lewis 1995, 1996), and provide a microenvironment suited to physiological needs (McNab 1982). Physical attributes and exposure of cavities to solar radiation can influence microclimatic conditions within roosts (Vaughan and O'Shea 1976; Vonnhof and Barclay 1997; Lausen 2001; Chruszcz and Barclay 2002). Bats are also in direct physical contact with a substrate (e.g., sandstone, shale, wood) while roosting, and because different substances conduct heat energy at different rates (Serway and Faughn 1989), bats cool at different rates depending on the nature of the substrate (Kurta 1985; Cossins and Bowler 1987). With tight energy budgets (Kurta et al. 1989a), bats may select appropriate thermal environments and roosting behaviours to achieve energy savings while minimizing costs. They may roost in clusters to minimize heat and water loss, and reproductive females may select roosts with different properties at different stages of reproduction to adjust for changes in thermoregulatory demands, group size, and environmental conditions.

An animal's environment shapes behaviour, necessitating the study of unique habitats to fully characterize a species' ecology. We examined the roosting behaviour and roost selection of a widespread species of bat, the big brown bat, *Eptesicus fuscus*. We studied a population roosting exclusively in rock crevices. While a number of studies have looked at aspects of tree-roosting (Brigham 1991; Betts 1995; Kalcounis 1995; Vonnhof 1995) and building-roosting (Audet and Fenton 1988; Holroyd 1993; Hamilton and Barclay 1994; Grinevitch et al. 1995; Williams and Brittingham 1997) populations of *E. fuscus*, this is the first study of roosting behaviour in a population roosting in rock crevices. Few studies have focussed on rock-roosting bat populations of any species (Tuttle and Heaney 1974; Trune and Slobodchikoff 1976; Vaughan and O'Shea 1976; Lewis 1996; Chruszcz and Barclay 2002), and little is known about the properties of any bat roosts, other than caves, owing to their inaccessibility (Kunz 1982; Nagorsen and Brigham 1993).

We investigated parasite load, group size, and roosting behaviours of reproductive female *E. fuscus* and measured the physical attributes of their rock-crevice roosts, including heat conductance of the roost substrate. We predicted that to minimize heat loss while roosting, reproductive females would select roost substrates that did not conduct heat well. We also predicted that roost-crevice openings would be small and the distance from level ground would be large to decrease vulnerability to terrestrial predators. Because exposure of a crevice to solar radiation alters thermal conditions, we predicted that aspect would be an important selection factor and that preferred aspect would change as physiological demands changed at each reproductive stage.

Methods

Study species

Eptesicus fuscus is widespread across much of North America. Individuals weigh ca. 18 g and feed on flying insects (van Zyll de Jong 1985). Parturition occurs in late June or early July, and in western North America most females give birth to one young (van Zyll de Jong 1985). During the summer months, adult females roost in maternity colonies

ranging in size from 5 to 700 individuals (Kurta and Baker 1990), but most colonies average fewer than 100 (van Zyll de Jong 1985). Natural roost sites for this species include rock crevices and tree hollows, but *E. fuscus* is also one of the most common species found in buildings (van Zyll de Jong 1985).

Study site

From May through August in 2000 and 2001, we conducted research in the South Saskatchewan River Valley (50°38'N, 110°11'W; 620 m asl) ca. 25 km southeast of the hamlet of Bindloss, Alberta. The terrain consists of eroded sandstone cliffs and hoodoo formations in the valley (badlands features) and flat grasslands above. Numerous drainage coulees run perpendicular to the valley. There are no buildings within 5 km of the study area. There are no trees other than several scattered clusters of cottonwoods (*Populus* spp.) close to the river's edge. Two basic types of rock make up the valley: cemented sandstone (hard boulder material) and non-cemented sandstone (solidified mud-sand, which erodes easily). Crevices exist in both types of material. The climate is arid, with rainfall averaging 12.7 cm between the beginning of June and the end of August (Environment Canada 1990). From June through August 2000 we recorded 9.8 cm of rain in the study area. Mean daily minimum/maximum temperatures during this period were 9.7/24.1°C in June, 15.3/31.3°C in July, and 13.7/28.8°C in August. Long-term values are 9.9/24.5°C in June, 12.0/27.5°C in July, and 10.7/26.8°C in August (Environment Canada 1990).

