Intraspecific Variation in Roost-site Selection by Little Brown Bats (*Myotis lucifugus*)

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ABSTRACT

Although many species of bats select roost sites in large trees that are in open areas, intraspecific variation in roost-site selection may exist. We collected data on the roosting behaviour of little brown bats in the Cypress Hills, Saskatchewan, to determine the extent of intraspecific variation in roost-site selection. In addition, we examined the thermal microclimate of the tree-roosts selected by bats, to determine if roost-microsite variation can explain why certain cavities are selected over others. We found little brown bats roosting in trees as well as buildings. With the exception of a male who roosted in a spruce (*Picea glauca*) stump, tree-roosts selected by male and female little brown bats were all in trembling aspen (*Populus tremuloides*) trees. We found variation in roost-site fidelity and differential use of torpor by male bats. Temperatures within conifer snag cavities differed from aspen cavities during the day, and mirrored ambient temperature, which tended to be warmer than aspen cavities. We propose that bats select cavities in aspens because they are susceptible to heart rot. Aspen trees with heart rot provide cavities with an intact sapwood shell that protects bats against harsh ambient conditions as well as predators, and provides a unique thermal microclimate. Our results suggest that the origin of a roost site may be unimportant to a bat, provided certain other requirements are met.

INTRODUCTION

Compared with nest-site selection by birds, relatively little is known about roost-site selection by bats, especially selection of natural roosts, such as tree cavities. Rather, the majority of ecological research on temperate insectivorous bats (Chiroptera: Vespertilionidae) has dealt with species roosting in human-made structures. The reason for this is that it is far easier to find and gain access to bats roosting in a human-made structure than in natural sites, such as tree cavities. As a result, however, our understanding of the cues that bats use to select sites under natural conditions, where human-made structures are not abundant, is limited.

Until very recently, the number of studies that examine selection of tree-roost sites by temperate bats has been low. However, as evidenced by the number of papers presented at this conference that address tree-roosting by bats, this is clearly changing (see papers in this volume by Betts, Chung-MacCoubrey, Crampton and Barclay, Kurta et al., Ormsbee, Sasse and Pekins, and Vonhof). Over different forest types and geographical regions, information on the cues that bats use to select roost sites under natural conditions is rapidly emerging. Despite differences in study areas and species, roost trees are typically large and in open areas. In addition, many bats that roost in aspen trees are secondarily using cavities originally excavated by primary cavity excavators (sapsuckers and other woodpeckers) for nest sites.

Although we heard at the conference that many species of bats select roost sites in large trees that are in open areas, intraspecific variation in roost-site selection has not been a focus of attention. However, in the Netherlands, the noctule bat (*Nyctalus noctula*) is found exclusively in tree cavities, while in central Europe individuals roost in buildings as well as tree cavities (van Heerdt and Sluiter 1965). Big brown bats in British Columbia roost in hollows of dead ponderosa pine trees (*Pinus ponderosa*), while the same species in Ontario roosts in human-made structures (Brigham 1991). Indeed, geographic differences, such as climatic conditions and prey availability, may explain differences seen in the type of roost selected. This leads to the question of how flexible the roosting behaviour of bats is in one area, where geographic differences are not a factor.

We collected data on the roosting behaviour of little brown bats in the Cypress Hills, Saskatchewan, to determine the extent of intraspecific variation in roost-site selection. In addition, we examined the thermal microclimate of the tree-roosts selected by bats to determine if roost-microsite variation can explain why certain cavities are selected relative to others. We propose that bats select cavities in aspen trees infected with heart rot because these trees provide cavities with an intact sapwood shell that protects against harsh ambient conditions, as well as predators, and provides a unique thermal microclimate within.

METHODS

Our study occurred from May to August, 1994. The study area was located within the West Block of Cypress Hills Provincial Park (49° 34′N, 109° 53′W), approximately 60 km southwest of Maple Creek, Saskatchewan, Canada. Lodgepole pine (*Pinus contorta*) forest, with little understorey, occupies dry sites above 1300 m, and white spruce (*Picea glauca*) forest occurs in cool, moist areas near wetlands and on north-facing slopes. Trembling aspen is found growing with white spruce near streams as well as in stands scattered throughout the hills on the edge of lodgepole pine stands (Sauchyn 1993).

