

ROOST SELECTION BY FOREST-LIVING FEMALE BIG BROWN BATS (*EPTESICUS FUSCUS*)

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Previous studies of forest-dwelling bats have identified physical features of trees and forests that correlate with the presence of bats by comparing roost sites to paired, randomly selected sites. This method may be limited if the absence of bats from random sites cannot be confirmed. Our purpose was to address roosting ecology of female big brown bats (*Eptesicus fuscus*) using a different approach. We quantified relative use of trees with 3 different types of cavity openings (long crevices, multiple holes, or single holes) and compared the relative use of these potential roosts to the availability of each roost type in the study area. Bats used trees with multiple holes and crevices significantly more often than expected based on their availability and trees with single holes less often than expected. Crevice roosts had significantly larger cavities than did single holes and roosting-group size was positively correlated with cavity volume. No relationship was found between cavity volume and tree height or stem diameter of roost trees, 2 variables that have been reported to correlate with roost selection in other studies of forest bats. Examination of our data suggests that the volume of roost cavities may be an important selection criterion for colonial, forest-living bats and that standard interpretations of the roost versus random-tree approach may not accurately identify patterns of roost selection in some systems.

Key words: cavity volume, Chiroptera, forests, radiotelemetry, roosting ecology, tree cavities

Many species of bats have evolved to spend at least part of their lives roosting in trees (Kunz and Lumsden 2003) and there is growing interest in identifying the roosting requirements of bats in forest ecosystems. A number of studies have provided critical insight into the roosting ecology of forest bats (e.g., Barclay and Brigham 1996; reviewed by Kunz and Lumsden [2003]). The standard paradigm used in such studies, which we term the random-tree comparison, is to track radio-tagged bats to roost sites and then compare physical characteristics of roost trees (e.g., height, diameter at breast height [DBH], density of surrounding forest, canopy cover, etc.) to randomly selected trees that are, presumably, not in use but available to bats (Brigham et al. 1997; Broders and Forbes 2004; Hutchinson and Lacki 2000; Mager and Nelson 2001; Sedgeley and O'Donnell 1999a; Vohnhof and Barclay 1996; Willis and Brigham 2005). A meta-analysis combining results of these studies indicates that, on average, roosts are in tall trees of relatively large DBH that have a relatively closed canopy (Kalcounis-Rüppell et al. 2005).

The random-tree comparison is important for understanding the roost requirements of forest bats because it identifies easily measured physical features of individual trees and forest stands often correlated with the presence of bats. However, in some systems, particularly where colonial-living species roost in tree cavities or under exfoliating bark, results of the random-tree comparison may need to be interpreted with caution for several reasons. First, forest-living bats tend to switch roost sites frequently but remain loyal to areas of forest (Kerth and König 1999; Kurta et al. 2002; Willis and Brigham 2004). Frequent roost switching coupled with fidelity to roosting areas means that randomly selected, nonroost trees, vacant on days when they are inspected for bats, may be used at other times (Kalcounis and Brigham 1998). Random tree cavities may be difficult to access and inspect so they are rarely examined for direct evidence of use by bats (but see Sedgeley and O'Donnell 1999b) with the consequence that the "control" group of randomly selected trees may not be a control at all. Second, the random-tree comparison typically assumes that all roost trees are equally valuable to bats. Despite frequent roost switching, some trees may be reused more frequently or by larger numbers of bats than others. However, few studies have monitored trees over the long term or accounted for differences in the relative use of different trees when comparing physical variables of roosts and nonroosts (Kurta et al. 2002). Third, the random-tree

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comparison does not quantify the relative availability or density of potential forest roost sites on the landscape (Sedgeley and O'Donnell 1999a). Thus, it does not provide information about the stability of populations of available roost trees, which are likely a limiting resource for many bat populations (Kunz and Lumsden 2003).

