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SECTION III ROOSTING

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

MATINA C. KALCOUNIS AND KERRY R. HECKER

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 Vohnhof). 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).

Variations in
Roosting Behaviour
by Little Brown Bats

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 sap-sucker 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

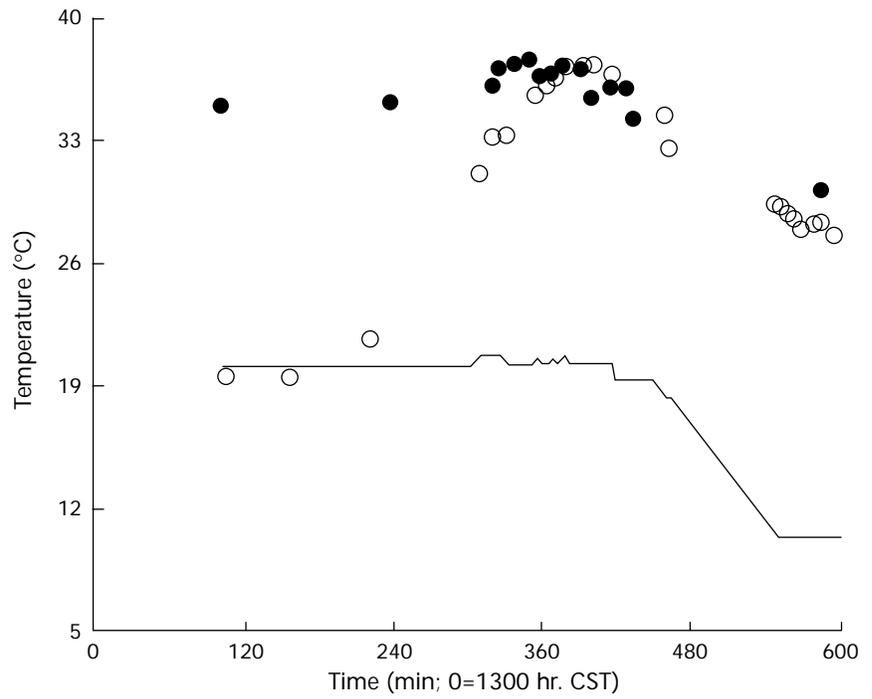


FIGURE 1 Temperature profiles of the two male bats. The bat roosting in the stump (●) stayed active while in the roost. The bat roosting in the aspen cavity (○) was torpid until approximately 1515 h and was active by 1900 h. Ambient temperature is shown by the solid line.

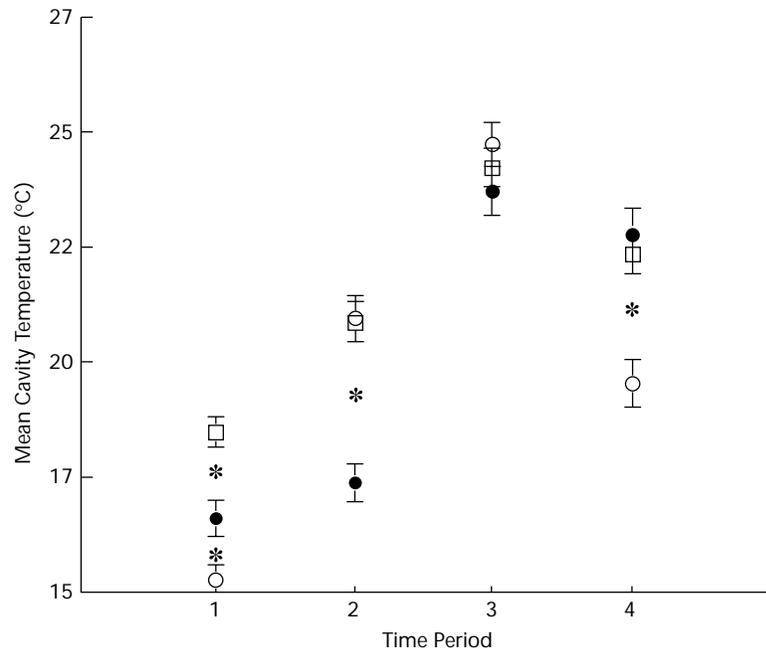


FIGURE 2 Mean (± 1 SE) temperatures of cavities in each of the four time periods (see text). Means separated by * are significantly different (Tukey's Test). Ambient (○), Roost (●), Snag (□).

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 intra-specific 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 ignarius*) 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 Columbia, 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.

ACKNOWLEDGEMENTS

We thank Robert Barclay and Mark Brigham for the invitation to present our work. David Gummer assisted us in the field, and we are especially grateful to him for leading us to the roost tree that we “misplaced.” We value the discussions that one, or both, of us have had with Darren Bender, Paul Bradshaw, Lisa Crampton, Scott Grindal, David Gummer, and Maarten Vonhof regarding this project. We appreciate the use of the Department of Biology, University of Regina Field Station, and acknowledge the hospitality of the West Block of Cypress Hills and Fort Walsh park administrators and employees. Financial support was provided by grants from the Regina Natural History Society, the Theodore Roosevelt Memorial Fund (American Museum of Natural History), and the Natural Science and Engineering Research Council of Canada (NSERC) in the form of research grants and University of Regina President's NSERC grants to Mark Brigham.

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Summer Roosting Ecology of Northern Long-eared Bats (*Myotis septentrionalis*) in the White Mountain National Forest

D. B. SASSE AND P. J. PEKINS

ABSTRACT

We studied the summer roosting ecology of female northern long-eared bats in the White Mountain National Forest of New Hampshire, and examined the importance of snag and stand characteristics at bat roosting sites. Radio-transmitters were used to track 26 northern long-eared bats to 47 roost trees; 39 (66%) were in snags. Roosts were in 14 *Fagus grandifolia*, 13 *Acer saccharum*, 8 *Betula alleghaniensis*, 6 *Acer rubrum*, and 5 other species. Roost snags were larger in diameter (mean = 41 cm; $p = 0.007$), taller (mean = 14.8 m; $p < 0.001$), had more bark remaining (mean = 78%; $p = 0.039$), and were less decayed than random samples of snags in the surrounding area. Characteristics of the surrounding stand were also related to roost sites; live trees had larger diameters ($p = 0.002$) and there was more snag basal area (3.9 m²/ha) in roost plots than the surrounding forest. We surveyed potential roost trees ($n = 104$) for bat activity in 1994 using ultrasonic bat detectors; 28 had bat activity and five were visually confirmed as roost trees.

INTRODUCTION

Roosts are critical habitat for bats; their availability may limit the number and distribution of certain species (Humphrey 1975). Roosts provide sites for hibernation, mating, rearing of young, and protection from weather and predators (Kunz 1982). Although specific information is minimal concerning summer roosting ecology of many New England bat species, most roost in tree cavities, crevices, man-made structures, and occasionally caves (Godin 1977).

Bats have low reproductive rates and long regeneration times, traits that make them vulnerable to population declines caused by high mortality or low recruitment (Hill and Smith 1984). Females of several species using the White Mountain National Forest (WMNF) form large groups (maternity colonies) during the summer, while males are thought to live singly or in small groups (Godin 1977). Thus, the habitat preferences of female bats may be disproportionately more important than that of males, because loss or

alteration of the habitat used by females may reduce recruitment. Therefore, the availability and protection of roosts meeting the needs of female bats may be critical in assuring the long-term survival of bat species.

There is scant information available on the particular habitat needs of female bats in New England, and none specific to the WMNF. Therefore, it is important to study the summer roosting ecology of bats in this area to understand the impact of timber harvests and wildlife management decisions that could affect the location and availability of habitat suitable for the rearing of juvenile bats. Knowledge of the ecology of tree-roosting bats is increasing, but most research relative to species of New England has occurred in the midwest (e.g., Constantine 1966; Kunz 1973; Caire et al. 1979; Gardner et al. 1991). No studies have investigated the summer roosting ecology of the northern long-eared bat (NLE) in New England, and except for the preliminary results of Foster (1993), published roost information concerning this species in forest habitats has come from accidental locations of single colonies rather than from planned studies (e.g., Brandon 1961; Mumford and Cope 1964; Cope and Humphrey 1972; Clark et al. 1987).

METHODS

This study was conducted in northern New England on the WMNF, which consists of 304,050 ha of land, approximately 97% forest. Nearly half the forest (139,300 ha) is open to timber management. Even-aged silviculture has been the primary management tool for the WMNF in the past, although recent practices have reduced clearcut sizes to a maximum of 12 ha. Currently, only about 1% of the managed half of the forest is under uneven-aged management, but this is expected to increase to 23% in the future. The WMNF is fairly mature, with the 70–89-year-old age class dominant, comprising 33% of the timber available for management (USDA Forest Service 1986).

Brooks et al. (1987) estimated that the most abundant timber type in northern New Hampshire was northern hardwoods (48%), such as sugar maple (*Acer saccharum*), beech (*Fagus grandifolia*), and yellow birch (*Betula alleghaniensis*), with spruce/fir (*Picea* spp./*Abies* spp., 26%) and pine (*Pinus* spp., 14%) comprising most of the remaining forest stands. The majority of northern hardwood stands (63%) are in the sawtimber size class, as are spruce/fir (48%) and pine (72%) stands (Frieswyk and Malley 1985).

We captured bats using mist nets placed across old roads, trails, and streams that are used as travel corridors leading to feeding areas, such as wetlands (Kunz and Kurta 1988). Trap sites were at least 1 km from developed areas to reduce the possibility of capturing bats that roosted in buildings. Nets were set before dusk and monitored every 10 minutes until dawn or capture of two female NLE weighing >7 g. Captured bats were identified to species and sex. Their reproductive state (based on palpation of the abdomen), mass, and time of capture were noted. Individuals were classified as adult or juvenile based upon the degree of ossification of the epiphyseal plates in the finger bones (Anthony 1988).

Females weighing >7 g were fitted with 0.65–0.8-g radio-transmitters

(Holohil Systems Inc., Carp, Ontario, Canada) glued on a shaved portion of the bat's upper back using Skin Bond (Pfizer Hospital Products Group Inc., Largo, Florida, U.S.A.; Wilkinson and Bradbury 1988). Each bat was located at a day roost using a Model TR-4 radio-telemetry receiver (Telonics, Mesa, Arizona, U.S.A.) and two- or three-element Yagi antennae. We counted bats leaving roost sites at dusk to estimate colony size and confirm roost location. The minimum distance between NLE roost and foraging area was estimated by measuring the distance from the site where a bat was captured to its roost tree (Brigham 1991).

Vegetative characteristics of roost sites were measured using variable-radius plots determined with a 10 basal area factor prism. Plot size varies with this technique based on the distance from the centre of the plot to the tree being measured. The diameter at breast height (DBH), height, and snag class of each roost were measured. A clinometer was used to measure tree height to the nearest 0.3 m. To be considered a snag, a tree had to be completely dead with no live branches. The percentage of bark remaining on the tree was visually estimated. Numerous studies have assigned snags into decay classes based on external characteristics of the snag in relation to wildlife use (e.g., Runde and Capen 1987; Welsh and Capen 1992; Bull and Holthausen 1993). Snags were placed into one of five classes based on the degree of decay of the tree (Table 1, modified from Cline et al. 1980 and Carbonneau 1986).

Measurement of the surrounding stand and forest included three levels of sampling. Roost-tree plots were centred on the roost, or if there were two roosts within 10 m of each other, the plot was centred between them. Four plots (stand plots) were located 60 m north, south, east, and west of the roost tree. Data from roost plots and associated stand plots were also combined to represent the roost stand. In cases where roost trees were within 60 m of each other, they were considered to be within the same stand, and the four stand plots were used for all roosts within that stand. Live and dead trees in the forest around the roost tree were sampled with four 1-km transects within the 1 km² around the roost. If several roost sites were within the same 1-km² block, the same transect plots were used for comparison with all roost plots and roost stand plots within that block. Transect plots were sampled every 200 m along the transect, yielding a total of 24 plots/km².

Species and diameter of all trees >10 cm DBH were recorded in all plots. All snags were measured using the same methods as for roost trees. Percentage of canopy coverage in each plot was measured with an ocular

TABLE 1 *Characteristics of snag classes based on increased degree of decay used to classify snags in the White Mountain National Forest, 1993–1994 (modified from Cline et al. 1980 and Carbonneau 1986).*

Class	Description
1	Recently dead. Still retains small twigs and branches.
2	No longer has small twigs.
3	Retains large branches > 2 m in length.
4	No large branches and is >6.5 m tall.
5	No large branches and is <6.5 m tall.

tube; one estimate was recorded 5 m from the centre of the plot in each of the cardinal directions. The average canopy coverage for the entire plot was calculated from these four measurements.