Data on roost-site selection in buildings by little brown bats were collected by watching the buildings in the study area at dusk, with the aid of a bat detector, to determine if bats were roosting in the building. Data on roost-site selection in trees by little brown bats were collected as part of a larger study looking at natural roost-site selection by big brown bats (Kalcounis 1995). Little brown bat tree-roost sites were found using two methods. First, while taking measurements of cavity microclimate of big brown bat (*Eptesicus fuscus*) roost and random available trees (Kalcounis 1995), we checked cavities for little brown bats. Second, we used radio-telemetry to locate roost trees. Individual little brown bats were captured in mist nets set in suspected foraging areas. Upon capture, 0.8-g, temperature-sensitive transmitters (BD-2T, Holohil Systems Ltd., Carp, Ontario) were attached using Skinbond cement. Bats were released soon after the cement had dried. Individuals carrying radio-transmitters were tracked to their roosts on the morning following capture using Merlin 12 (Custom Electronics, Urbana, Illinois) portable telemetry receivers and hand-held, 5-element Yagi antennae. When a suspected roost tree was located, we observed it at dusk to ensure that it was being used by bats, and to determine the number of bats roosting in the tree. Bats carrying radio-transmitters were tracked to their roosts every day until the transmitter fell off or the signal was no longer heard. For each day that we tracked bats, we determined if they were active or torpid in the roost.

Thermal Microclimate Within Cavities

To compare temperature profiles of the cavities selected by bats (old sapsucker holes in aspen trees) with those not selected (cavities in conifer snags), temperature-sensitive radio-transmitters were used. Snags were defined as dead white spruce or lodgepole pine trees with cavities. Transmitters were placed in cavities by climbing the trees and suspending the transmitter in the cavity using monofilament line. Two cavities of each type were selected at random.

Temperatures in both cavity types were compared to ambient temperatures. Each sampling day was divided into four time periods reflecting early morning (period 1: 0000h–0559h), mid-morning (period 2: 0600h–1159h), afternoon (period 3: 1200h–1759h), and evening (period 4: 1800h–2359h) time blocks.

To measure temperatures, we used an automated telemetry receiver (Lotek SRX 400 telemetry receiver using Event Log Version 2.62, W18 data-logging software, Lotek Engineering Inc., Aurora, Ontario). The receiver was programmed to record the temperature, for each transmitter, every hour for each 24-hour period from 13 to 26 July. To determine whether ambient and cavity temperature profiles differed, we performed one-way analysis of variance (ANOVA) tests using mean temperatures within the four time periods.

RESULTS

Roost-Site Selection by Little Brown Bats

We found two little brown bat building-roosts, both of which were maternity colonies. One maternity colony was located in the park headquarters building in the West Block of Cypress Hills Provincial Park. The bats roosted in the attic and under the cedar shingles of an east-facing section of the roof. They have used the structure for at least four years (see Kalcounis and Brigham 1994). The mean colony size in 1992 and 1993 was 23 with a range of 2 to 72 (Kalcounis and Brigham 1994). The other building-roost was located in a farmhouse abandoned for one year. The farmhouse had broken windows through which the bats emerged. During an emergence in June 1994, over 250 little brown bats were counted.

We found six little brown bat tree-roosts, one of which housed a maternity colony. While taking measurements within the cavity of a random available tree for Kalcounis (1995), a colony of 23 little brown bats was found in an old sapsucker (Red-naped or Yellow-bellied subspecies of *Sphyrapicus varius*) hole in a live trembling aspen tree. The two individuals captured from this colony were juvenile females too small to carry transmitters. The colony remained in the roost tree for three days.

The remaining five roost sites were located by radio-tracking two adult male little brown bats. The two bats were caught on 6 and 7 July, respectively, which allowed us to radio-track them simultaneously. Both males roosted solitarily. We were able to track the first male bat for eight consecutive days, and found that it roosted exclusively in a crack in a spruce stump. We were able to track the second male bat for 19 consecutive days and found that it roosted exclusively in aspen trees; however, it switched between four different cavities in four different trees. Details of the male little brown bat roost-tree characteristics are given in Table 1. All aspen trees had symptoms of fungal heart rot in the form of conks (fungal fruiting bodies).

In addition to variation between the males in the type of roost selected and fidelity to particular roost sites, the males differed with respect to the use of torpor while in the roost. Of the eight days that we were able to track the males simultaneously, both bats remained active in the roost for seven days. On one day, however, the stump-roosting male remained active while the other male roosting in a live aspen tree used torpor (Figure 1).