Several recent studies have demonstrated that colonies of forest bats form fission–fusion societies composed of a number of roosting groups spread among multiple cavities on a given day (e.g., Kerth and König 1999; Kurta et al. 2002; O'Donnell 2000; Willis and Brigham 2004). The colony, on the whole, may be too large to fit into any one tree cavity but individuals still remain loyal to an area of forest. As they switch roosts over time, they end up roosting with their colony mates in other trees (Willis and Brigham 2004). If large colonies and roosting groups provide fitness benefits for bats, then the space available inside roost cavities may be an important factor influencing roost selection. However, despite the potential importance of cavity volume, few studies have measured this variable to determine if it is correlated with the use of trees by bats (Sedgeley and O'Donnell 2004).

The big brown bat (*Eptesicus fuscus*) is a common vesperilionid ranging from southern Canada to northwestern South America (Kurta and Baker 1990). In the Cypress Hills of Saskatchewan, Canada, female big brown bats form maternity groups within cavities in trembling aspen trees (*Populus tremuloides*) and conform to a fission–fusion colony structure (Willis and Brigham 2004). Individuals switch between roost trees about every 2 days but remain loyal to their colony mates and specific patches of forest within and between years. These bats also reuse the same individual trees within and between years (Kalcounis and Brigham 1998; Willis and Brigham 2004; Willis et al. 2003). The utility of the random-tree comparison is diminished in the Cypress Hills, and potentially other study areas, because, as observed by Kalcounis and Brigham (1998) and one of us (CKRW), virtually every aspen tree with an opening contains bat guano, indicating previous use. However, even though all potential roosts appear to be used, bats may still prefer certain trees relative to others. Some roosts are characterized by long crevices extending along the length of the trunk, some have several circular openings (hereafter holes), formed either from branch scars or by primary cavity excavators (e.g., woodpeckers), and some have just a single hole. Roost-opening type is an easily measured characteristic that may influence the roost selection decisions of bats (e.g., Sedgeley and O'Donnell 2004).

Our specific objectives were to quantify the relative use of trees with long crevices (hereafter crevices), multiple holes, or single holes by roosting groups of reproductive female big brown bats; to quantify the relative availability of each type of roost tree on the landscape; to determine if bats use each roost type as often as expected based on its relative availability; and to determine if the various roost types differ in their internal volume and, thus, the amount of space they provide for roosting groups of bats.

MATERIALS AND METHODS

We captured and radiotracked bats between 1 June and 20 August in 2000–2002 in Cypress Hills Provincial Park, Saskatchewan, Canada (49°34'N, 109°53'W). For details of the study area see Sauchyn (1993) and Willis and Brigham (2004). All protocols were approved by the University of Regina President's Committee on Animal Care in accordance with guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998) and guidelines set by the Canadian Council for Animal Care. Adult female big brown bats were captured in mist nets while emerging from roost trees and, occasionally, while foraging. We netted at roost trees infrequently to minimize disturbance to bats, never more often than once every 7 days (mean = 15.6 days \pm 8.5 SD, range = 7–30 days). We radiotracked female bats exclusively because males were rare in the study area (over 3 years, only 2 males were captured at foraging areas and none during netting sessions at roost trees). We recorded the reproductive class and mass of all individuals. Reproductive status of females was assessed by gentle palpation of the abdomen to discern pregnancy, and expression of milk or the presence of bare patches around the nipples indicated lactation. Based on the reproductive status of the majority of bats captured at roosts, we also divided each year of the study into early-pregnancy, late-pregnancy, and lactation periods. The terms early pregnancy and late pregnancy reflect our ability to detect embryos by palpation because many bats captured early in the season almost certainly carried offspring that were too small for us to detect. The start of the late-pregnancy period was delineated by the 1st capture of a detectably pregnant bat (12–18 June) and the start of the lactation period by the 1st capture of a lactating bat (6–16 July). Typically, we did not capture pregnant bats after capturing lactating individuals, but on 1 night in 2000 we captured both pregnant ($n = 2$) and lactating ($n = 4$) individuals from the same roost. This netting session defined the start of the lactation period for that year.