Basal area (m²/ha) of live and dead stems was computed for roost-tree plots, roost stands, and the surrounding forest. Measurements of basal area for each roost-tree plot within a single stand were treated as separate samples, and a composite basal area was computed from them to represent the basal area of the roost-tree plot of each stand. The same was done for the roost stand plots and forest transect plots.

Differences in snag DBH, height, bark remaining, and snag class in roost plot, roost stand plot, roost stands, and forest transect plots were tested using the General Linear Model ANOVA module of the Systat for Windows statistical package. Comparisons of live tree diameter, canopy closure, and basal area between these groups were similarly made with this program. Pairwise comparisons between groups were made using Tukey tests. Differences in colony size and foraging distance were also made using the General Linear Model ANOVA. Statistical significance for all tests was set at the $p < 0.05$ level. We present data as means ± 1 SE.

A pilot study was initiated in 1994 to investigate the usefulness of bat detectors as tools for locating roost trees. Broadband ultrasonic bat detectors (Anabat II) linked with sound-activated microcassette tape-recorders were used to sample bat activity at potential roost trees (Krusic 1995). These systems were contained within watertight boxes and were raised into the air with ropes slung over snag branches as close to cavity openings as possible. Detectors were placed at snags about 45 minutes before dusk and left in place for one hour. Tapes were then analyzed for the presence of bat vocalizations. At snags with bat activity, observers returned the next night to perform an exit count to confirm bat roosts. Echolocation calls were recorded at confirmed roost trees with more sensitive tape-recorders, and bats were identified to genus using the Bat Tools software program developed by C. Neefus and R. Krusic at the University of New Hampshire.

Based on 1993 roost-tree data, five criteria were used to describe potential roost trees:

1. The tree was completely dead.
2. DBH was > 25 cm.
3. Snag height was > 6.5 m.
4. The snag retained branches from which to hang detector boxes.
5. There was a visible cavity or crevice.

Transects were laid out through the forest at elevations similar to 1993 roost sites to identify snags that met these characteristics. The DBH, height, and snag class were measured on potential roost trees. We located 104 snags (53 softwood, 51 hardwood) along 31 transects totalling about 4 km in length.

RESULTS

We trapped 281 bats during 87 nights at 18 sites during a total of 752 net-hours. The most common species were the little brown bat (108

individuals, 71%) and northern long-eared bat (75 individuals, 27%). Three big brown bats (*Eptesicus fuscus*), two red bats (*Lasiurus borealis*), two hoary bats (*Lasiurus cinereus*), and one silver-haired bat (*Lasionycteris noctavagans*) were also captured.

One pregnant *M. septentrionalis* was captured in 1993 (7 July); eight pregnant individuals were captured from 8 June to 1 July, and a lactating female was captured on 11 and 25 July 1994. The first juvenile *M. septentrionalis* was captured on 3 August 1993 and on 22 July 1994. Based on this information, we estimated the date of parturition as 2 July. There were no captures of reproductive *M. lucifugus*, but maternity colonies existed because juveniles were captured on 26 July 1993, and 23 and 31 July 1994.

We affixed radio-transmitters to 32 *M. septentrionalis* of which 26 (81%) were relocated at their roost sites. Forty-seven roost trees were found; 14 beech, 13 sugar maple, 8 yellow birch, 6 red maple (*Acer rubrum*), 2 big-tooth aspen (*Populus grandidentata*), and 1 each of black cherry (*Prunus serotina*), hemlock (*Tsuga canadensis*), paper birch (*Betula papyrifera*), and white ash (*Fraxinus americana*). Sixty-six percent (39) of the roosts were in snags. Some roost sites were “clustered” together, rather than dispersed in a random pattern throughout the forest.

Bats tended to move often between roost sites, which presumably affected the number of bats observed at exit counts. Bats were relocated an average of 4.5 times (range 1–16) over 1–19 days (mean = 8 ± 5.2); the mean number of roost sites per bat was 2.2 (range 1–5). Two roosts located in 1993 were also used by similarly sized groups in 1994. At roosts where bats were observed and exit counts were performed more than once, 38% were occupied more than half the time, only 17% were used continuously. The mean distance between *M. septentrionalis* foraging areas and roost trees was 602 m (SE 66.6, range 60–1719 m).

We performed exit counts at 43 of 47 roost trees. Bats were only seen at 29 of 47 sites because foliage obscured visibility at certain trees. Thirty-five (75%) roosts at which exit counts were done were used by <10 bats, 11% were used by 11–24 bats, and 15% were occupied by >24 bats. The maximum group size was 36 bats observed at two separate roosts. There were no significant differences in DBH, bark remaining, height, or snag class between snags used by groups of more than 10 bats than those used by smaller groups. There was no difference in maximum group size in live versus dead trees, but five of seven roosts with >24 bats were in snags. The average group size significantly decreased after parturition, falling from 10.8 ± 2.6 to 3.5 ± 1.6 ; $p = 0.021$.

Roost snags had larger diameters, greater height, more bark, and lower snag-class values than did available snags (Table 2). Live trees in roost-tree plots had larger DBH than did live trees in transect plots (Table 2). Canopy closure of roost stands was significantly lower than in available stands ($p = 0.019$), most roost trees were located in stands that had >75% canopy cover. Snags in roost stands were taller and had lower-class values than snags in available stands. There was no difference in mean snag DBH between roost plots, stand plots, and transect plots, although mean DBH of live trees in roost stands was greater than that in available stands (Table 2).

Comparison of all snags in roost plots, roost stand plots, and forest transect plots revealed significant differences in snag height and snag-class values (Table 2). Bats roosted in plots with taller snags than found in the

TABLE 2 Comparison of physical characteristics of *Myotis septentrionalis* roost and available sites in the White Mountain National Forest, 1993–1994.

Level of comparison	Snag DBH (cm)		Snag height (m)		Snag bark (%)		Snag class		Canopy (%)		Live DBH (cm)		Snag basal area (m ² /ha)	
	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
<i>Snag</i>														
Roost	40.9	2.8	14.8	1.0	78	5.6	2.8	0.3	83	1.4	n/a	n/a	n/a	n/a
Available	33.0	1.0	8.8	0.4	66	1.9	3.7	0.1	86	3.5	n/a	n/a	n/a	n/a
p-value	0.007		<0.001		0.039		0.001		0.513		n/a		n/a	
<i>Plot</i>														
Roost	36.4	2.0	12.2 ^{ab}	0.7	71	4.0	3.2 ^a	0.2	83	3.5	30.8 ^a	0.6	3.9 ^{ab}	0.3
Stand	32.2	1.7	8.0 ^a	0.6	68	3.5	3.6	0.2	82 ^a	2.2	29.8	0.4	2.3 ^a	0.3
Transect	33.5	1.3	8.6 ^b	0.5	64	2.6	3.8 ^a	0.1	88 ^a	1.7	28.8 ^a	0.3	1.9 ^b	0.3
p-value	0.254		<0.001		0.138		0.02		0.06		0.001		<0.001	
<i>Stand</i>														
Roost	34.0	1.3	10.4	0.5	71	2.6	2.8	0.1	82	1.9	30.1	0.3	n/a	n/a
Available	33.5	1.3	8.6	0.5	64	2.6	3.4	0.1	88	1.7	28.8	0.3	n/a	n/a
p-value	0.754		0.01		0.08		0.04		0.019		0.001		n/a	

^{ab} Tukey test indicated a significant difference between these groups ($p < 0.05$).

surrounding stand ($p = 0.002$) or forest ($p < 0.001$). There was no difference in the degree of decay of snags in roost and roost stand plots, but roost plots had less decayed snags than did forest transect plots ($p = 0.014$). Live trees in roost plots were significantly larger than those in forest transect plots ($p = 0.002$; Table 2).

There were differences among snags used for the above comparisons. Hardwood snags were taller (mean 11 m \pm 0.3) than softwood snags ($p < 0.05$), but softwood snags (mean 3.1 \pm 0.2) were less decayed than hardwood snags (mean 3.7 \pm 0.1; $p = 0.003$). However, there were no significant differences in snag height or bark remaining between hardwood and softwood snags.

There were no differences in the amount of hardwood, softwood, or total live-tree basal area between roost plots, roost stands, and the surrounding forest, but there was significantly more total snag basal area in roost plots than elsewhere. Bat-roost stands had significantly more live hardwood (mean 18.1 m²/ha \pm 1.5) than softwood basal area (mean 8.8 m²/ha \pm 3; $p < 0.001$).

We placed bat detectors at 104 snags from mid-July through mid-August 1994. Echolocation calls were recorded at 28 snags (27%), of which five (5%) were visually confirmed to be roost sites. Three of the confirmed roosts were in hardwood trees (yellow birch, paper birch, and red maple). Two roosts with confirmed use by *Myotis* bats were in white pine (*Pinus strobus*) and hemlock, both having low canopy closures (25% and 0%). When only confirmed roosts were considered, 3 of 41 (8%) snags > 45 cm DBH were used, while only 2 of 64 (3%) snags < 45 cm were used. Although our sample size was too low for statistical analysis, bats seemed to avoid small, older snags; class three and four snags < 45 cm DBH were not used.

The species of trees used by northern long-eared bats mirrored the basic composition of the forest in the White Mountains, which is dominated by northern hardwoods, such as beech, maple, and yellow birch. Females consistently roosted in areas with snags which were larger in diameter, greater in height, had more bark remaining, and were less decayed than those randomly available in the forest. Diameter and height of the roost tree are important characteristics of roosts of several vespertilionids (Barclay et al. 1988; Campbell 1993; other papers in this volume). The 1983 U.S. Forest Service inventory of timberland in northern New Hampshire (Brooks et al. 1987) found that 26% (sampling error = 8%) of hardwood trees >12.7 cm DBH with observed cavities were snags. However, 66% of *M. septentrionalis* roosts and most of those with high exit counts were in snags. Although snag preference is presumed, *M. septentrionalis* also roosted in locations with higher mean live-tree diameters, indicating that snag characteristics alone may not adequately describe their roosting ecology, and that stand-level characteristics may play an important role in roost choice. Because of the relative abundance of tree cavities, areas with large tree diameters are associated with increased bat activity and species diversity (Gerrell 1988; Thomas 1988).

Although *M. septentrionalis* used roost stands with lower canopy closure than those available, this may not be biologically significant because most of their roosts had >75% canopy closure. Measurements at ground level may overestimate the amount of canopy coverage at the roost cavity if small trees that shade the ground do not reach above the cavity. These visual estimates, as well as those of bark remaining on snags, may not have been discriminating enough to accurately measure these variables.

Our study represents an initial documentation of the use of a softwood (hemlock) tree as a roost site by *M. septentrionalis* bats. This tree represented only one of 47 *M. septentrionalis* roosts located via radio-telemetry, and an overall preference for hardwood snags is evident. Softwood basal area was only about half that of hardwoods and only a small percentage of that was attributable to snags. Hardwood snags also had larger diameters than softwoods; large diameter was a significant characteristic of roost trees of *M. septentrionalis*. The elevation of softwood stands may also preclude bats from using them as roost sites in this region because northern hardwoods generally predominate below 850 m, where most bats were captured (Leak and Graber 1974).

A northern long-eared bat and a little brown bat used the same yellow birch roost tree on different days in this study (Sasse 1995). While it is not unusual for several species to share hibernacula or roost sites in man-made structures, it is not often observed in tree-dwelling bats, and has only been reported once before for *M. septentrionalis* (Kunz 1982; Foster 1993). However, this behaviour may be more common than previously thought. The practice of conducting exit counts at tree roosts to determine colony size may require detection and identification of species-specific echolocation calls so as to discriminate between multiple species using the same roost site.

As the majority of bats captured on the WMNF were little brown bats, it is likely that the two *Myotis* roosts located with bat detectors were used by this species. Each of these roosts was located in an area with low canopy coverage, unlike those of *M. septentrionalis*, but similar to those of other *Myotis* bats near the extreme edge of their range (Kurta et al. 1993). Until the software used in analysis of bat vocalizations is capable of accurate identification, species determination will require capture of bats as they leave the roosts or internal examination of the roost.

Few studies have been performed in which individual trees were examined for bat use due to the difficulty of determining bat presence, as well as the small percentage of trees occupied at any one time. Gardner et al. (1991) scanned over 2,000 potential roost trees with a bat detector while creating a disturbance, but found only one Indiana bat roost. However, they later determined that bats do not always vocalize after a disturbance; thus, their results were likely conservative. Barclay et al. (1988) found 32 different silver-haired bat roosts by visually searching bark folds and other exterior crevices in trees within a 2 km² area in Manitoba. However, the total number of trees examined and the number of trees searched more than once was not given, so an estimate of usage rates cannot be made. Gysel (1961) studied animal use of 989 cavities in Michigan and estimated that 10% of cavities in beech/maple stands and none of those in oak/hickory stands were used by bats (species not reported). Silver-haired bats roosted behind the loose bark of only 2% of snags examined in a study on wildlife use of cavities in the upper Piedmont of South Carolina (Carmichael and Guynn 1983).