Captures

We captured bats by placing mist nets across coulees and between hoodoo formations in flyway areas. The bottom of the nets ranged from 0 to ca. 5 m above the ground. Adult bats were distinguished from juvenile bats by examining the joints in the fingers, adults have fully ossified epiphyses (Anthony 1988). We classified females as non-reproductive, pregnant, lactating, or postlactating (Racey 1988). By gently palpating the abdomen we could detect pregnancy. Pregnancy was confirmed by subsequent recapture of all but two bats later in the season. We confirmed lactation by expressing milk from enlarged teats. Postlactating females had hair regrowth around the periphery of the teats and we were unable to express milk. Each individual was examined visually for parasites, and by running our fingers through the fur we were able to detect the presence of ticks. We placed a numbered coloured plastic split-band onto one forearm of each individual for identification. All animals were cared for in accordance with the principles and guidelines of the Canadian Council of Animal Care.

To locate roosts, we attached 0.7-g radio transmitters (Holohil Systems, Carp, Ont.) to reproductive females using Skinbond® surgical adhesive (Smith and Nephew United, Inc., Largo, Fla.). As recommended by Aldridge and Brigham (1988), transmitter mass was less than 5% of a bat's body mass.

From 6 June to 26 August 2000 (77 days in total), we located roosts during the day on each day that an individual carried an active tag. We used a Merlin 12 receiver (Custom Electronics, Nokomis, Fla.) with either a five-element or a three-element Yagi antenna. We accessed roosts by climbing

or using ladders or ropes. Roosts were observed at emergence to confirm the position of exit(s) and to count bats. In 2001, we tracked radio-tagged bats between 18 May and 7 August (47 days in total) to determine whether previous roosts were reused.

Crevice

In 2000, we identified 72 roost sites and measured slope, aspect, dimensions and shape of the opening, depth, and distance to level ground above and below the roost. We also described the crevices in the following manner: constituent rock material (cemented or non-cemented sandstone), open or closed to rain, orientation (horizontal, vertical, or diagonal), side of the river (northwest or southeast), and type of crevice. The latter description involved classifying the crevice into one of three categories based on the diversity of crevices in the area: crack (long fissure), slab (having a thin outer wall), or erosion tube/hole (eroded hollow area). The opening shape and dimensions of each crevice were used to calculate the opening area.

We compared the heat conductance of the two types of rock with that of wood. Rock samples were taken from the study site and chiselled to 4 cm thickness. We took 4 cm thick wood samples from an attic known to have roosting *E. fuscus* (Hamilton and Barclay 1994). Volumes were determined by immersing the samples in water and measuring the volume displaced.

We conducted two experiments to quantify the heat-conductance properties of the materials. In the first, we heated rocks in an oven at 93°C for 1 h. All rocks were placed on cooling racks and a Thermochron iButton (model DS1921, Dallas Semiconductor Corp., Dallas, Tex.) was placed on the rock to record rock temperature each minute. The experiment ended when the rocks reached room temperature. Room temperature was measured using an additional iButton. The second experiment involved heating a rectangular plastic bag with 19 g of water (simulating the body of *E. fuscus*) to 38°C in a water bath. We then placed the heated bag on the sample (rock or wood) with a temperature-sensitive radio transmitter (Holohil Systems) taped lightly to the top of the bag. The entire system was covered with a layer of neoprene to minimize heat loss to the air above the water bag. We recorded the bag's temperature every minute until the bag reached room temperature. Cooling curves were compared statistically to determine differences in heat-retention and -conductance capacities.

We collected data for randomly selected crevices to compare with those for crevices used by bats. Randomly selected crevices were not known to be roost sites. Radio-tagged *E. fuscus* roosted predominantly in a 1.25-km stretch of the valley for most of the summer, and we measured 25 m long sections along both sides of the river in this stretch of valley. We randomly selected a section, a distance (0–25 m) to walk into the section, and a distance to walk away from the river. When we had moved the indicated distances, we located the nearest crevice large enough for at least one bat to roost in. We measured the same characteristics for the random crevices as for roost crevices. We measured 36 randomly selected crevices on the northwest side of the river but only 14

on the southeast side, owing to the smaller area with suitable terrain.