Thermal Microclimate Within Cavities

Mean temperatures differed significantly in time periods 1 ($F = 21.33$, $df = 2$, $p < 0.001$), 2 ($F = 20.06$, $df = 2$, $p < 0.001$), and 4 ($F = 11.64$, $df = 2$, $p < 0.001$). Roost cavities were significantly warmer than ambient temperature, but significantly cooler than conifer snags during time period 1 (Figure 2). In time period 2, roost cavities were significantly

TABLE 1 *Characteristics of male little brown bat tree-roosts. The male bat who roosted in the spruce stump is referred to as Bat A. The male who switched aspen tree-roosts is referred to as Bat B.*

Bat	Tree condition	Tree species	Tree height (m)	DBH (cm)	Origin of cavity	Cavity entrance height (m)	Number of cavities in tree	Dates occupied
A	dead, stump	spruce	2.2	38.2	split wood	—	—	6–14 July
B	dead, snag	aspen	6.1	33.3	sapsucker	5.7	3	8 July, 14 July
B	live	aspen	31.2	35.0	sapsucker	12.0	1	9–10 July, 16 July
B	live	aspen	39.4	36.7	branch scar	7.7	1	11–13 July, 15 July
B	dead, standing	aspen	12.6	25.1	sapsucker	8.1	>5	17–22 July, 27 July

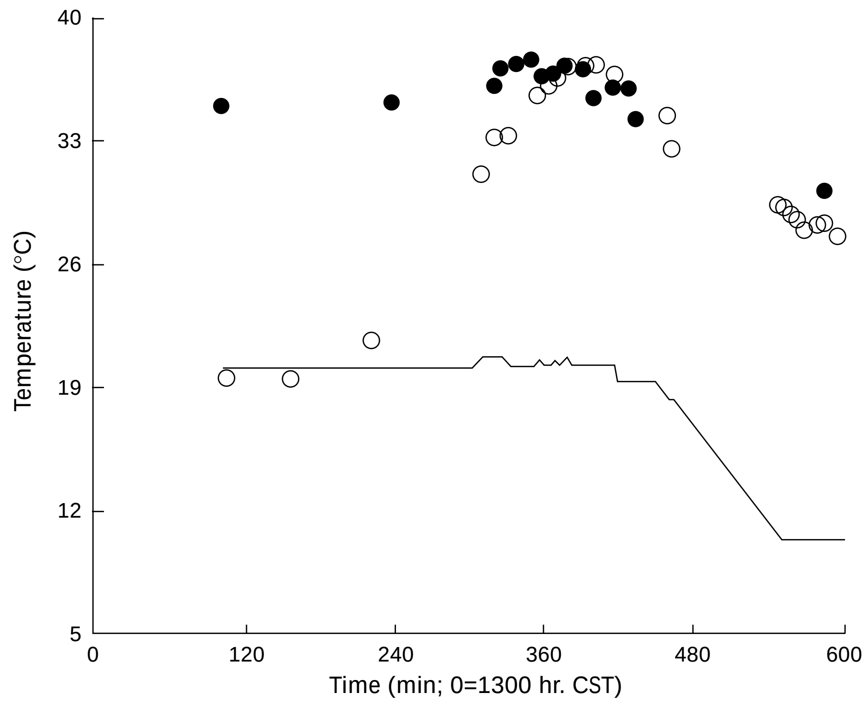

FIGURE 1 *Temperature profiles of the two male bats. The bat roosting in the stump (●) stayed active while in the roost. The bat roosting in the aspen cavity (○) was torpid until approximately 1515 h and was active by 1900 h. Ambient temperature is shown by the solid line.*