The underlying assumption of our pilot study was that snags without recorded bat activity are not roost sites, which may not be true in all cases. Since each potential roost tree was only surveyed once, it is possible that they were used on other occasions. If placement of the detector was such that it did not record the echolocation calls of bats departing from a tree, we may have overlooked roost sites. This could occur if a snag had multiple cavities or if the bat exited a cavity that was outside the detector's sensing range. This did happen on one occasion when a hand-held detector failed to record vocalizations from a bat exiting a cavity at the top of the tree, while picking up signals from bats leaving a cavity near the base. A false negative could also be obtained if the bats moved to a different roost after their calls were recorded the first night; thus, no bats would be observed at that snag when we returned on the following evening. Unwarranted follow-up exit counts are also caused by bats flying near the detector rather than exiting from the snag being studied.

The 5% occupation rate (based on actual observation) is probably lower than the true rate of potential roost-tree use. Results of our radio-telemetry data and other studies indicate that tree-dwelling bats often move between several roost sites, and although a particular snag is not occupied on one day, it may be occupied on another (Lewis 1995). Additionally, the sources of false negative results outlined above make it likely that more than 5% of potential roosts may be in use at any one time. The criteria we used in choosing snags to survey may not have been descriptive enough of potential roost trees, and with refinement to limit the number of snags that need to be surveyed, this technique could prove useful in locating roost trees of several different bat species.

Information about external attributes of roosts used by female northern long-eared bats will allow identification of habitat suitable for use by maternity colonies of this species, and perhaps other cavity-dwelling bats. Conservation efforts should focus on maximizing snag basal area in stands near foraging areas, such as wetlands, thereby providing bats with a number of tall, large-diameter snags with a range of microclimates and physical traits. Further research concerning the availability and distribution of suitable roosting habitat in managed and unmanaged areas of the forest in relation to elevation and foraging habitat may be warranted, and could necessitate changes in existing forest management standards for retention of snags and other wildlife trees in order to maintain bat population levels.

ACKNOWLEDGEMENTS

This research was conducted in partial fulfilment of the requirements for the degree of Master of Science in Wildlife at the University of New Hampshire by D. B. Sasse. Funding for the research was provided by the University of New Hampshire and the U.S. Forest Service, Northeastern Forest Experiment Station, Durham, N.H. Thanks go to Mariko Yamasaki, Dr. Christopher Neefus, and Dr. Michelle Scott for their guidance and support in carrying out this project. Fieldwork was performed with the aid of John Zimmer, Tom Giffen, Jim Sweeney, Greg Russell, Ian Warden, Aimee Lalla, and Matt Tarr, and others from the University of New Hampshire and the U.S. Forest Service.

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Ecological, Behavioural, and Thermal Observations of a Peripheral Population of Indiana Bats (*Myotis sodalis*)

ALLEN KURTA, KIMBERLY J. WILLIAMS, AND ROBERT MIES

ABSTRACT

We studied roost-tree selection, inter-roost movements, and body temperature of 23 adult female and juvenile Indiana bats over a three-year period. Bats selected their roost tree on the basis of species and diameter, but the amount of exfoliating bark was not a factor. These bats roosted exclusively in green ash (*Fraxinus pennsylvanica*) with a mean diameter of 40.9 ± 1.2 cm (SE; $n = 23$). Unlike Indiana bats in the centre of their range, those in Michigan never used silver maple (*Acer saccharinum*), never roosted in a shaded area, and never roosted in a healthy, living tree. The bats changed roost trees every 2.9 days, on average, moving from 1 to 178 m to an alternate tree. Pregnant females changed roosts most often, and lactating bats, the least. Overall, roost-switching was not satisfactorily explained by hypotheses based on predator avoidance, interruption of parasite life cycles, tracking of food resources, or environmental conditions. The ephemeral nature of bark roosts may be a factor in frequent roost-switching, but it has not been adequately tested. The number of trees occupied by the group each year varied from five to 18, although two to four trees each year were used most heavily. Contrary to published information, these bats were not adversely affected by body temperatures of 35–40°C.

INTRODUCTION

Guidelines for management of endangered species generally are derived from studies performed near the centre of an animal's geographic range, where populations are large and stable and, therefore, easier to work with than those on the periphery. Nevertheless, peripheral populations are worthy of attention. If one accepts the classical view that peripheral populations are waging a constant battle with extinction, then the declining health of an outlying group may be an early warning of potential problems for the main population. Conversely, recent analyses suggest that peripheral populations are more likely to survive than centrally located ones, and ultimately, peripheral areas may become critical refugia for a

species (Lomolino and Channell 1995). In any event, a prudent management plan should specifically address peripheral, as well as central, populations, because vegetative and climatic conditions often differ across a species' range, and guidelines formulated for one group may not be applicable to the other (e.g., Lewis 1993).

The Indiana bat ranges across much of the eastern United States (Thomson 1982). Disturbance during hibernation and intentional modification of major hibernacula led to serious declines in population size during the 1960s and early 1970s, and consequently, the species was declared endangered in 1973 (Richter et al. 1993). Hibernating Indiana bats are now well protected, but the species continues to decline, suggesting problems in summer as well (Clawson 1987). During the warm-weather months, these bats roost primarily under exfoliating bark, in upland woodlots and riparian forests. To date, summer roosting habits have been most extensively studied in Illinois (Gardner et al. 1991) and Missouri (Calahan 1993), in the heart of the species' distribution.

In the present report, we describe a multi-year study of a summer population of Indiana bats, roosting only 15 km from the northern edge of their range. Our goals were to provide baseline, ecological, and behavioural data, applicable to the management of this species in northern areas, and to make comparisons with previous studies performed in the core of the species' range. We were particularly interested in factors affecting roost selection and roost fidelity, but we also examined the question of body temperature. Based on laboratory experiments, Henshaw and Folk (1966) suggested that body temperatures of only 34–35°C were fatal to this bat. If true, such a low, lethal body temperature would have a profound ecological impact, severely limiting the types of roost sites that this tree-dwelling animal could use.

METHODS

Ecological and Behavioural Observations

The study took place near Vermontville, Eaton County, Michigan, from 30 June 1991 to 15 August 1993. Indiana bats were captured in mist nets while flying over streams or in flight paths leading from their roosts. After capture, some dorsal fur was trimmed with scissors, and a 0.7-g radio-transmitter (Holohil Systems Inc., Woodlawn, Ontario) was attached using a surgical adhesive (Skin-Bond). The roost tree was located on subsequent days, using a three-element Yagi antenna and receiver (Wildlife Instruments, TRX-2000S). Transmitters remained attached and functional for up to 11 days.

Population size was determined by counting bats as they left their roost, between sunset and 50 minutes after sunset. We consistently observed trees that sheltered an Indiana bat with a functioning transmitter. In addition, we made counts at other roost trees (originally detected by radio-tracking), when multiple observers were available, or when we did not have a transmitter on any bat.

To characterize the habitat, we established 0.1-ha, circular plots surrounding each roost, and identified every tree >10 cm DBH within the plots. If plots for adjacent roosts overlapped, we only used data from the

first roost that was discovered to maintain independence of the data. We measured diameter at breast height (DBH) and determined the height of each roost tree and the preferred exit point using a clinometer. We also classified each tree according to the amount of loose bark that was present using a system recommended by Gardner et al. (1991). A rating of high was given to trees with $\geq 25\%$ loose bark, medium $\geq 10\%$ but $< 25\%$, and low was $\geq 0\%$ but $< 10\%$.

In this report, we include information obtained from five of eight roost trees previously described in Kurta et al. (1993a). We discarded data on three trees (roosts F, G, and H) mentioned in that paper because those roosts were discovered only by accidentally observing bats leaving the trees at dusk. The recent demonstration that a similar species, the northern bat (*M. septentrionalis*), also roosted occasionally under bark in this wetland (Foster 1993), necessitated that we re-evaluate the data using only trees located by actually radio-tracking Indiana bats.

Thermal Observations

Radio-transmitters used in 1992 and 1993 were temperature sensitive, and allowed us to determine the surface temperature of the bat while it was in the roost. Data were not taken in a systematic manner in 1992, but in 1993, body temperature was recorded every 30 minutes between sunrise and sunset. During both years, ambient temperature in the shade was simultaneously measured with a mercury thermometer. To avoid disturbance, temperatures were recorded more than 100 m from the roost. Although we would like to have monitored roost ambient temperature at the same time as body temperature, this was not practical because, as described later, the bats frequently changed roosts and used many different trees.

Statistics

All means are followed by \pm one standard error and then the range in parentheses. Comparisons between two groups were performed using the normal approximation to the Wilcoxon Two-sample Test, whereas tests involving more than two categories relied on the chi-squared approximation to the Kruskal-Wallis Test. Tests involving enumeration data (contingency tables) were performed using chi-squared tests or, when expected frequencies fell below five, Fisher's Exact Test. We used Spearman's Rank Test to examine potential correlation between variables. All tests were two-tailed and used a significance level of 0.05.

RESULTS

Maternity Roost Parameters

We radio-tracked 23 Indiana bats and located the roost tree on 130 of 141 days that the transmitters were functional. The bats included six pregnant individuals, seven lactating bats, five post-lactating/non-reproductive females, and five juveniles. The bats roosted primarily under the exfoliating bark of 23 different trees. All roost trees were dead or nearly dead green ash that had lost most or all of their major branches; any living branches that remained were < 3 cm in diameter. Average DBH of roost trees was 40.9 ± 1.2 (30–52) cm. Mean roost-tree height was 25.1 ± 1.6 (8–47) m, and mean exit height was 9.9 ± 0.9 (1.4–18) m. Roost trees

were on average 38.7 ± 7.1 (1–147) m away from another tree used as a roost in the same year and 17.3 ± 4.5 (1–111) m away from the nearest tree used as a roost during any of the three years. There were no significant differences among years in DBH, height, exit height, or nearest-neighbour distance (all $p > 0.12$).

Analysis of Woody Vegetation

All roosts were in an unshaded, 5-ha wetland and surrounded by up to 1 m of standing water. Our vegetation analysis yielded nine non-overlapping plots that contained 99 green ashes, 34 silver maples, nine American elms (*Ulmus americana*), and two barkless, unidentifiable trunks. Although this area was forested pasture at one time, it has been persistently inundated for 15 years, leading to the death of most trees and the imminent death of the rest. Consequently, many trees appeared suitable for Indiana bats (i.e., loose and peeling bark was present on the trunks). Within our plots, 66 green ashes were suitable (16 actual roosts and 50 apparently unused), as were 21 silver maples, and two American elms. Because of the small sample of elms, we excluded them from further analyses.

Evidence for Roost Selectivity

Were Indiana bats selective in choice of roost tree? We examined three potential modes of selectivity—by tree species, DBH, and the amount of exfoliating bark present on the trunk. Within our plots, 76% of the 87 potential roost trees (excluding elm) were green ashes, whereas 24% were silver maples. Using these values as expected proportions, we determined that the probability of all 23 roosts being green ash as the result of chance was less than 0.005 ($X^2 = 7.32$; $d.f. = 1$), and we concluded that the bats were choosing green ash over silver maple.

Were Indiana bats more likely to use a tree with a large amount of loose and peeling bark? Following Gardner et al. (1991), we ranked 12 roost trees as high, nine as medium, and two as low. This distribution differed from random ($X^2 = 6.87$; $d.f. = 2$; $p < 0.01$), and superficially supports the hypothesis. However, within our sample of 50 suitable green ashes that were not used as roosts, the distribution of high, medium, and low was 21, 13, and 16, respectively. There was no significant difference ($X^2 = 4.73$; $d.f. = 2$; $p > 0.09$) between roost and non-roost samples, and hence, no evidence that the amount of loose bark was a factor in roost selection.

Although the amount of loose bark was not important, the size of the tree was. The diameter of roost trees (mean = 40.9 ± 1.2 cm; $n = 23$) was significantly greater ($z = 3.85$; $p < 0.0001$) and significantly less variable ($F_{22, 49} = 3.03$; $p = 0.006$) than the diameter of suitable, non-roost green ashes (mean = 33.4 ± 1.4 cm; $n = 50$) within our plots. Diameter of non-roost trees varied from 11 to 70 cm, whereas trees used by females and young were tightly grouped between 30 and 52 cm.