To measure roost availability we randomly selected numbers as outlined above, but after moving the appropriate distances, we searched within a 1-m radius for any crevice large enough for a single bat to fit in. If such a crevice was found, it was deemed an available roost. We repeated this 19 times on the northwest side of the river and 14 times on the southeast side.

Statistical analyses

We transformed data (e.g., \log_{10} , squaring, cubing, square root) to meet assumptions of normality and variance homogeneity. We used an α value of 0.05 and present means \pm standard error (SE). SYSTAT 7.0.1 for Windows was used for performing *t* tests, analyses of covariance (ANCOVAs), ANOVAs, and regressions. Chi-squared tests were performed using Statistix 4.1. Yates' correction factor was applied to all χ^2 tests with 1 degree of freedom (Zar 1984).

Statistical tests of circular data (aspect) were performed as outlined in Fisher (1993). Aspects for 46 roosts and 36 randomly selected crevices from the northwest side of the river were compared using a nonparametric statistical procedure (Fisher 1993, p. 115) to determine if roost aspect was different from what was randomly available. The test statistic can be evaluated using the χ^2 distribution. Using the same method we determined whether aspect differed for roosts used by reproductive (pregnant, lactating) and postlactating bats. We calculated mean directions as outlined in Fisher (1993, p. 31).

Results

Captures

Based on captures and roost observations, the bats we followed during this study formed one maternity "colony". We defined a colony as a group of individuals that roosted together regularly. Although roostmates changed from day to day when several roosts were being used at one time, individuals were always from the larger group, deemed the colony, which consisted of adult females and their pups. We banded 34 adult females, and because few unbanded individuals were caught at the end of the season, we believe that this represented most if not all of the adult females constituting the colony. We recaptured 22 of these females at least once during the study period. We also captured 18 juveniles (9 females, 9 males) in association with the maternity colony (in some cases mothers were captured with attached juveniles). On one occasion in 2001 we found two adult males roosting with the adult females. These males were juveniles born and banded in 2000. Adult male *E. fuscus* were regularly captured in the study area, but did not roost with the females and were thus not part of the maternity colony.

Of the 27 adult female *E. fuscus* inspected for ectoparasites, 5 did not have any (18.5% uninfected) and 22 had one or more types of ectoparasites. Twelve had soft-bodied ticks (*Ornithodoros* sp., likely *Ornithodoros alectorobius kelleyi*, W. Samuel, personal communication; 1–7 ticks per individual), 2 had bed bugs (*Cimex pilosellus*), 11 had mites (unidentified wing and ear mites), and 7 had bat fleas (*Myodopsylla* sp.).

In 2000, we attached 30 radio transmitters to 22 females (some females were tagged more than once). We tagged 11 pregnant females. We tagged 11 lactating females, the first on 6 July. One pregnant bat became lactating and two lactating bats became postlactating during the life of the transmitter, as confirmed via recapture. We radio-tagged 11 postlactating bats, the first on 30 July. Radio transmitters remained attached to the bat for between 1 and 18 days (7.4 ± 0.8 days). The last radio transmitters were attached on 20 August and these bats (along with other untagged *E. fuscus*) were still in the area on 26 August, when the study ended.

Roosting behaviour

The maternity colony was a cohesive group of individuals. The entire colony often roosted as one large group, but at other times roosted as several small groups during pregnancy and lactation. On several occasions we observed individuals roosting in contact with one another as one group. Emergence counts of *E. fuscus* occupying any one roost ranged from 1 to 37, with a group size of 8.25 ± 0.96 bats (median = 4.5 bats, $n = 92$ roosting groups). Five of the 11 (45%) pregnant bats roosted alone at least once during the life of their transmitter (79 bat-days roosting in a group, 11 bat-days alone (12.2%)). One of the 11 (9%) lactating bats roosted with her pup but no other bats (on the day following the birth of her pup; 59 bat-days in a group, 1 bat-day away from a group (1.7%)). Nine of the 11 (82%) postlactating bats roosted alone at least once (45 bat-days in a group, 49 bat-days alone (52.7%)). The proportion of bat-days spent roosting alone differed significantly across reproductive stages ($\chi^2 = 62.2$, $df = 2$, $P < 0.001$). The frequency of roosting alone increased as the postlactation period progressed, although adults often returned to roost with the group for a day after a period of roosting alone. For example, one female roosted with the pup-dominated group the day after tagging, then roosted alone for a day. For the next 17 days she roosted with the pup-dominated group six times and was out of the main roosting area for a total of 11 days (on 2 of these days we confirmed that she was roosting alone). Adult females roosted alone significantly more often after 14 August than earlier in the postlactation stage (1–14 August, 13 bat-days alone out of 55 bat-days; 14–25 August, 36 out of 39 bat-days; $\chi^2 = 56.1$, $df = 1$, $P < 0.001$).