We distinguished volant juveniles from adults based on fusion of the phalangeal epiphyses (Anthony 1988). Adult females were outfitted with blue, numbered, plastic, split-ring forearm bands (National Band and Tag Company, Newport, Kentucky) and 0.7-g radio-transmitters (BD-2T, Holohil Systems Ltd., Carp, Ontario, Canada). With fine scissors, we trimmed a small area of dorsal fur between the scapulae and affixed transmitters to the exposed skin using surgical adhesive (Skin-Bond, Smith and Nephew United, Largo, Florida). Transmitter mass represented less than 5% of each bat's body mass (Aldridge and Brigham 1988). We released bats within several hours of capture and tracked them to their roosts on as many days as possible using hand-held telemetry receivers (R-1000, Communication Specialists Inc., Orange, California) and 5-element Yagi antennas (AF Antronics, Inc., Urbana, Illinois). When roost trees were located, they were observed at dusk to confirm the presence of bats and to count roosting-group size. All roost trees had cavity openings that fell into 1 of 3 categories: single holes, (small, approximately 5- to 7-cm diameter, circular openings), multiple holes (>1 circular openings, 5- to 7-cm diameter) into the same roost cavity, and crevices (noncircular openings greater than 15 cm in length). We climbed multiple-hole trees (see below) and used heavy-gauge wire to determine if cavities were continuous from 1 hole to the next. We also measured the height of roost trees using a clinometer, and recorded DBH.

We used 3 different metrics of roost-selection behavior to assess whether bats exhibit preferences for trees with crevices, multiple holes, or single holes. The 1st was simply the total number of roost trees of each type used by bats over the course of the study. The 2nd was the total number of tracking days during which bats were radiotracked to roost trees of each type. This metric accounts for the

selective reuse of some trees, and for use of trees by multiple radio-tagged bats, because it treats each day for each individual as the sampling unit. For example, if we radiotracked 3 bats to the same tree on 1 day, or if 1 bat reused the same tree on 3 different days, we recorded 3 tracking days for that tree. It is unlikely that consecutive tracking days are independent samples, in the strictest statistical sense, because the roost-selection decisions of individuals on a given day are likely influenced by their roosting behavior on previous days and the behavior of their colony mates. However, when used in conjunction with roost type and roosting-group size (see below), tracking days could allow for strengthened inferences about roost selection. We did not include nontagged bats captured during netting sessions at roost sites in our calculations of tracking days but we did include the bats we radiotracked to those trees. The 3rd metric quantified the sizes of roosting groups using different roost types. Whenever possible, we counted numbers of bats emerging from roost trees at dusk. Emergence counts taken on nights when we netted at roosts were not included because some bats may not have emerged while nets were in place.

During 2001, we assessed the relative availability of trees with crevices, multiple holes, and single holes in the study area. We defined nine 0.79-ha circular (50-m-radius) sampling plots in a stand of forest containing a large number of big brown bat roost trees, roosting area 1 (the best studied of 3 big brown bat roosting areas identified in the study area [see Willis and Brigham 2004]). We selected plots by 1st delineating 5 east-to-west-running transects evenly spaced at 300-m intervals along a 1.5-km stretch of the north-south hiking trail that roughly bisected roosting area 1. Each transect was 1,000 m long (i.e., 500 m on each side of the trail). Two plots were situated at random distances along each of 4 transects and 1 plot was defined on the 5th transect. Within each plot we counted the total number of aspen trees (> 30 cm DBH), as well as the number of aspens with crevices, multiple holes, or single holes. We used the relative proportions of each of these types of cavities to generate expected values for comparison with each of the 3 metrics of roost selection described above.

During 2001 and 2002 we climbed trees with unoccupied but previously used roost cavities to measure the volumes of crevice, multiple-hole, and single-hole cavities. We used heavy-gauge wire to measure distances from the roost opening to the top, bottom, and back wall of cavities (Sedgeley and O'Donnell 1999b). We also measured the thickness of the cavity wall at the roost opening and the tree's circumference at the height of the roost opening. For trees with crevices greater than 1 m in length, we recorded all measurements within 30 cm of the top and 30 cm of the bottom of the cavity to ensure that we accounted for variation in cavity dimensions over their entire length. These measurements allowed us to calculate the effective volume available inside roost cavities. All cavities were roughly cylindrical in shape and we assumed they were cylinders to calculate cavity volume.