Roost Loyalty Within Years

Individuals were not highly faithful to a particular tree. Seventeen of the 23 bats switched trees at least once, yielding a total of 37 roost changes. On the day that a bat was first located, we did not know whether it had changed roosts or had remained in the same tree; therefore, we deleted the first day from our analyses. Thirty-seven roost changes over the remaining 107 observation days indicated that Indiana bats typically

changed roosts every 2.9 days. Modal number of roost changes/bat was only two, but changes/bat varied from zero to six. Number of changes was positively correlated with number of days that the bat was monitored ($r_s = 0.70$; $n = 23$; $p = 0.0002$; Figure 1).

Some changes were to trees that the bat had previously roosted in, and others were to trees that we had not tracked that individual to before. Modal number of different trees used by each bat also was only two, but individuals used from one to four. Number of different trees used by each bat also was correlated with number of observation days ($r_s = 0.71$; $n = 23$; $p = 0.0001$; Figure 1).

Average distance for all 37 roost changes was 74.2 ± 7.6 (1–178) m. Among adults, distance moved was independent of reproductive condition ($X^2 = 0.78$; $d.f. = 2$; $p = 0.67$), and there was no difference between adult females and juveniles ($z = 0.29$; $p = 0.77$); distance moved was independent of year ($X^2 = 3.04$; $d.f. = 2$; $p = 0.22$). Were bats simply moving to the nearest available tree? If so, the distribution of roost-change distances should be the same as the distribution of distances between each roost and its nearest neighbour in that year (Figure 2). The two, however, differed significantly (Fisher's Exact Test: $p = 0.007$). Although 67% of within-year, nearest-neighbour distances were ≤ 50 m, only 27% of roost-change distances were that small.

We compared the tendency to change roosts among adult females using a 3×2 contingency table; the three columns represented reproductive condition, and the rows represented the number of occasions that a bat was observed in the same roost as on the previous day versus a roost different from that used the previous observation day. Roost-switching was not randomly distributed among reproductive conditions ($X^2 = 6.82$; $d.f. = 2$; $p < 0.05$). For pregnant bats, we recorded 19 days on which a roost change occurred and 20 days on which it did not, indicating a 49% chance that a pregnant bat would not be in the same roost on consecutive days. For lactating and post-lactating/non-reproductive females, we recorded 7 changes versus 28 non-changes (20%), and 6 changes versus 13 non-changes (32%), respectively. Juveniles switched roosts on 5 days and remained in the same tree on 10 days (33%), a frequency virtually identical to that of the post-lactating females ($X^2 = 0.01$; $d.f. = 1$; $p > 0.5$).

To investigate whether roost-switching was related to ambient temperature, we examined the correlation between roost-emergence counts and minimum ambient temperature the day of the observation (usually occurring near dawn when bats are selecting a roost) and maximum temperature on the day before the count (which might determine whether bats return the next morning). Temperatures were obtained from a recording station at Charlotte, 14 km ESE of the study site. We restricted our analysis to trees at which we made ≥ 10 emergence counts in any one year, after 14 May, but before 17 July, which was the earliest date that volant juveniles were captured. We performed five analyses on four roost trees, but there was no consistent relationship between the environmental variables and roost population size. Two trees showed significant correlations between population size and both temperatures, two roosts had no significant correlations, and one displayed a significant relationship with minimum temperature, but not maximum (Table 1).

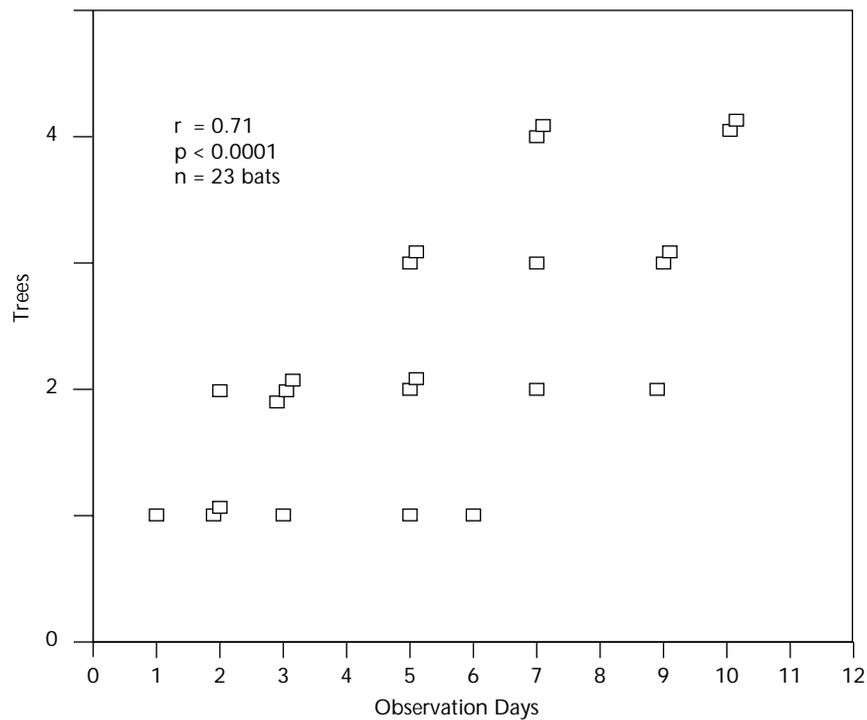
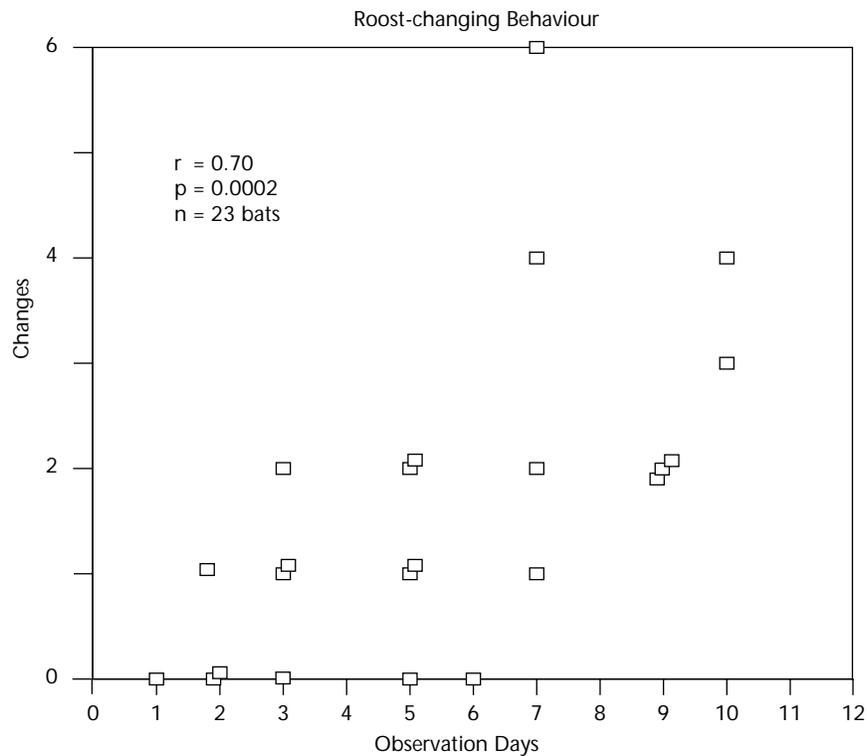


FIGURE 1 *Roost-changing behaviour. (Top) The relationship between number of roost changes and number of days that the bat was located. (Bottom) The relationship between number of different trees used and number of days that the bat was located.*

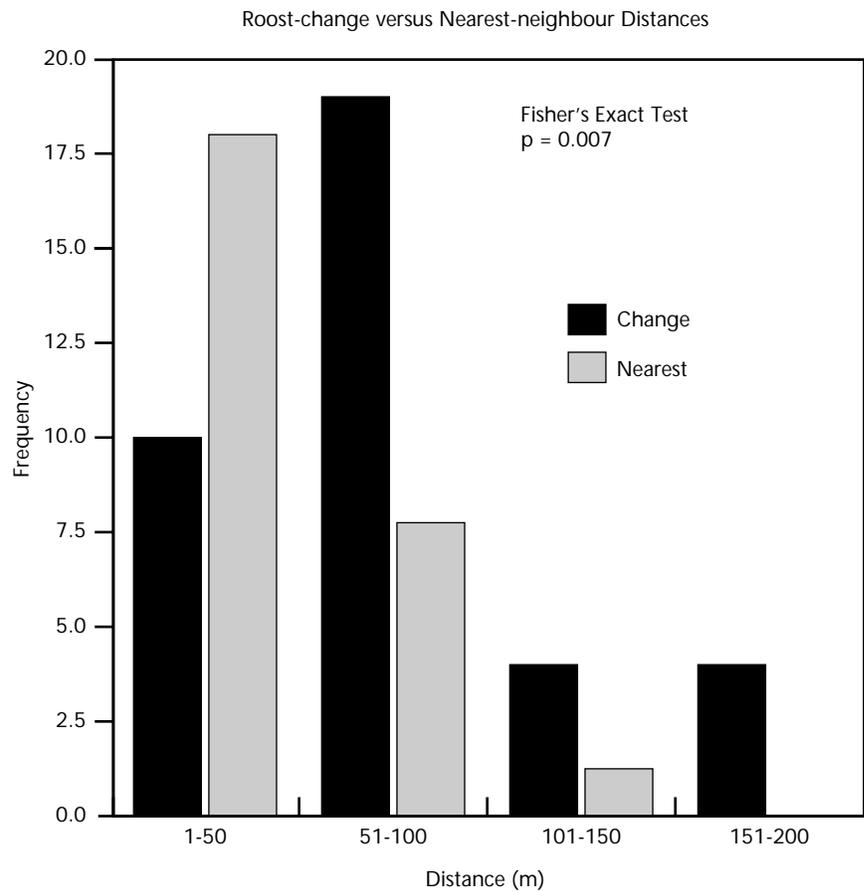


FIGURE 2 *Roost-change distances compared to nearest-neighbour distances within that year. Nearest-neighbour distances were measured only for trees to which Indiana bats were actually radio-tracked in that year.*

Population Size and
Relative Importance
of Roosts

We made emergence counts on 161 dates, observing 1–7 roosts on any given night, for a total of 283 observations. On 113 occasions (40%) no bats left the roost; occasionally the lack of bats was due to cold or wet weather, but we attributed most instances to the bats' tendency to concentrate activity at some trees and rarely occupy others (see below). During 20 of the remaining 170 nights (12%), only a single bat emerged. Twelve observations of solitary emergence were of seven bats carrying trans-

TABLE 1 *Rank correlations between number of bats leaving a tree and the maximum ambient temperature recorded on the previous day and the minimum ambient temperature recorded on the morning of the count.*

Roost/year	<i>n</i>	Range of dates	Maximum temperature (°C)	Minimum temperature (°C)
2A/1992	14	30 May–15 July	$r_s = -0.27; p = 0.34$	$r_s = 0.02; p = 0.95$
2E/1992	13	16 June–10 July	$r_s = 0.50; p = 0.08$	$r_s = 0.56; p = 0.047$
2A/1993	25	19 May–10 July	$r_s = -0.18; p = 0.38$	$r_s = -0.15; p = 0.48$
3B/1993	16	1 June–15 July	$r_s = 0.70; p = 0.003$	$r_s = 0.84; p = 0.0001$
3F/1993	22	14 June–14 July	$r_s = -0.56; p = 0.007$	$r_s = -0.59; p = 0.004$

mitters, so we knew that at least one juvenile and three pregnant, one lactating, and two post-lactating females roosted alone on at least one night. The other 150 emergences involved 2–45 bats, and most (89%) involved 2–21 bats (Figure 3).

To determine whether roost populations were consistently larger after young became volant, we compared emergence counts made before and after 17 July, in 1992 and 1993, the two years during which field work spanned the entire spring–summer roosting period (Figure 4). To minimize complications resulting from migration, we also limited the data to counts made between 14 May and 15 August. There was no significant difference in population size before and after 17 July, in either 1992 ($z = 0.92$; $p = 0.36$) or 1993 ($z = 1.06$; $p = 0.29$). This suggested that Indiana bats occupied a greater number of trees within the wetland soon after the young became volant, or that some dispersed to other areas.