Female *E. fuscus* switched roosts frequently. In 2000, we identified 72 roosts, 55 (76%) of which were used only once, 14 (19%) twice, 2 (3%) three times, and 1 (1%) four times. Roosts were occupied for 2.01 ± 0.18 consecutive days (range 1–7 consecutive days; median = 1 day). Most roosts (62, or 86%) were used during only one reproductive period, although one deep (>38 cm) erosion hole was used during all three reproductive periods, and 9 roosts were used during two reproductive periods. We located 14 roosts during pregnancy, 19 during lactation, and 59 during postlactation. During postlactation, bats frequently roosted alone, thus accounting for the large number of roosts found during that period.

Roosts were close to water, and all but one were within 400 m of the South Saskatchewan River. From 6 June through 10 August 2000, individuals from the colony roosted along a 1.25-km length of the river valley (main roosting area). After 10 August, the postlactating females spread out over a

4.41-km length that extended both upriver and downriver from the main roosting area.

Until 29 July 2000, female *E. fuscus* roosted only on the northwest side of the river, although we found two adult males on the southeast side. On 29 July, the colony roosted on the southeast side of the river for the first time. This move occurred 1 day before we captured and tagged the first postlactating female. The two sides of the river differ in aspect, with crevices on the northwest side facing predominantly southeast and crevices on the southeast side of the river facing predominantly west and south. The sides of the river also differed in crevice availability, the northwest side having significantly more crevices ($\chi^2 = 4.63$, $df = 1$, $P < 0.05$). By the end of the 2000 study period we had located 18 roosts (25%) on the southeast side of the river and 54 (75%) on the northwest side. This does not differ from the expected distribution of roosts based on availability ($\chi^2 = 0.03$, $df = 1$, $P > 0.9$). However, the distribution of roosts throughout the season changed significantly: of the 28 roosts used prior to 29 July, none were on the southeast side, but after this date, 18 of the 44 roosts were on the southeast side ($\chi^2 = 11.2$, $df = 1$, $P < 0.001$).

In 2001 we captured 28 of the *E. fuscus* banded in 2000 and we located roosts on 47 days via radiotelemetry. Thirteen rock crevice roosts identified in 2000 were reused in 2001 and 4 new rock-crevice roosts were discovered, all within the main roosting area. These new roosts were not measured and were not included in any statistical analyses. One roost used in 2000 was occupied by a nesting merlin (*Falco columbarius*) in 2001.

Roost selection

We compared randomly selected crevices (50) with roosts (72 roosts identified, 62 fully measured and described; Table 1). Roosts had significantly smaller openings and shorter distances from level ground above than randomly selected crevices. Roosts did not differ from randomly selected crevices in depth, distance to level ground below, or slope of the ground containing the opening. On the northwest side, roosts did not differ in aspect from randomly selected crevices. Roosts were significantly different in orientation from randomly selected crevices: more roosts were sloped (vertical or diagonal) than those that were randomly available. Roosts used during pregnancy (12), lactation (20), and postlactation (23) differed in depth (ANOVA, $F_{[2,52]} = 6.02$, $P = 0.004$), lactation roosts (64.1 ± 7.7 cm) being significantly deeper than roosts used during postlactation (37.0 ± 3.9 cm, $P = 0.0047$), and deeper, but not quite significantly so, than roosts used during pregnancy (40.6 ± 7.5 cm, $P = 0.051$). Roosts also differed in opening size ($F_{[2,52]} = 3.89$, $P = 0.027$; overall opening area 213 ± 36 cm²), postlactation roosts (136 ± 34 cm²) having significantly smaller openings than lactation roosts (239 ± 46 cm², $P = 0.029$). Roosts used during pregnancy and lactation differed significantly in aspect ($126 \pm 9^\circ$) from postlactation roosts ($177 \pm 9^\circ$; χ^2 equivalent = 23, $df = 1$, $P < 0.05$).