We used chi-square tests to compare the frequencies of roosts and tracking days to expected values based on the relative availability of different potential roost types. Nonnormal data were log-transformed where necessary. Significance of all null hypothesis tests was assessed at $P < 0.05$. Analyses were conducted using SYSTAT Version 9 (SPSS Inc., Chicago, Illinois).

RESULTS

We counted 361 aspen trees in the nine 0.79-ha plots. Only 8.3% ($n = 30$) of these had cavities. The density of potential roost sites in this roosting area of forest is therefore approximately 4.2 potential roosts per hectare. Twenty percent (6/30)

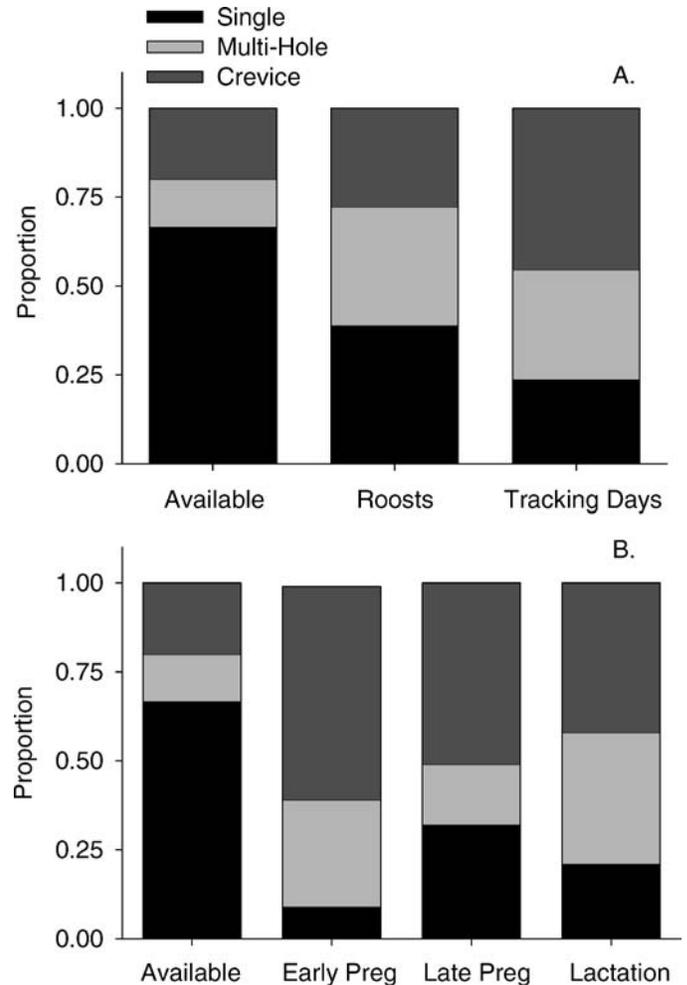


FIG. 1.—A) Proportions of available roost trees (Available, $n = 30$), roost trees used by big brown bats (Roosts, $n = 54$), and total tracking days (Tracking Days, $n = 317$) falling into 3 categories based on the type of cavity in the tree: single holes (black), multiple holes (Multi-hole, light gray), and crevices (dark gray). B) Proportions of available trees of each type plotted alongside proportions of tracking days to each roost type during early-pregnancy (Early-Preg, $n = 43$ days), late-pregnancy (Late Preg, $n = 113$ days), and lactation ($n = 161$ days) periods.

of the trees with cavities had crevices and 13% (4/30) had multiple holes, whereas the majority (67%, 20/30) had single holes. We used these proportions to calculate expected values for comparison to the number of trees of each type to which we tracked bats, and the total number of tracking days we found bats in trees of each type.