Based on emergence counts, we estimated the relative importance of roost trees by calculating the number of “bat-days” that each was occupied; one bat-day equals one bat using a tree for one day. Indiana bats did not use each tree to the same extent, but seemed to prefer two to four particular trees every year (Figure 5). In 1993, for example, four roosts (1D, 2A, 3B, and 3F), out of 18 that were occupied, accounted for 579 (80%) of 721 bat-days; in contrast, eight other trees (1B, 1E, 2F, 3D, 3I, 3J, 3L, and 3M) contributed a total of only 13 (2%) bat-days. During the

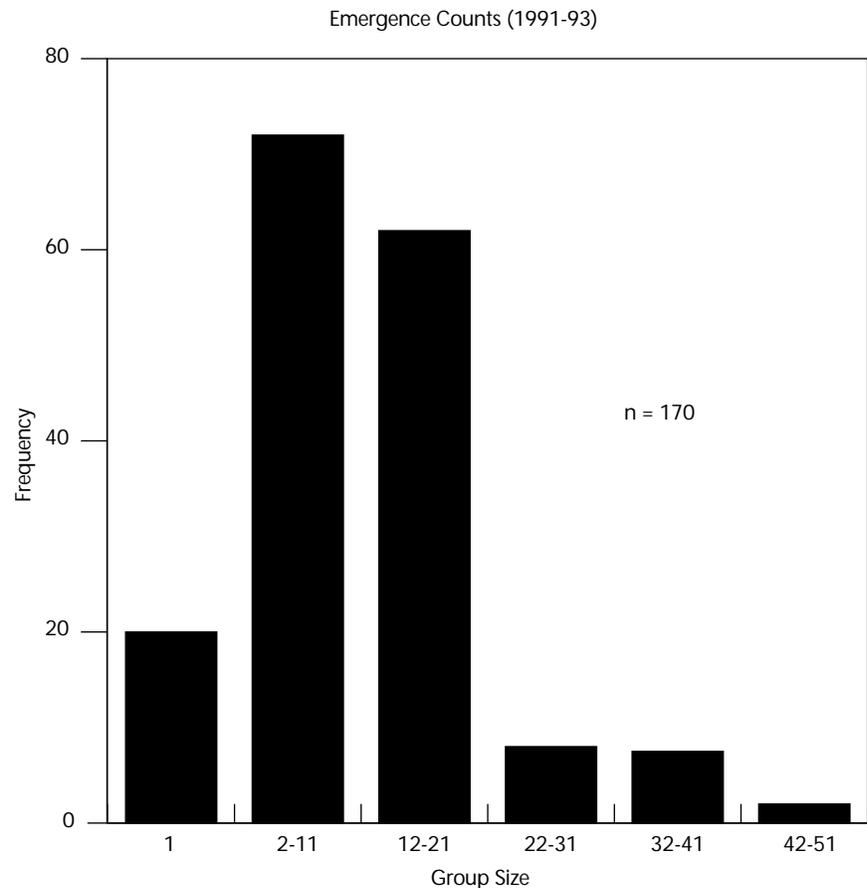


FIGURE 3 Histogram showing frequency of roost population sizes.

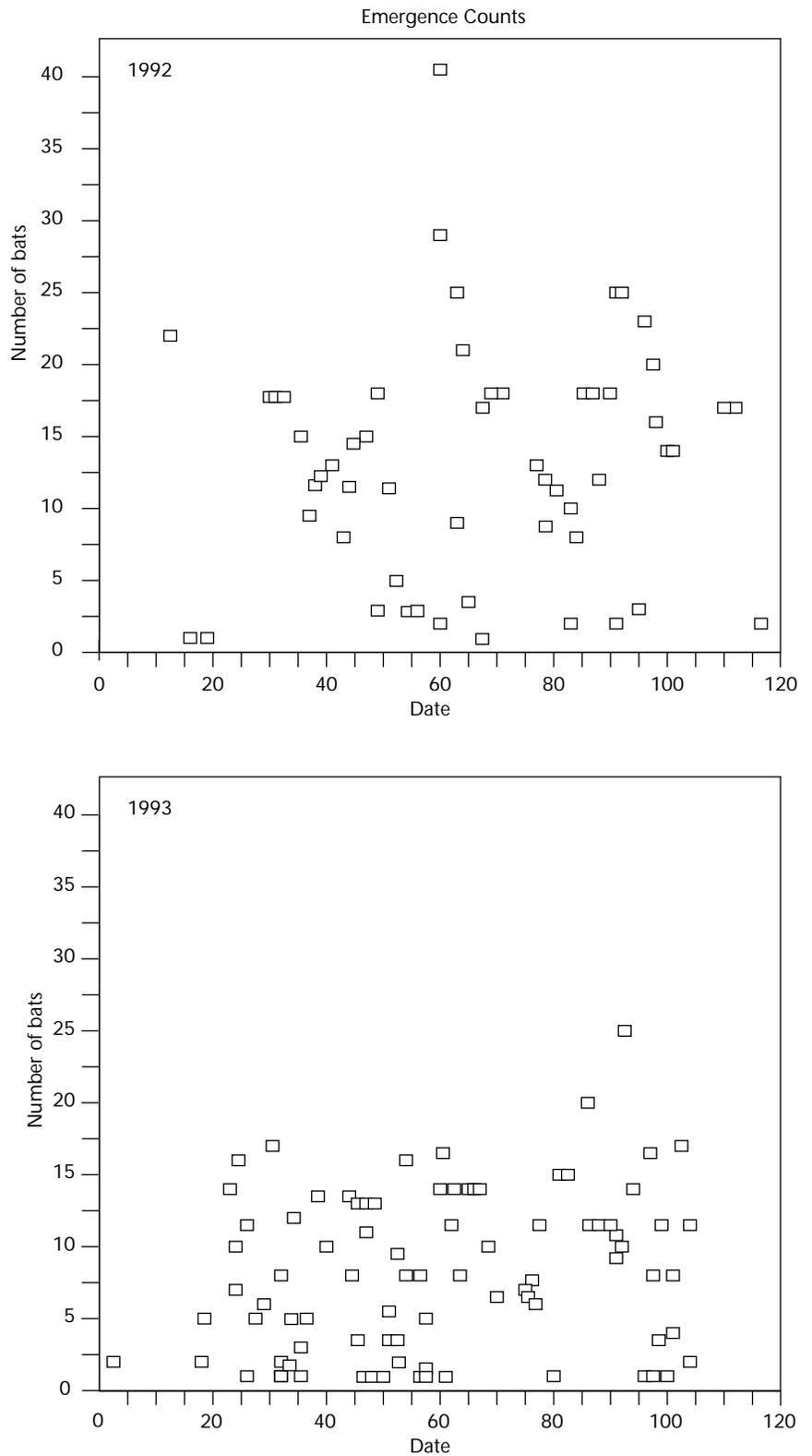


FIGURE 4 Emergence counts by date in 1992 and 1993. Dates are numbered sequentially beginning with 1 May as day 1. Day 78 is 17 July, the first date on which volant juveniles were recorded.

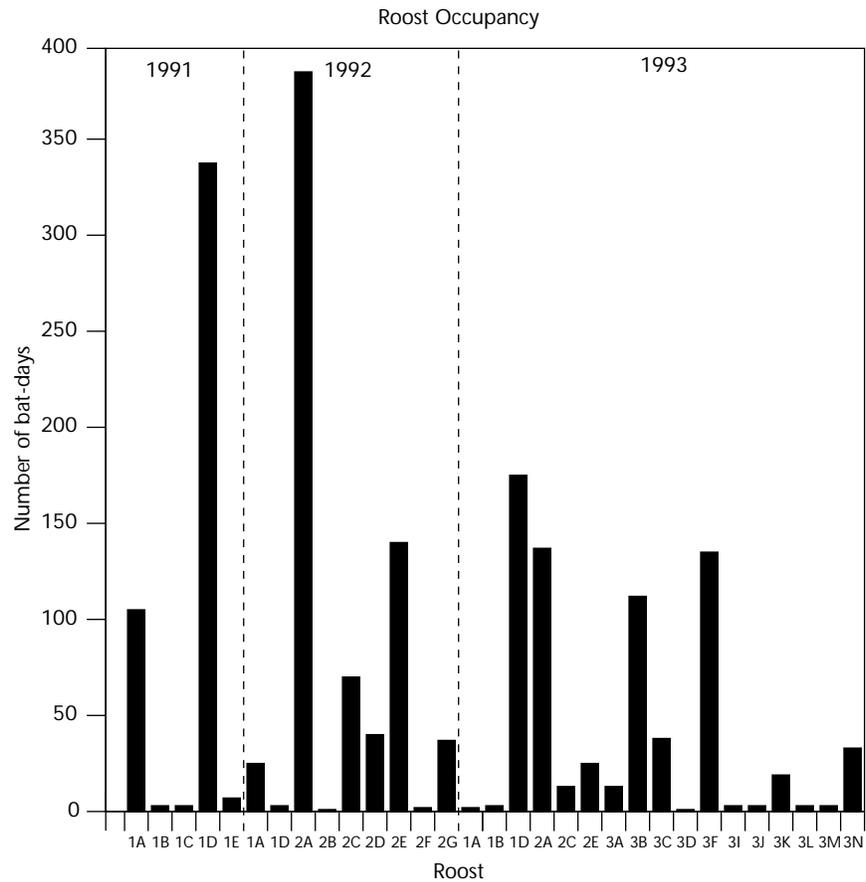


FIGURE 5 Number of bat-days for each roost tree in each year. Code names for each roost consisted of a number representing the year of discovery (1–3 for 1991–93), and a letter assigned in order of its discovery in that year. Roosts 3E, 3G, and 3H were used by adult males and were not included.

three years, six trees (1A, 1D, 2A, 2E, 3B, and 3F) were used most heavily, but there was no statistical difference in DBH, tree height, exit height, or amount of bark between these trees and the other 17 roosts (all $p < 0.05$).

Body Temperature

During 1992 and 1993, we remotely recorded body (skin) temperatures (T_b) of 17 Indiana bats, on 1–10 days each. Although Henshaw and Folk (1966) believed that T_b 's above 35°C were harmful to Indiana bats, 14 of our bats (82%) achieved a T_b greater than 35°C on at least one day, and mean maximum T_b of those animals was $37.9 \pm 0.3^\circ\text{C}$ ($n = 17$). Some bats exceeded 35°C for as many as 12 consecutive hours, and others exceeded it on as many as six consecutive days. Six of seven bats monitored in May or June, when high temperatures were presumed to be most deleterious (Henshaw and Folk 1966), reached a $T_b > 35^\circ\text{C}$, and the one that did not was only monitored for a single day after a cool (8°C) night—a situation often leading to torpor in insectivorous bats. The highest T_b recorded in either year was 40.3°C , at sunset on a day when air temperature (T_a) external to the roost was only 22°C . The highest T_a was 33°C , and it corresponded to a T_b of 37.7°C .

Thermal Observations

In a laboratory study of Indiana bats captured at caves, Henshaw and Folk (1966: 228) stated that T_b was maintained close to ambient, and that “body temperatures of 34–35°C were frequently fatal.” Although Gardner et al. (1991) cautioned that the results of Henshaw and Folk (1966) might not apply to bats at maternity colonies, no data on body temperature existed for Indiana bats on their summer range, prior to the present study. During 1992 and 1993, 82% of the bats achieved a maximum T_b exceeding 35°C. These high temperatures often were maintained for hours and on consecutive days, yet the bats never vacated the wetland for more shaded and presumably cooler roosts. The highest T_b was over 40°C, and it was recorded at a time when T_a was only 22°C and direct solar radiation was impossible (i.e., at sunset); such a large differential under these conditions suggested that the high T_b was achieved physiologically and was not environmentally induced. In addition, the average maximum T_b (37.9°C) was within the range of normal T_b for small mammals (Hart 1971). Our observations strongly suggested that there was no stress associated with a T_b of 35–40°C and that the results of Henshaw and Folk (1966) do not apply to Indiana bats on their summer range.

Roost Selectivity

The wetland at Vermontville provides an unusual opportunity to test elements of roost selectivity, without many of the confounding factors present in other studies of tree-roosting bats. Presumably, the high concentration of roost trees is the reason these bats did not use other nearby areas for roosting during the entire, three-year period. Having all roosts in the same, small wetland minimizes the confounding effects of differences in stand composition, amount of shade, subcanopy development, distance to foraging grounds, etc. In addition, use of only a single species of tree allows us to examine preferences in diameter and amount of exfoliating bark without the confounding effects of multiple tree species.

Female and juvenile Indiana bats in Michigan apparently select their roost tree on the basis of species and diameter, but not the amount of loose and peeling bark. Choice of roost species in Missouri simply reflects the composition of the surrounding forest (Calahan 1993), but our analysis indicates that green ash is chosen more often than expected based on its abundance in the Michigan wetland. Indiana bats roost in silver maple in both Illinois (Gardner et al. 1991) and Missouri (Calahan 1993), so its lack of use in Michigan is surprising.