To compare the rates of cooling of the two types of rock material, we used a nonlinear regression model of the form $y = (a - c)^{b \times x} + c$, where y is rock temperature, a is the temperature at time zero, c is room temperature, and b is a decay factor describing the slope of the curve. The two types

Table 1. Statistical comparisons of roost crevices with randomly selected crevices.

	Opening size (cm ²)		Distance from level ground above (m)		Depth (cm)		Distance from level ground below (m)		Slope of ground (deg.)		Aspect (deg.)		Orientation	
	Roost crevices	Random crevices	Roost crevices	Random crevices	Roost crevices	Random crevices	Roost crevices	Random crevices	Roost crevices	Random crevices	Roost crevices	Random crevices	Roost crevices	Random crevices
	203 ± 25	2189 ± 1563	6.3 ± 1.2	3.6 ± 1.0	47 ± 4	48 ± 8	4.2 ± 0.6	5.3 ± 1.4	85 ± 4	74 ± 5	128 ± 9	113 ± 8	Diagonal/vertical	Horizontal
Test statistic	<i>t</i> = 2.61		<i>t</i> = 2.18		<i>t</i> = 1.44		<i>t</i> = 0.82		<i>t</i> = 1.84		$\chi^2_{\text{equivalent}} = 0.68$		$\chi^2 = 13.3$	
df	87.4		101		78		59.8		109		1		1	
<i>P</i>	0.011		0.032		0.155		0.418		0.068		>0.05		<0.001	

Note: Values are given as the mean ± SE.

of rock differed significantly ($F_{[1,15]} = 14.1, P = 0.002$) in heat conductance, with cemented sandstone ($n = 12$ rocks, $b = -0.0297 \pm 0.001 \cdot \text{min}^{-1}$) cooling more slowly than non-cemented sandstone ($n = 6, b = -0.0333 \pm 0.002 \cdot \text{min}^{-1}$) after being heated. We included volume in the model as a covariate and it accounted for a significant portion of the variation ($F_{[1,15]} = 18.7, P < 0.001$). We also compared the cooling curves for the heated water bag cooled on cemented sandstone ($n = 12$), non-cemented sandstone ($n = 6$), and wood from the attic ($n = 3$). We performed an ANCOVA to determine whether type of substrate affected the shape of the water bag's cooling curve. We included volume of the substrate in the model as a covariate but this did not explain a significant portion of the variation ($F_{[1,17]} = 0.21, P = 0.65$). Type of substrate significantly affected the cooling curves ($F_{[1,17]} = 28.6, P < 0.001$). Cemented sandstone cooled faster (mean $b = -9.26 \times 10^{-4} \pm 4.21 \times 10^{-5} \cdot \text{min}^{-1}$) than non-cemented sandstone (mean $b = -7.22 \times 10^{-4} \pm 4.96 \times 10^{-5} \cdot \text{min}^{-1}; P = 0.034$) and wood (mean $b = -5.26 \times 10^{-4} \pm 3.43 \times 10^{-5} \cdot \text{min}^{-1}; P = 0.001$). Non-cemented sandstone did not differ significantly from wood ($P = 0.2$). The proportion of roosts made of non-cemented sandstone (33 out of 62) did not differ from what was randomly available ($\chi^2 = 0.02, \text{df} = 1, P = 0.89$).

We classified roosts into three main types: tubes/holes ($n = 32$), cracks ($n = 20$), and slabs ($n = 10$). Selection of roosts based on type did not differ in the three reproductive stages ($\chi^2 = 2.02, \text{df} = 4, P = 0.73$). We classified roosts as "open to rain" ($n = 26$), or "closed to rain" ($n = 36$). On rainy days ($n = 15$) and days with no rain ($n = 63$), the proportion of roosts that were closed to rain versus open to rain did not differ ($\chi^2 = 0.87, \text{df} = 1, P > 0.5$).