Bats did not use the 3 different roost types in proportions equal to their availability (Fig. 1). We tracked 61 bats to 54 different roost trees on 317 tracking days between 2000 and 2002. Twenty-eight percent (15/54) of roost trees had crevices, 33% (18/54) had multiple holes, and 39% (21/54) had single holes. These proportions are significantly different from expected based on the availability of potential roost trees in roosting area 1 ($\chi^2 = 24.1$, $d.f. = 2$, $P < 0.001$; Fig. 1A). The difference was even more pronounced when using tracking days as the metric. Overall, we tracked bats to trees with

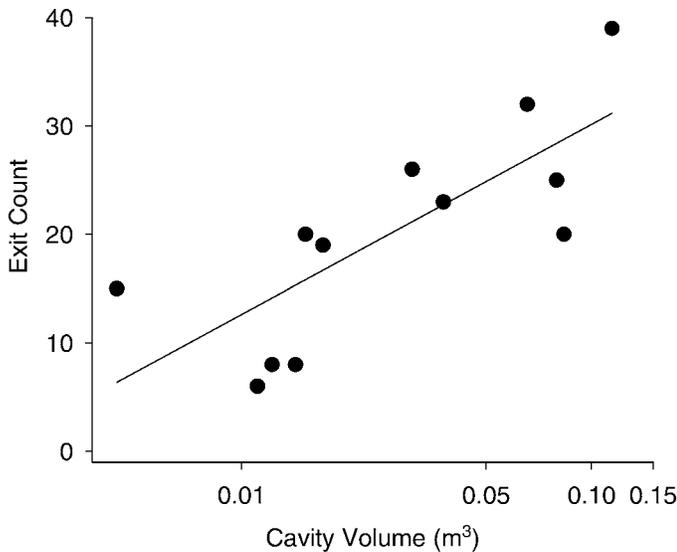


FIG. 2.—The relationship between the average number of big brown bats emerging from tree roost cavities at dusk (emergence count) and the volume of the cavities. See “Results” for regression results.

crevices on 48% (151/317), multiple-hole trees on 29% (92/317), and single-hole trees on 23% (74/317) of tracking days ($\chi^2 = 268.8$, $d.f. = 2$, $P < 0.001$; Fig. 1A). When we subdivided the data by reproductive period, there was a significant difference between expected values based on available cavity trees and the number of tracking days for each roost type during early pregnancy ($\chi^2 = 65.6$, $d.f. = 2$, $P < 0.001$, $n = 43$ days; Fig. 1B), late pregnancy ($\chi^2 = 77.0$, $d.f. = 2$, $P < 0.001$, $n = 113$ days; Fig. 1B), and lactation ($\chi^2 = 156.9$, $d.f. = 2$, $P < 0.001$, $n = 161$ days; Fig. 1B). There was also a significant difference in the relative number of tracking days for each of the 3 roost types between reproductive periods ($\chi^2 = 20.1$, $d.f. = 4$, $P < 0.001$; Fig. 1B). Bats tended to use a much larger proportion of multiple-hole cavities during early pregnancy and lactation, relative to late pregnancy, and the importance of crevices was clear across all reproductive stages (Fig. 1B).

We used a general linear model to assess whether volume of 18 roost cavities was related to tree height or DBH and found no significant relationship ($r^2 = 0.04$, $F = 0.28$, $d.f. = 2, 15$, $P = 0.76$). A significant difference was found in cavity volume between crevice cavities ($0.057 \text{ m}^3 \pm 0.054 \text{ SD}$, $n = 11$), multiple holes ($0.021 \pm 0.028 \text{ m}^3$, $n = 13$), and single holes ($0.008 \pm 0.007 \text{ m}^3$, $n = 10$; analysis of variance, $F = 8.14$, $d.f. = 2, 31$, $P = 0.001$). Trees with crevices had significantly larger cavities than those with single holes (Tukey’s test, $P = 0.001$) and, although not statistically significant, there was a trend for trees with crevices to have larger cavities than multiple-hole trees ($P = 0.09$) and for multiple-hole trees to have larger cavities than single-hole trees ($P = 0.10$).