The preference for green ash over silver maple, and for roosts of intermediate diameter may be related to thermal properties of the trees. Kurta and Williams (1994; A. Kurta, unpubl. data) recorded ambient temperatures under the bark of two Michigan roosts, from 3 August to 3 September 1994, and the highest temperatures were only 34.8 and 36.1°C—about 10°C lower than reported for more southern regions (Gardner et al. 1991). Unlike bats in southern states that may select a roost to avoid heat (Gardner et al. 1991), Indiana bats in the cooler climate of Michigan may be selecting a tree on the basis of its warmth.

Solar heating would be most important to bats in northern areas during the morning, when the body-to-ambient-temperature differential is

greatest and the cost of thermoregulation is highest (Studier 1981). Large-diameter trees would have too much thermal inertia and heat too slowly in northern areas. In contrast, slower heating may be advantageous in warmer regions, and interestingly, maximum (not mean) diameters of roost trees in Missouri and Illinois (Calahan 1993; Gardner et al. 1991) appear greater than those in Michigan, although such a comparison is confounded by the presence of multiple tree species in the southern studies. In the north, small trees would warm quickly in the morning sun, but they presumably are less desirable for roosting because they also would provide a less stable thermal environment, fewer opportunities for clustering, and fewer roosting sites under the bark than a slightly larger tree (Gardner et al. 1991). Similarly, the preference for green ash over silver maple may stem from differences in the colour or texture of the bark (green ash is darker and rougher) and their effects on heating and cooling rates. We are currently measuring thermal properties of green ash and silver maple of varying diameters to test these hypotheses.

Implicit in the suitability system developed by Gardner et al. (1991) is that a tree with more exfoliating bark has more potential roost sites, and presumably is more likely to be used by Indiana bats than a tree with a lower ranking (less loose bark). However, our study indicates that this is not true for green ash. Indiana bats did not choose trees of high suitability more often than expected based on their abundance in the wetland. Calahan (1993) also indicates that the amount of bark present on a tree does not differ between roost and non-roost trees, but his technique apparently does not distinguish between bark that is loose and peeling (i.e., available for roosting) and bark that is held tightly to the trunk (i.e., not available for roosting). Although the amount of exfoliating bark does not reliably predict present use, it may be a useful indicator of habitat quality, because trees with large amounts of loose bark presumably maintain at least some of that bark for a longer period of time, and hence, such trees would be available for roosting further into the future.

Lack of Roost Fidelity

Throughout their range, individual Indiana bats apparently use a number of roost trees (Calahan 1993; Gardner et al. 1991; the present study), and this lack of fidelity to a single resting place appears typical of tree-roosting species in general (Brigham 1991; Foster 1993). How many trees are required? The number of roost trees used by each Indiana bat is correlated with the number of observation days (Figure 1), which suggests that the number of roosts that an individual occupies throughout the year is greater than the maximum (four) observed in our study. In 1993, the entire group used at least 18 different trees, but whether each bat visits this many roost trees over an entire season is unknown.

The use of multiple roost trees by Indiana bats in Missouri led Calahan (1993) to distinguish between “primary” and “alternate” roost trees. A “primary” roost is one that shelters at least 30 bats on at least two days, and “alternate” roosts are all others. Unfortunately, Calahan’s (1991) system is not applicable to our bats, and probably is not useful for any colony of small-to-moderate population size. Although one of our trees from 1991 (1D; Kurta et al. 1993a) would be considered “primary,” none of the trees occupied in 1992 or 1993 meets the minimum population size and residency requirements to be called “primary” (Figure 4).

Nevertheless, one can demonstrate empirically that some trees are favoured over others by calculating the number of bat-days that each is occupied (Figure 5).

Reasons for switching roosts are not well understood for any bat, including Indiana bats (Lewis 1995). Some species may track their food resources, changing roosts as foraging sites change, to minimize commuting distances (Kunz 1982). However, 78% of roost-change distances in our study were less than 100 m (Figure 2); such distances are trivial for a volant animal and argue against this hypothesis.

Predator avoidance and interruption of parasite cycles also are potential reasons for changing roosts (Kunz 1982; Marshall 1982; Merilä and Allander 1995). However, roost-switching is not likely to be an effective behaviour, either for fooling predators or avoiding parasites, unless all bats abandon a roost simultaneously. Even though individual Indiana bats change roosts every 2.9 days in Michigan, some trees remain occupied, at least by a few bats, for weeks at a time (e.g., Figure 1 in Kurta 1993a); prolonged occupancy of certain trees with major fluctuations in population size occurs in Missouri and Indiana as well (Calahan 1993; Humphrey et al. 1977). Also, roost-change distances in our study were as low as 1 m, and 19% were less than 25 m (Figure 2). Such short distances in an open wetland are not likely to hide bats from sharp-eyed, aerial predators or persistent, terrestrial carnivores.

Biologists from southern states suggest that Indiana bats change roosts in response to external environmental conditions, moving to different trees with different microclimates (Calahan 1993; Gardner et al. 1991; Humphrey et al. 1977). Much of this argument, as it pertains to Indiana bats, centres around the bats avoiding high summer temperatures or precipitation, particularly in exposed roosts, and using living trees, such as shagbark hickories (*Carya ovata*), as alternate roosts. However, the bats in Michigan challenge the generality of these ideas because they never roost in shaded areas, never use a living tree, and population size is not consistently correlated with either maximum or minimum ambient temperatures (Table 1). In addition, one would expect all bats to leave a particular tree when environmental conditions change dramatically, but this is not always the case. Favoured roost trees, in Michigan and elsewhere, often are in continual use for weeks or months, even though population size and ambient conditions fluctuate greatly (Calahan 1993; Humphrey et al. 1977; Kurta et al. 1993a, b). We surmise that Indiana bats occasionally do move in response to temperature changes. Nevertheless, the statistical evidence is weak and ambiguous (Table 1; Calahan 1993), suggesting that temperature is not the only, or even primary, reason for changing roosts.

The ephemerality of bark roosts may contribute to the low fidelity of Indiana bats and other tree-dwelling species (Brigham 1991; Kurta et al. 1993a; Lewis 1995). Bark roosts are prone to sudden destruction from wind, rain, and other factors (e.g., Gardner et al. 1991; Kurta 1995), and bats may frequently change trees to reassess the value of known roosts and to discover additional, high-quality ones. In our study, the majority of roost trees are rarely visited, and even then by only a few bats (Figure 5); assuming that ephemerality is a factor in roost-switching, this suggests that the emphasis is on reassessing known roosts and secondarily on identifying new ones. If ephemerality is important, we predict that Indiana

bats that roost in more permanent sites, such as tree cavities or under the bark of living shagbark hickories (e.g., Humphrey et al. 1977; Kurta et al. 1993b), will move less often than Indiana bats that roost under bark of dead trees.

In our study, roost-changing occurred most often in pregnancy and least often during lactation. Pregnant bats may change more frequently to reacquaint themselves with the condition of their roost trees after hibernation (a corollary of the ephemerality hypothesis). At our study site, many trees lost bark over winter, one became firewood, and one roost area was taken over by a nesting pair of brown creepers (*Certhia familiaris*; Kurta and Foster 1995). Lactating mothers, in contrast, have already located alternate roosts and may be reluctant to move their offspring, especially when burdened by a transmitter, because of the unusually large size of young bats (Kurta and Kunz 1987).

Management
Implications

Use of multiple roosts is a tremendously important factor in the management of Indiana bats and other tree-dwelling species. The area needed to sustain an individual tree-roosting bat, compared to similar-sized rodents and insectivores, is enormous, and is a function of the number of trees required, the density of suitable trees, and the distance between all roosts and suitable foraging grounds. In regions such as the midwestern United States, where forests often are young and highly fragmented, these distances may become (or already are) high enough to be limiting for some species. The large number of tree-roosting bats that are endangered or threatened (Anonymous 1995) indicates that further research on roosting dynamics is urgently needed. In addition, the large geographic range of most tree-dwelling species (Barbour and Davis 1969) and potential differences in roosting behaviour between central and peripheral populations (the present study; Kurta et al. 1993a) make it imperative that management plans address the needs of both groups.

ACKNOWLEDGEMENTS

We thank the Borntagers for access to their property. Funding was provided by grants from the EMU Graduate School, National Science Foundation (USE-8952309), and Nongame Program of the Michigan Department of Natural Resources to AK, as well as grants from the Theodore Roosevelt Memorial Fund, Sigma Xi, and Helwig Scholarship Fund to KJW. S. Gaitens, R. Foster, M. Lucas, D. Mania, M. McGuire, C. Price, and D. Viele aided with the field work.

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Bat Species Composition and Roost Use in Pinyon-Juniper Woodlands of New Mexico

ALICE L. CHUNG-MACCOUBREY

ABSTRACT

Bat species composition and structures used for maternity colony roosts were investigated in pinyon-juniper habitats of the Cibola National Forest. I mist netted 10 sites with permanent water on four different nights during the summer of 1995. Number of species and total numbers of bats captured ranged from 0–11 species at a site and 0–134 bats in a night. *Myotis californicus*, *M. ciliolabrum*, *M. volans*, *M. thysanodes*, *Eptesicus fuscus*, *Lasionycteris noctivagans*, *Lasiurus cinereus*, and *Tadarida brasiliensis* were captured at ≥ 5 sites, although not always in high numbers. Species captured at < 5 sites were either locally abundant (e.g., *M. evotis*) or a rarity (e.g., *Euderma maculatum*). Radio-telemetry was used to study maternity-roost use by three federal Category 2 candidate species. Three *M. thysanodes*, one *M. evotis*, and two *M. volans* roosts were located. *M. thysanodes* and *M. volans* roosts with 30 to over 200 bats were found in ponderosa pine snags and live ponderosa pine (*Pinus ponderosa*) with long, vertical cracks. These snag and live-tree roosts were located in ponderosa pine stringers in drainages between pinyon-juniper slopes or at the interface of ponderosa pine and pinyon-juniper habitats. *M. evotis* used live and dead junipers exclusively for colony and solitary roosts.

INTRODUCTION

Insectivorous bats consume large quantities of insects each night to support the high energetic costs of flight and reproduction, and to permit storage of energy as fat for the winter (Kunz 1982; O'Shea and Vaughan 1977). Thus, bats may have a large impact on insect populations, insect activity, and many insect-related ecological processes (such as herbivory, pollination, disease transmission, etc.). These far-reaching influences suggest that bats may play an important role in ecosystem function, balance, and integrity. Despite their diversity, abundance, and importance in the environment, little is known of the biology, life history, and habitat requirements of bats in the American Southwest.

Of the 26 bat species found in New Mexico, two are federally endangered and 13 are federal Category 2 candidates. Future decisions relating

to bats for land management, ecosystem management, and federal/state status determinations may largely depend on information provided by current research on geographic presence/absence, habitat associations, life histories, foraging and roost requirements, and other critical needs and threats.

In the Southwest, surface water, appropriate roosts, and food are essential components of suitable bat habitat. Water is very important to insectivorous bats because of their high protein diet and high rates of evaporative water loss (McNab 1982). However, suitable maternity roosts may be most critical to successful reproduction of bats because they provide a microclimate that facilitates gestation and rapid growth of pups (Humphrey 1975). Knowledge of which structures provide a suitable microclimate for reproduction is essential for effective management of bat habitat and populations. Thus, the objectives of this study were to (1) examine species composition, relative abundance, and reproductive timing of bats that use water resources in pinyon-juniper habitats; and (2) identify types of roosts used by maternity colonies of select Category 2 candidate species.

MATERIALS AND METHODS

To determine species composition, I sampled bats by placing mist nets over relatively permanent bodies of water in pinyon-juniper habitats. Ten netting sites were chosen among the Sandia, Manzano, Magdalena, Gallinas, and San Mateo mountains of the Cibola National Forest ($34^{\circ} 10'N$, $107^{\circ} 26'W$). Site selection was based on habitat type (pinyon-juniper), geographic location, and permanency of the water source. Water sources were perennial streams, well- and spring-supplied steel tanks, or dirt stock tanks. Following methods described in Kunz and Kurta (1988), each site was netted four times at approximately 2–3-week intervals beginning in May and ending in August 1995. Nets were opened at sunset and were closed after activity had substantially subsided (typically between 2330 and 0100 h). After species, sex, age, reproductive status, and body measurements were recorded, bats were weighed and released.