Discussion

Reproductive female *E. fuscus* selected rock-crevice roosts with certain physical attributes, and changed their behaviour over the summer. Because the physiological requirements of reproductive females change over the course of a season, one expects to find associated behavioural changes, such as clustering to reduce heat loss (Kunz 1982; McNab 1982; Tuttle and Stevenson 1982; Roverud and Chappell 1991) and choosing a roost with an appropriate thermal regime (Vaughan and O'Shea 1976; Churchill et al. 1997).

During pregnancy and lactation, the maternity colony we studied sometimes existed as several small groups, but at other times as one large group. This group "fluidity" is similar to the roosting behaviour of *E. fuscus* and *Chalinolobus tuberculatus* using tree cavities (Brigham 1991; Kalcounis 1995; O'Donnell 2000), but unlike the more stable group composition and roost fidelity observed in colonies of *E. fuscus* roosting in buildings (Brigham and Fenton 1986; Brigham 1991; Holroyd 1993). This suggests that natural behavioural patterns may not be present in groups roosting in man-made roost structures, where protection from predators is greater, more microclimate options may exist, and alternative roost structures may be absent. Female *E. fuscus* in our study area roosted alone more frequently during post-lactation and this behaviour was pronounced during the latter part of postlactation. The clustering behaviour observed in pregnancy and lactation, and reduced clustering during postlactation, are consistent with the finding that pregnant

and lactating females used torpor less than did postlactating females (Lausen 2001; see also Hamilton and Barclay 1994). Clustering reduces energy expended to replace lost metabolic heat, and can decrease evaporative water loss (Studier 1970; Wang and Wolowyk 1988; Kurta et al. 1989b), which may be most important for lactating bats (Kurta et al. 1990; Wilde et al. 1995), especially in an arid environment such as our study area. The costs of torpor are reduced for postlactating female bats, and roosting singly facilitates the use of torpor (Licht and Leitner 1967; Trune and Slobodchikoff 1976). Postlactating *E. fuscus* roosting in buildings frequently roost away from the maternity roost and use torpor more (Hamilton and Barclay 1994). Postlactating *C. tuberculatus* also roost solitarily more often than pregnant and lactating individuals (O'Donnell and Sedgely 1999).

Aspect and slope can influence roost microclimate because of differences in absorption of solar radiation (Rosenburg 1974). During pregnancy and lactation, roosts did not differ in aspect or slope from what was randomly available. With the onset of postlactation, females began roosting on both sides of the river, and within a longer stretch of the valley. Lower roost availability on the southeast side explained the unequal numbers of roosts on the two sides, but the sudden change in behaviour observed at the end of July is best explained by microclimate differences resulting from differences in aspect between the sides (Lausen 2001). Roosts selected during postlactation faced significantly more south and would have received less direct sunlight at dawn than the roosts used during pregnancy and lactation (Lausen 2001). Aspect has been identified as an important factor for *E. fuscus* selecting roosts in tree cavities (Kalcounis 1995). We suggest that in rocky areas, aspect is important for selecting the larger roosting area along the river valley, and the side of the river occupied.

After weaning, postlactating female *E. fuscus* forage increasingly far from the maternity roost (L. Wilkinson, personal communication), and lower roost fidelity has been found for other postlactating female bats (reviewed in Lewis 1995). In our study, adult females periodically returned to roost with the pup-dominated group between periods of roosting alone, perhaps reflecting underlying social bonds that are not yet understood.

Female *E. fuscus* switched roosts frequently. A large number of roosts were used by the colony during one season, and few were reused, which is similar to the behaviour of *Antrozous pallidus* (Lewis 1996; Vaughan and O'Shea 1976) and *C. tuberculatus* (O'Donnell and Sedgely 1999). *Eptesicus fuscus* switch roosts frequently in some geographic locations but not others (reviewed in Lewis 1995). For bats in general, frequent roost switching has been attributed to microclimate, avoidance of ectoparasites, predator avoidance, and human disturbance (reviewed in Lewis 1995), and correlated with roost availability and permanency (Kunz 1982; Lewis 1996). Rock-crevice availability was high in our area, and although rock crevices might be expected to have a high degree of permanency, several roosts were destroyed or altered by erosion during heavy rain. High availability and erodability of rock crevices may thus have promoted roost switching.