We performed emergence counts at 5 crevice trees, 5 multiple-hole trees, and 2 single-hole trees for which we also measured cavity volumes. Bats used some of these trees repeatedly and counts were performed on multiple evenings (3.4 ± 2.1 emergence counts per tree, range = 1–6 emergence counts per tree) at all but 3 trees (1 crevice tree, 1 multiple-hole

tree, 1 single-hole tree). We averaged emergence count values for trees monitored more than once. Excluding the 2 single-hole trees and including cavity volume as a covariate, we found no significant difference between numbers of bats emerging from crevice roosts versus multiple-hole roosts (analysis of covariance [ANCOVA], $F = 1.281$, $d.f. = 1, 1, 7$, $P = 0.30$), but there was a significant effect of cavity volume on emergence count (ANCOVA, $F = 11.49$, $d.f. = 1, 1, 7$, $P = 0.01$). With the 2 single-hole trees included in the analysis, there was a significant linear relationship between the logarithm of cavity volume and average emergence count ($r^2 = 0.59$, $n = 12$, $P = 0.003$; Fig. 2).

DISCUSSION

Our data indicate that female big brown bats in the Cypress Hills select certain tree roosts relative to the availability of potential roost trees on the landscape and that their selection is correlated with the space available inside cavities. Trees with crevices and multiple holes were chosen more often, whereas trees with a single hole were used less often than expected based on their abundance. Preferred roost types had larger cavities and cavity volume was positively correlated with roosting-group size. Thus, more bats used large cavities more often than expected based on the availability of potential roosts. Cavity volume was not correlated with tree height or DBH, variables that have been found to predict roost selection in most studies (Kalcounis-Rüppell et al. 2005).

The random-tree comparison, typically used to characterize roosting-habitat selection by forest bats (e.g., Brigham et al. 1997; Hutchinson and Lacki 2000; Mager and Nelson 2001; Sedgely and O’Donnell 1999a; Vonhof and Barclay 1996; Willis and Brigham 2005), would not have detected the patterns we observed for several reasons. First, most if not all potential cavities in our study area are likely used by bats at some point (Kalcounis and Brigham 1998), so comparing randomly selected cavities and known roost trees would reveal little about roost selection. It is often difficult to access tree cavities and thus few studies inspect random trees for evidence of use by bats (but see Sedgely and O’Donnell 1999b). Therefore, it is unknown whether this potential limitation of random-tree comparison applies in other systems. Second, the random-tree comparison would not have considered different categories of roost trees (e.g., crevices, multiple holes, and single holes). Random-tree comparison studies typically group all roost trees into 1 category. Third, in most studies, roost tree is treated as the sole experimental unit, and tree reuse is not considered (but see Willis and Brigham 2005). We found that the indices tracking days and emergence counts provided additional information about the relative importance of different roost types for the big brown bat population in the Cypress Hills. Interpreted in isolation, each of the metrics we employed is likely complicated by inherent statistical biases, but using all 3 in conjunction improved our ability to make inferences about roost selection and could allow for stronger interpretive inference in future studies.

The availability of trees with cavities was low in our study area. We found about 4 potential roost trees per hectare

compared to an overall stem density of about 51 trees/ha. The density of crevice trees, the most preferred roost sites, was even lower, at about 0.8 trees/ha. Lewis (1995) suggested that bats roosting in rare but permanent or near-permanent structures should exhibit high fidelity to them, whereas those roosting in more ephemeral structures should switch between sites frequently. Our findings are consistent with this hypothesis in the sense that preferred roost sites (trees with large cavities) are rare, apparently long lasting, and reused by individual big brown bats and roosting groups within and between years, some for up to 10 years and possibly longer (Willis and Brigham 2004; Willis et al. 2003). However, if roost abundance and ephemerality were the key drivers of roost switching in this study area then big brown bats should rarely switch trees, even within years, and this is clearly not the case (Kalcounis and Brigham 1998; Willis and Brigham 2004). Recent work suggests that roost switching by colonial bats in forests helps bats maintain long-term social relationships between colony members distributed among multiple roost trees on a given night (Kerth and König 1999; O'Donnell 2000; Willis and Brigham 2004). Switching may also help bats learn about and remember roost locations (Kurta et al. 2002). In this scenario, individual roost trees are just small components of much larger "forest roosts," composed of a group of actual and potential roost trees in a local area. The roosting area on the whole, and not an individual roost tree, is analogous to physically spacious roost sites such as those in caves, mines, or buildings (Willis and Brigham 2004). Long-term monitoring of individual bats and roost trees is needed to understand the relative importance of sociality and roost ephemerality to patterns of roosting behavior in forests.