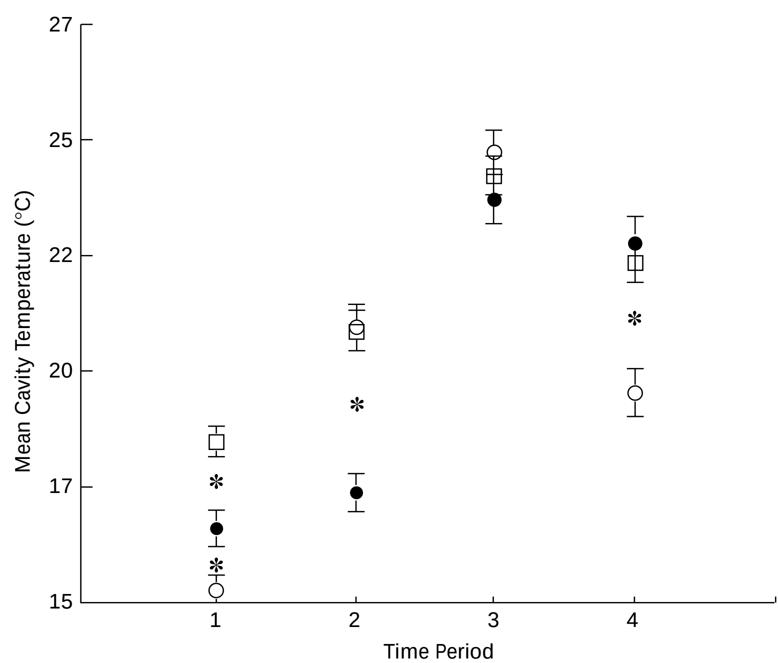

FIGURE 2 *Mean (±1 SE) temperatures of cavities in each of the four time periods (see text). Means separated by * are significantly different (Tukey's Test). Ambient (○), Roost (●), Snag (□).*

warmer than ambient temperature and snags, which did not differ from one another (Figure 2). In time period 4, both cavity types were significantly warmer than ambient temperature (Figure 2).

DISCUSSION

Our results demonstrate that within an area there is considerable intraspecific variation in little brown bat roost-site selection, with bats roosting in both live and dead trees as well as buildings. With the exception of the spruce stump, there was little variation in the type of tree-roost selected by male and female little brown bats. We found variation in roost-site fidelity and differential use of torpor by male bats. These results suggest that the origin of a roost site may be unimportant to a bat, provided that certain other requirements are met. Indeed, the roosting behaviour of little brown bats in Cypress Hills is flexible enough that they were found roosting in buildings, as well as aspen trees. Presumably, little brown bats are able to use human-made structures for roosts, provided that the human-made structures are of appropriate dimensions and provide a suitable microclimate within.

Bats used more than one roost tree. There are several reasons why some of the bats in our study may have switched tree-roosts. When the roost microclimate or distance to foraging area changes, bats may respond by switching to more preferred sites (Kunz 1982; Lewis 1995). Bats may switch roosts to avoid predators (Barclay et al. 1982; Kunz 1982; Wilkinson 1985; Audet 1990; Lewis 1995; but see Fenton and Rautenbach 1986) or large populations of ectoparasites (Wilkinson 1985; Lewis 1995).

Some species of bat that switch roosts frequently remain faithful to particular areas (Lewis 1995). Even though one male little brown bat switched roosts frequently, he often returned to previously used roost trees, suggesting fidelity to a particular group of roost trees rather than a single roost tree. Big brown bats in the Cypress Hills exhibit similar roost-switching behaviour (Kalcounis 1995), as did bats in many studies presented at the conference (see papers in this volume by Betts, Crampton and Barclay, Kurta et al., Vonhof).

With the exception of the spruce stump, all tree-roosts were in aspen trees. Most cavities within the aspen had been excavated and used as nest sites by sapsuckers. Sapsuckers and other woodpeckers are primary cavity excavators. The use of aspen by primary cavity excavators is related to the relatively soft wood and susceptibility to heart rot of these trees. False tinder rot (*Fomes igniarius*) is a major cause of decay in aspen (Basham 1958; Peterson and Peterson 1992). False tinder rot infects aspen through roots or broken branches (Basham 1958), and induces extensive decay of the heartwood while sparing the sapwood, which remains as a tough, living, outer shell (Kilham 1971). Hoof-shaped conks are characteristic external indicators of false tinder rot (Peterson and Peterson 1992), and may be the cues that primary cavity excavators use to select aspen with decayed heartwood. Thus, in the absence of sapwood rot, an aspen infected with false tinder rot provides ideal conditions for nesting primary cavity excavators that are capable of getting through the sapwood layer. Infected aspen trees provide cavities with a shell that protects against harsh, ambient conditions, as well as from predators not strong enough to chew through the sapwood layer or small enough to fit through the entrance hole.