From the end of June through early August, radio-telemetry was used to track reproductive females to maternity roosts. The Gallinas mountains northwest of Magdalena were chosen for the telemetry study because pinyon-juniper is the primary habitat type of this range, and numerous permanent water sources are dispersed throughout. I netted over water sources to obtain pregnant or lactating long-legged myotis (*M. volans*), fringed myotis (*M. thysanodes*), or long-eared myotis (*M. evotis*), all of which are federal Category 2 candidate species. Only one female of a species was radio-tagged per site per night to avoid tracking bats from the same roost. After clipping fur from between the shoulder-blades, a 0.50–0.67-g radio-transmitter (Holohil Systems, Ltd.) was secured with surgical glue, and the bat was released after the glue had dried (approximately 30 minutes). The following days were spent attempting to locate the bat and identify its roost. If a roost was located, I counted bats exiting at dusk to determine total occupancy of the roost.

RESULTS

From three to 11 species were captured at each site (Table 1). However, all species caught at a site were not necessarily captured on any one night. Number of captures per night at each site was variable between netting events. Numbers of bats caught at any one site in a night ranged from

TABLE 1 Sites at which each species was captured. Sites are ordered by mountain range.

Species	Sandia		Manzano		Gallina		Madgalena	San Mateo		
	1	2	3	4	5	6	7	8	9	10
<i>Myotis californicus</i> and <i>ciliolabrum</i> ^{a,b} California and small-footed myotis	×	×	×	×	×	×	×	×	×	×
<i>M. volans</i> ^b Long-legged myotis		×	×		×	×	×	×	×	×
<i>Eptesicus fuscus</i> Big brown bat	×	×	×		×	×	×	×	×	
<i>Lasionycteris noctivagans</i> Silver-haired bat	×	×	×	×			×	×	×	×
<i>Lasiurus cinereus</i> Hoary bat	×	×	×	×			×	×	×	
<i>M. thysanodes</i> ^b Fringed bat					×	×	×	×	×	
<i>Tadarida brasiliensis</i> Mexican free-tailed bat				×			×	×	×	×
<i>M. evotis</i> ^b Long-eared myotis					×	×			×	×
<i>M. auriculus</i> Southwestern myotis			×			×	×			×
<i>M. yumanensis</i> ^b Yuma myotis						×	×			×
<i>Antrozous pallidus</i> Pallid bat						×	×			
<i>M. lucifugus occultus</i> ^b Little brown myotis							×			
<i>Pipistrellus hesperus</i> Western pipistrelle										×
<i>Idionycteris phyllotis</i> ^b Allen's lappet-browed bat										×
<i>Euderma maculatum</i> ^b Spotted bat										×

^a These species could not be distinguished in the field and are thus reported together. *M. ciliolabrum* is a federal Category 2 Candidate.

^b Federal Category 2 candidate species.

TABLE 2 Total number of bats caught on each netting occasion by site. Sites are arranged by mountain range.

Netting occasion	Sandia		Manzano		Gallina		Madgalena	San Mateo		
	1	2	3	4	5	6	7	8	9	10
#1	3	23	10	2	64	19	100	6	11	15
#2	0	23	16	5	13	2	134	58	41	8
#3	1	0	52	6	43	44	42	29	97	4
#4	3	2	41	0	27	23	24	51	30	15

0 to 134 (Table 2). *Myotis californicus*, *M. ciliolabrum*, *M. volans*, *M. thysanodes*, *Eptesicus fuscus*, *Lasionycteris noctivagans*, *Lasiurus cinereus*, and *Tadarida brasiliensis* were captured at many or most netting sites (≥ 5 sites; Table 1), although not always in high numbers. Species that were caught at < 5 sites were either locally abundant at their site of capture (e.g., *M. evotis* or *M. auricolus*) or rare (e.g., *Euderma maculatum* or *Idionycteris phyllotis*).

Capture of females who were obviously pregnant began around the second and third weeks of June. Lactating females were caught beginning the first week of July and were still being captured in early August. Post-lactating females were captured starting the first week of August.

In the Gallinas mountains, two long-legged, one long-eared, and three fringed myotis maternity roosts were identified. Long-legged and fringed myotis roosts were in ponderosa pine snags or live ponderosa pines with long, vertical cracks and loose bark. Vertical cracks were most likely due to lightning strikes. Long-legged myotis roosts contained 67 to over 200 bats, and fringed myotis roosts contained 30 to 40 bats. A single, long-eared myotis roost of five bats was found in a cavity within the dead trunk of a live juniper (*Juniperus* sp.). All maternity roosts were vacant by late August/early September. Of the five ponderosa pine roosts, two were in isolated stands of ponderosa pine (stringers) running the lengths of arroyos in pinyon-juniper (*Pinus edulis*—*Juniperus* sp.) habitat, and three were located at the interface of pinyon-juniper and ponderosa pine habitats.

Lactating long-legged and long-eared myotis radio-tagged in late July/early August were not found in colony roosts, but changed roosts daily. Long-legged myotis females moved amongst pinyon snags and roosted underneath the sloughing bark. Long-eared myotis females moved amongst live and dead junipers (primarily *Juniperus monosperma*) and roosted within the twisted folds of the trunks.

DISCUSSION

This first season, all or a large portion of the bat species that use water and other resources in pinyon-juniper habitats of central New Mexico were identified. Total captures were generally lower in the Sandia and Manzano mountains, most likely due to the fewer number of suitable watering sites in pinyon-juniper habitats of these mountains (pers. obs.).

Netting success between nights was highly variable in both species composition and total captures. Thus, four nettings were probably the minimum necessary to reflect the entire complement of species using a site throughout the season. Many factors affect the species and number of bats captured, including weather, moon phase, site location, overall availability of water, reproductive status of bats, changes in foraging patterns, previous captures, and ability to avoid nets (Reith 1982; Kunz and Kurta 1988). Although many factors may affect netting results, mist netting still provides information, such as geographic distribution, species composition, relative abundance, and timing of activities. Mist netting data from this study may be used by managers for making future status determinations of federal Category 2 candidate species, managing bat habitat, and evaluating land-management practices, and by researchers for designing roost, foraging, and reproductive studies.

Within pinyon-juniper habitats, hard ponderosa pine snags or live ponderosa pines with cracks or loose bark may be important sites for long-legged and fringed myotis maternity colonies. Site fidelity is correlated with permanency of the roost type (Lewis 1995). Thus, bat species that use permanent structures, such as caves, are more likely to reuse the same roost on a daily and annual basis than species that use foliage roosts. However, site fidelity is inversely correlated with availability of the roost type (Lewis 1995). The ponderosa pine roosts used by bats in this study are persistent for many years, but are not in great abundance in pinyon-juniper habitats. Thus, these bats are likely to occupy the same roosts year after year. Female long-eared myotis that were radio-tagged in this study used junipers exclusively (primarily *Juniperus monosperma*) for both colony and solitary roosts. Because of the high availability of junipers, long-eared myotis may not exhibit site fidelity to the same degree as long-legged and fringed myotis. Nevertheless, inadvertent disturbance or loss of any colony roost may potentially displace hundreds of pregnant females or females and young. Because of the low reproductive rate of bats (approximately one young per year), such an occurrence could have a large impact on the local population (Humphrey 1975). Bats evicted from maternity roosts produce fewer offspring after moving to the new roost (Brigham and Fenton 1986). The abundant use of both live and dead trees by bats in pinyon-juniper habitats has important implications in the regulation of fuelwood harvest and salvage logging in the Southwest. To manage for bats in pinyon-juniper habitats, more steps must be taken to ensure that active colony roosts are not disturbed, that potential roost trees remain available for future use, that a diverse food base is cultivated, and a sufficient number and dispersion of water sources are available for use by local populations.

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Characteristics, Use, and Distribution of Day Roosts Selected by Female *Myotis volans* (Long-legged Myotis) in Forested Habitat of the Central Oregon Cascades

PATRICIA C. ORMSBEE

ABSTRACT

I tracked female *Myotis volans* using radio-telemetry during July and August 1993, 1994, and 1995 in two drainages (Quentin Creek and Lookout Creek) of the Central Oregon Cascades. Analysis of the data indicates large snags and hollow cedar trees are important day roosts. Individuals radio-tagged at the same night roost did not use one common day roost. Individual bats roosted in one roost for several days, or used multiple day roosts within distinct areas. The area in Quentin Creek encompassing one night roost and all known day roosts covered 3,258 ha, and the area in Lookout Creek encompassed 6,391 ha. Distributing solitary day roosts and patches of roosts across the landscape, protecting the microclimate of roosts, and conducting further research on the types and distribution of day roosts would be reasonable steps towards providing day roost habitat for this species and gaining further understanding of its day roost ecology.

INTRODUCTION

Myotis volans is a forest-dwelling bat found in the Oregon Cascades. It inhabits arid rangelands and montane forests across the western United States and Canada (Nagorsen and Brigham 1993). This species was identified by the Forest Ecosystem Management Assessment Team (FEMAT) as being associated with old growth, in need of further study, and of concern because of the limited distribution of old-growth habitat within western Washington and Oregon, and northern California (Thomas et al. 1993). *M. volans* was federally listed in the USA as a Category 2 species in November 1994.

I collected data on day roost characteristics, use, and distribution for female *M. volans*. I explored five questions of interest concerning day roosts: (1) What are the physical characteristics of day roosts selected by female *M. volans*? (2) Do female *M. volans* found night roosting together, use one common day roost? (3) Do female *M. volans* use more than one

day roost? (4) If they do use more than one day roost, how are the roosts distributed in relation to one another? (5) How large an area encompasses the night roosts and day roosts of female *M. volans* associated with the same night roost? This report presents a preliminary exploration of the data and further analysis is forthcoming.

STUDY AREA

Study sites were located in the central Oregon Cascades in the Willamette National Forest. I collected data in 1993, 1994, and 1995 in Lookout Creek drainage, which lies east of Blue River Reservoir; and in Quentin Creek drainage in 1994, which lies northeast of Blue River Reservoir. These sites were selected because they had accessible bridges that served as night roosts for female *M. volans* and the drainages were relatively accessible. A variety of potential day roosts were present (cliff faces, caves, snags, and trees) over a matrix of varying stand conditions (natural seral stages, managed stands with and without residual snags and trees).

METHODS AND MATERIALS

I captured female *M. volans* at two bridge sites between 0330 and 0430 h during July and August. Lactating and pregnant females were selected over females of unknown reproductive status. I radio-tagged 22 bats with 0.55 to 0.65-g BD-2B radio-transmitters (Holohil Systems Inc., Carp, Ontario). I radio-tagged one individual in both 1994 and 1995. Because it did not return to the same day roosts in 1995 as it had used in 1994, I counted it as two separate bats for my analysis.

A location for each radio-tagged bat that stayed within the study area was mapped daily based on compass readings, or roost location, for the life of the radio or until it was shed. Verification of an exact day roost for each radio-tagged bat was attempted once every 24 hours during daylight. Roost locations and characteristics, including species, DBH, height, and decay class (Appendix 1) were recorded.

The design of my study did not call for in-depth observations of bat activity at the day roosts. However, on six occasions I returned to four different roosts at dusk to observe radio-marked bats exiting from their day roosts (fly-out). Three of these roosts were *Psuedotsuega menziesii* snags in decay classes 1 and 2. The fourth roost was a large-diameter *Thuja plicata* in decay class 0.5.

Statistical Methods

Simple statistics were calculated using Paradox version 4.5 (Borland Int. Inc.), and JMP statistical software version 3.1 (SAS Institute Inc.). I used simple linear regression to explore the relationship between the days a bat was radio-tracked and the number of roosts associated with it. For this analysis, I used “roost sites,” which included both verified roosts, and compass locations of unique sites where a specific roost structure was not verified. The response variable—number of roost sites—was square-root-transformed as it was count data, and the transformation resulted in a

more normal distribution. I also ran a simple linear regression of the days a bat was radio-tracked against the size of the area encompassing day roost sites of the individual (roost areas). I eliminated one outlier for this analysis as the roost area of this bat was over three times the size of the largest roost area used by the other bats.

JMP software was used for cluster analysis as a visual tool for mapping roost sites. I used GIS to determine distances between roosts, distances from day roosts to night roosts, and the area encompassing day roost sites (verified roosts and compass locations) for individual bats. This analysis was completed exclusive of roosts selected on the morning that a radio-marked bat was released. The area of landscape polygons encompassing day and night roosts for each drainage was measured using GIS.