There are 2 potential explanations to account for aggregations of bats at roost sites (Wilkinson 1985). Passive aggregation would occur at sites attractive to the same individuals on the same days. For example, if roosts are characterized by different but specific microclimate conditions then bats of the same reproductive class might select the same sites. In contrast, active aggregations occur if bats share roost sites because of preferences for each other, regardless of specific roost features (Wilkinson 1985). Big brown bats do form active associations with other bats in their roosting areas in the Cypress Hills (Willis and Brigham 2004) but differences in roost selection that we observed among the 3 reproductive periods suggest that passive aggregation at certain trees with attractive characteristics may still play a role. Big brown bats tend to share roost sites with a greater number of different individuals during late pregnancy relative to early pregnancy or lactation (Willis and Brigham 2004). Bats must cope with cold temperatures and limited insect availability during early pregnancy in the Cypress Hills so they should benefit from selecting "warm trees" (if such trees exist), whereas lactating bats also are predicted to select warm sites to avoid torpor. Thermal constraints during late pregnancy may be relaxed relative to early pregnancy in the Cypress Hills because by late pregnancy the weather is typically warmer. Thermal constraints may be relaxed during late pregnancy relative to lactation, as well, because heavily pregnant bats likely rely on deep torpor more

heavily, in part because of added flight costs (Chruszcz and Barclay 2002; Lausen and Barclay 2003; Willis 2006). Thus, during late pregnancy, individuals may switch between many different roost trees, with less consideration of their thermal properties, to maintain and renew associations with large numbers of colony members before energetically demanding lactation (Willis and Brigham 2004). Early-pregnant and lactating bats switch roosts with equal frequency but end up roosting with fewer different individuals because they aggregate at relatively few preferred trees. Examination of our data on differential roost selection during the 3 reproductive periods supports this hypothesis, with multiple-hole trees being the "preferred trees." Multiple-hole trees were even less common than crevice trees but also were used significantly more often than their availability would predict during early pregnancy and lactation, but not during late pregnancy (Fig. 1B). Crevice openings were often more than 1 m long and likely exposed bats to high levels of circulating air and convective cooling, which can have dramatic implications for energy expenditure (Bakken and Kunz 1988). Multiple-hole trees, with much smaller roost openings, could reduce convective cooling. Although cavities tended to be smaller in multiple-hole trees than in trees with crevices, there was considerable overlap in volume between these 2 types of roosts and some multiple-hole trees with large cavities often housed large roosting groups. Differences in roost selection between reproductive periods, then, may be the result of a trade-off between maximizing cavity volume and group size, and minimizing exposure to convective cooling during energetically stressful periods. Experiments, similar to those of Kerth et al. (2001), manipulating roost temperature and possibly air circulation in different types of natural tree roost cavities, would help resolve questions about the importance of social thermoregulation versus the thermal properties of roost sites, themselves, to roost selection.

Forest management plans for colonial bats should consider that bats switch roost trees regularly and that all roost trees may not necessarily be equal in terms of their importance to bats. Some roost trees with preferred characteristics may be used for longer periods by larger numbers of bats, and some trees may be abandoned and then reused, both within and between years. Many interpretations of random-tree comparison results may not account for these patterns. The random-tree comparison does provide valuable information about tree and forest-stand features that are correlated with the presence of bats if the absence of bats from random trees can be confirmed. However, longer-term monitoring of bats and roost trees, beyond the life of individual radiotransmitters, is needed to gain a better understanding of the relative importance of different types of roost trees and forest types to bat populations.

The rarity of preferred roost structures in our study area, coupled with loyalty by bats to small patches of forest, highlights the potential sensitivity of forest-living bats to human impacts such as clear-cut logging. The removal of even a small section of this forest roosting area could be detrimental to the stability of the colony roosting there. Examination of our data suggests that forest management schemes must consider

roosting areas of forest as a relevant "habitat unit" for bats. It is essential that future studies quantify rates of loss and recruitment of potential roost structures within forests and determine the effects of roost-tree dynamics on survival and fitness in bat populations.

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