Cavity-roosting bats, like various birds, are secondary cavity users. As secondary cavity users, bats choose cavities from among those already excavated, and are therefore constrained by the primary cavity excavators' preference for nesting sites and the decay characteristics of the tree and cavity. The selection of nest sites by primary cavity excavators probably influences the population numbers and community composition of bats in the Cypress Hills, just as the local distributions and abundances of several secondary cavity-nesting birds are enhanced by old nest cavities (Daily 1993).

Preference for aspen trees has been shown for many primary cavity-excavating species. Throughout the North American breeding ranges of sapsuckers and other woodpeckers, most of the excavated nest holes are in aspen trees (Arizona, Li and Martin 1991; Colorado, Crockett and Hadow 1975, Winternitz and Cahn 1983; New Hampshire, Kilham 1971; British Columbia, Erksine and McClaren 1972, Peterson and Gauthier 1985, Keisker 1987, Harestad and Keisker 1989). Even when aspen is not the dominant tree species in a forest, primary cavity excavators choose it over other species with a higher availability. In the Interior Douglas-fir Biogeoclimatic zone of southern British Colombia, 87.7% of all primary cavity-excavating birds were found nesting in aspen trees, despite a relative availability in a random sample of only 53.6% (Harestad and Keisker 1989). As part of a study that examined reproductive success of cavity-nesting birds, aspen trees provided greater than 96% of all nest sites for primary cavity excavators, even though aspen constituted only 12% of all tree species in random plots (Li and Martin 1991).

In the Cypress Hills, suitability and selection of aspen for nesting, and subsequent roosting, seem to be determined both by their availability as the only dominant hardwood, and by decay characteristics. Selection by bats of aspen trees over white spruce and lodgepole pine is not surprising given the difference in decay characteristics of the trees. White spruce and lodgepole pine are softwoods, which do not have the same decay characteristics of hardwoods, such as aspen. In conifers, heartwood and sapwood both decay more rapidly, which precludes the formation of a solid outer shell of sapwood (McClelland 1977).

Primary cavity excavators in the Cypress Hills are limited in the number of species of tree that they can select for excavation, as aspen is the only abundant tree with suitable decay characteristics. The decay dynamics of balsam poplars (*Populus balsamifera*) are similar to aspen; however, balsam poplars are not abundant in the Cypress Hills. Where the distribution of aspen overlaps with that of other trees with similar decay characteristics, such as western larch (*Larix occidentalis*) and paper birch (*Betula papyrifera*) in the Rocky Mountain forests of north-western Montana, primary cavity excavators prefer nesting in western larch (McClelland et al. 1979).

Temperatures in aspen cavities tended to be warmer than ambient temperature at night (periods 1 and 4) and cooler than ambient temperature during the day (periods 2 and 3). During the day, temperatures within conifer snag cavities differed from aspen cavities and mirrored ambient temperature, which tended to be approximately 5°C warmer than aspen cavities. The dichotomy in temperatures between aspen cavities and conifer snag cavities suggests that it may be the effect of warm ambient temperature that influences selection of aspen over conifer snags.

The different decay dynamics of softwoods and hardwoods should influence temperature regimes within cavities of snags and aspen trees. Cavities in conifer snags are also available as roost sites to bats in the Cypress Hills. Despite their availability, cavities in snags were never used as roost sites. The formation of a solid outer shell in aspen may not only protect bats from predators, but may also provide a buffer from high ambient temperatures. Decaying conifers do not form this solid outer shell.

Burnett and August's (1981) study on the energy budgets of a maternity colony of building-roosting little brown bats offers insight as to why the daytime difference between aspen and snag cavities may be an important criterion in the selection of roost sites by little brown bats. At noon, unoccupied little brown bat roosts in their study were 30°C as compared with 35°C for occupied roosts. The thermoneutral zone for little brown bats is between 32.5°C to 37.5°C, which puts the temperature of occupied roosts within the thermoneutral zone. By occupying a roost, little browns increase the temperature by 5°C. It follows then, that an unoccupied roost that is much warmer than 30°C would be unsuitable for little brown bats because once occupied, the temperature within the roost would approach, or exceed, the upper level of the thermoneutral zone. For this reason, we suggest that the temperature difference between aspen and snag cavities during time period 2 renders snag cavities less suitable as little brown bat roost sites. To test this, temperature profiles of aspen cavities occupied by little brown bats are required.

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