The colony displayed fidelity to the roosting area but less to individual roosts, as also occurs in some tree-roosting bats (Kunz 1982; Kalcounis 1995; O'Donnell and Sedgely 1999).

While most roosts were not reused in one season, they were reused between years. Seventy-six percent (13 of 17) of roosts recorded in 2001 were used in 2000. This supports the observation that year-to-year fidelity is higher when roost permanency is greater (Lewis 1995).

Avoidance of ectoparasites has been used to explain frequent roost switching in rock-roosting *A. pallidus* (Lewis 1993, 1996). Over 80% of the adult female *E. fuscus* in our study were infested with at least one type of ectoparasite, and 44% had ticks. Ticks can remain in the rock crevices awaiting hosts and some species feed on bats for several days, detaching between nymphal instars and then reattaching to feed at each stage (Allan 2001). Switching roosts and avoiding reusing them within a season may reduce ectoparasite load.

Frequent roost switching might also be attributed to predator avoidance (Kunz 1982; Wilkinson 1985; Lewis 1995). Potential predators in our study area included short-eared owls (*Asio flammeus*), merlins, bull snakes (*Pituophis melanoleucus*), coyotes (*Canis latrans*), great horned owls (*Bubo virginianus*), and rattle snakes (*Crotalus viridis*; Holloway 1998). A bull snake consumed two radio-tagged *E. fuscus* on 9 July 2000. We also discovered an extralimital population of bushy-tailed wood rats (*Neotoma cinerea*), which may take bats from roosts (Lewis 1996). Wood rats approached closely when bats vocalized during handling or entanglement in mist nets.

Risk of predation may also explain physical attributes of roosts. Crevices selected as roosts had smaller openings and were farther from level ground above than what was randomly available. Small openings may provide protection from predators (Tidemann and Flavel 1987), but because microclimate is also affected by opening size (Lausen 2001), predation risk may not be the only explanation for this preference.

Roosts were not selected for shape (i.e., slab, crack, hole/tube), but for dimensions. All roosts had smaller openings and were more vertical than what was randomly available. Rock-crevice roosts used during lactation were deeper than those used during pregnancy and postlactation. Deeper roosts are also selected by lactating *A. pallidus* (Lewis 1996; Vaughan and O'Shea 1976) and lactating *Myotis evotis* (Chruszcz and Barclay 2002), and have more moderate, stable temperature regimes than shallow crevices (Vaughan and O'Shea 1976; Lausen 2001; Chruszcz and Barclay 2002). Postlactation roosts had smaller openings than lactation roosts, perhaps reflecting the smaller size of groups during postlactation.

Crevice substrate was not an important physical attribute in selection of roosts by *E. fuscus*, despite the fact that individuals cool at different rates on different substrates (Kurta 1985), and that in a cluster of bats, those in contact with a rock substrate are cooler than those roosting off the substrate (Twente 1955). Although differences in heat conduction by the different substrates were statistically significant, they may not be biologically significant. For example, we used a plastic bag with water, while living bats are furred, have physiological response mechanisms, and may not cool significantly differently on the two types of rock substrate. A smaller bat (ca. 7 g) in our study area, *M. evotis*, roosts exclusively in cemented sandstone (Holloway 1998; Chruszcz and Barclay 2002). These bats, unlike *E. fuscus*, roost soli-

tarily and use torpor every day regardless of reproductive state (Chruszcz and Barclay 2002). Cemented sandstone is a “heat sink” during the day, absorbing the sun’s energy and radiating at a slower rate than non-cemented sandstone, but it is less insulating than non-cemented sandstone. Chruszcz and Barclay (2002) suggested that *M. evotis*, a small gleaning bat, may be forced to use torpor every day to balance its energy budget, and we suggest that its choice of rock substrate may facilitate this. In contrast, *E. fuscus*, weighing more than twice as much, aggregating in groups, and not using torpor every day (Lausen 2001), may be unaffected by differences in substrate heat conductance, or perhaps other roost attributes have greater fitness consequences.

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