RESULTS

Radio-Tracking	<p>Out of 22 bats that I radio-tagged, I tracked 16 to day roosts. The other six bats were either not located after the first day, or the signal could not be pinned down to a distinct location. Fifteen bats were tracked for two or more days, and 13 of these used multiple roost sites (verified roosts and compass locations). The average number of days that bats ($n = 16$) were radio-tracked was 8.25 ($SE = 1.3$) and ranged from 1 to 24.</p>
Physical Characteristics of Day Roosts	<p>A total of 41 day roosts used by 16 individuals (one bat was radio-tracked during two separate seasons, and is accounted for twice) were located. Snags comprised 88% ($n = 36$) of all roosts. Live <i>P. menziiesii</i> (Douglas-fir) comprised 10% ($n = 4$), and one rock crevice was selected as a roost.</p> <p>The average height of all roosts was 40.0 m ($SE = 2.5$) and ranged from 13.4 to 71.5 m. The average DBH for all snags and trees used as day roosts was 100.2 cm ($SE = 6.08$) and ranged from 34.0 to 194.0 cm. Nearly half (47%) of the snags were decay classes 1 and 2, <i>P. menziiesii</i> averaging 108 cm ($SE = 7.4$) DBH, and 45.8 m ($SE = 2.9$) tall. Nine (25%) of the snags used as day roosts were decay classes 3 and 4, <i>P. menziiesii</i> averaging 99.1 cm ($SE = 10.1$) DBH, and 32.7 m ($SE = 5.7$) tall. The remaining snags were <i>Tsuga heterophylla</i> (western hemlock) snags (14%, $n = 5$), mostly in decay classes 1 and 2 ($n = 4$), and <i>Thuja plicata</i> (western redcedar) snags (11%, $n = 4$), mostly in decay class 0.5 ($n = 3$).</p>
Use of Day and Night Roosts	<p>Bats were located at day roosts on 93 occasions. On two occasions, two bats that were radio-tagged at the same night roost were found using the same day roost at the same time. None of the radio-tagged bats were found using the same day roost at different times.</p>
Multiple Day Roosts	<p>The average number of days spent at a day roost for all radio-tagged bats ($n = 16$) was 2.16 ($SE = 0.27$) and ranged from 1 to 7 days. Fourteen bats were radio-tracked to day roost sites (verified roosts and compass locations) on more than one day. Thirteen of these bats used at least two roost sites over the time they were tracked.</p> <p>There was a weak relationship between the number of days a bat was radio-tracked and the number of roost sites it used (one-tailed p-value = 0.02). This implies that the more days a bat is radio-tracked the more</p>

roost sites it will be found using. The number of days a bat was tracked did not affect the size of roost area (one-tailed p-value = 0.77). This implies that regardless of the number of days these bats were tracked, they tended to roost within a discrete area (n = 12).

Distribution of
Roost Sites

Multiple day roost sites (verified roosts and compass locations) of individual bats occurred within an average area of 11.42 ha (SE = 3.9) for 12 bats, and within 175 ha for one bat. The average distance between day roosts (verified roosts only) of individual bats was 412.5 m for 11 bats, and 3,693 m for one bat.

The average distance of day roosts (exclusive of day roosts selected on the morning that a bat was released) from the night roost was 2.46 km and ranged from 0.71 km to 6.47 km. The area encompassing all day roosts (n = 26) and the night roost for Quentin Creek drainage covered 3,258 ha. The area encompassing all day roosts (n = 15) and the night roost for Lookout Creek drainage covered 6,391 ha.

Fly-Out

I witnessed 3 to 12 bats exit the *P. menziiesii* snags. Over 300 bats exited from the *Thuja plicata* roost on two separate occasions, and many of the bats were observed exiting and returning to the roost, behaviour that is typical of neonatal bats testing their flight skills (Perlmeier, 1995 and pers. comm.). Large accumulations of guano were present at the base of this and one other hollow tree in the same cedar grove. Three evenings later, not a single bat exited either roost. Sheets placed at the base of both roosts to catch guano indicated the bats did not return to either roost over the rest of the summer.

DISCUSSION

Roost Characteristics
and Function

While relatively large-diameter, tall *P. menziiesii* snags dominate the type of roost selected by individual bats in this study, other types of day roosts may be of equal or more critical value to the ecology of *M. volans*. For instance, only a few *Thuja plicata* snags in decay class 0.5 were selected, and could be interpreted as minor contributors to the pool of day roosts. Fire-hollowed *Thuja plicata* are relatively rare compared to *P. menziiesii* snags, but provide large chambers or cavities that can house large numbers of bats, and provide different microclimate conditions compared to the cracks and crevices typical of *P. menziiesii* snags. The difference in physical characteristics, and the discrepancy in the number of bats I witnessed during fly-out indicate that different types of day roosts serve different functions. Further study to quantify these differences could be valuable in fully understanding the roost ecology of this species.

There could be many reasons for female *M. volans* to select different types of day roosts, and vary the number of roost-mates. One hypothesis is that reproductive females who are caring for altricial pups that are not able to thermoregulate, echolocate, or fly, increase the safety and energy conservation for themselves and their pups by roosting in one location as a large group. Once the pups are more independent of their mothers, learning a variety of roosts and foraging sites in smaller, less competitive groups could increase a pup's chance of survival.

Use The low occurrence of radio-tagged bats day roosting together, and the fact that no two bats used the same day roost on separate occasions, suggest that the radio-tagged bats did not share a single common day roost. Too few bats were radio-tagged at any one time to draw conclusions about how these bats interact at the day roosts as a whole group.

The bats in this study generally used more than one day roost. Roosting habits of bats are variable and influenced by reproductive status, environmental conditions, such as proximity to food sources, parasite load, threat of predation, or microclimatic conditions, and social organization (Kunz 1982). Lewis (1995) reported similar factors influencing roost switching. The use of multiple roosts by female *M. volans* could be a result of any one or all of these influences.

Use of several roosts has been attributed to predator avoidance for some species of bats in tropical zones. In temperate regions, such as the Pacific Northwest, predation on bats by raptors and some mammals is probably opportunistic, and there is little evidence that bats are a major food source for other species of wildlife (Fenton 1983). Results from pellet analysis of *Strix occidentalis* (northern spotted owl) within the Oregon Cascades for an area encompassing this study site produced only occasional records of bat remains (Swindle, pers. comm.).

The linear regression results indicate that there is some sort of relationship between the number of tracking days and the number of roosts used by an individual, yet the results were weak, in part because of the small sample size. My analysis only included data for verified roosts or locations. There were occasions where a bat was tracked to a roost one day, not found the next, and relocated at the same or a different roost the day after. It is likely that the bat was at an alternate roost on the day it was not found, yet these events were not used in the analysis. An effective analysis of this type would require a larger sample size where the number of days that each bat is tracked covers more than a few days to offset occasions when a bat spends several days at one roost.

Distribution I have reasonably strong evidence that the size of a roost area was not influenced by the number of days that a bat was tracked. While this supports the idea that some of these bats use discrete roost areas, again the sample size is small and further testing with a larger sample would be logical before inferring these results beyond the scope of this study.

The distribution of multiple day roosts for individual bats within relatively small areas is consistent with the work of Taylor and Savva (1988), who found several species of Tasmanian bats using multiple day roosts. They hypothesized that the bats' fidelity was to a roost area rather than to a specific roost. Kunz (1982) suggested that most bats use one or more alternate roosts, and found that fidelity to a home area rather than a specific roost was common among foliage-roosting bats. Kunz (1982) suggested that roost fidelity is partially based on abundance and permanence of roosts. Lewis (1995) reviewed roost fidelity and lability for 43 species of bats and found fidelity to be related to permanence of the roost and inversely related to roost availability. Because of the temporary nature of snags, using several roosts in a discrete area that provides desirable habitat conditions may be a better strategy than being loyal to one snag and risking the need to relocate at an inopportune time.

Selection of day roosts by female *M. volans* involves biological, environmental, and temporal considerations at more than one geographic or physical scale. This study and discussion barely scratches the complex surface of day roost selection. Humphrey (1975) hypothesized that the distribution of nearctic bat species was associated with the availability of roost structures. His work indicated that nursery roosts are a prime resource in determining distribution and abundance of nearctic bats. Ensuring adequate roost distribution and abundance for snag-dependent species, such as *M. volans*, in forested habitats of the Pacific Northwest will require maintenance of adequate snag resources over time, especially on lands designated for commercial forestry.

Solitary *P. menziiesii* snags and patches distributed across an entire watershed would provide one level of day roost habitat for female *M. volans*. Management strategies specific to identified roost areas may be the most effective approach to maintaining or increasing roost structures for these sites. Monitoring use and roost microclimates will be important in determining long-term use of these areas, and any changes to roost microclimates.

Maintaining the microclimate of hollow trees and rock outcrops used as roosts may require vegetation protection or management out to 240 m (Chen et al., 1993). In many cases, reserve buffers could be counterproductive to maintaining the microclimate around day roosts. If vegetation is left to grow within a buffer, it could change the temperature and air flow of the roost. Protection of roosts in harvest units, along stand edges, or in forest gaps may require removal of vegetation. Monitoring temperature and use at these more permanent roost structures would be valuable in designing appropriate management strategies.

Further study on the concept of day roost areas and day roost fidelity would be helpful in better understanding and managing for roost types and distribution. Day roosts are one component of the ecology of *M. volans*. Other components, such as foraging areas and hibernacula, are not well understood and may also play an important role in the distribution and stability of this species. The results of this study are from a limited geographic area with a relatively small sample size of bats, and I recommend taking this into consideration before applying the results to other areas.

ACKNOWLEDGEMENTS

My thanks to Stuart Perlmeter for his technical and emotional support, insight, and sense of humour. My thanks to Aimee Hart, Maddie Rowan, Miyah Yoder, and Joannie Humphries for their patience and endless hours of field and computer work. I thank Bill McComb, John Hayes, and Dick Holthausen for their comments and review, and to Rosanna Costello for GIS support.

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APPENDIX 1 Decay classes for snags (adapted from Neitro et al. 1985).

Typical attributes	Decay class				
	0.5	1	2	3	4
Percent dead	± 50%	100%	100%	100%	100%
Branches	80–100%	80–100%	few—no branches	limb stubs to none	none
Bark	80–100%	80–100%	varies	varies	0–50%
Condition	hard	hard	hard/soft	soft	soft
Height	± full	full—broken top	broken top	upper bole gone	less than 50% full

Bats and Bridges: Patterns of Night Roost Activity in the Willamette National Forest

STUART I. PERLMETER

ABSTRACT

Intraspecific and interspecific differences in night roosting activity of *Myotis lucifugus* and *Myotis volans* were investigated at bridges used as night roosts in the Willamette National Forest. Data collected for this study included night roost temperatures, occupancy rates, night roost population structure, and temporal patterns of cluster formation and dispersal for both species. Results indicated that bats select larger bridges that maintain higher night-time temperatures compared with smaller bridges. Multiple regression analysis indicated that roost size and daily solar radiation levels significantly influenced night roost temperatures. The number of bats observed at night roosts was positively related to minutes after sunset, roost size, and night roost temperature differentials. I present a model calculating night roost energy expenditure. Significant differences in the location, time of year, and patterns of night roost activity were found in *M. lucifugus* and *M. volans*. Males showed a strong trend towards roosting alone, while clusters were composed almost exclusively of females. Differences in activity levels between *M. lucifugus* and *M. volans* may be related to differences in the length and timing of gestation, foraging strategies, and the role of social groupings at night roosts.

INTRODUCTION

For many species of bats, parturition is marked by the formation of large, conspicuous maternity colonies at suitable day roost sites. For many of these maternity colonies a less conspicuous social grouping forms nightly when bats retreat to a night roost. Depending on the species and the availability of sites in a geographic area, bats use a variety of natural and artificial structures as night roosts (Kunz 1982).

The function of night roosting in bats can be divided into three broad categories: (1) social; (2) thermoregulation and energetic; and (3) environmental. These categories are not mutually exclusive and their influence will differ depending on the species, gender, and internal status of the individual. For an extensive review of literature on night roosts see Kunz (1982). Suggested social benefits for bats using night roosts include main-

taining a close association with a group of conspecifics, particularly between females and their offspring (Howell 1979; Vaughan 1976), as information centres (Howell 1979; Wilkinson 1992), or to calm members of the aggregation and thereby reduce individual metabolic rates (Trune and Slobodchikoff 1976).

The majority of studies of night roosting have emphasized the thermoregulatory and energetic benefits of night roosting in the context of a bat's daily time budget. In optimal modelling theory (Krebs and Kacelnik 1991), the decision to use a night roost and for what length of time is a subset of adaptive behaviours that function to enhance a bat's energetic efficiency. While bats should be adapted to maximize food intake as expeditiously and efficiently as possible, taking refuge in a night roost with a favourable microclimate also can reduce an evening's metabolic expenditure. Additional savings in nightly energy expenditures can be achieved by forming densely packed clusters (Anthony et al. 1981; Barclay 1982; Burnett and August 1981; Kurta 1985).

Environmental and microclimatic variables are frequently cited as affecting the occupancy rate at night roosts. These variables include ambient temperatures outside the roost microenvironment (Anthony et al. 1981; Barclay 1982; O'Shea and Vaughan 1977), the availability of sufficient levels of prey (Anthony et al. 1981), and lunar phase (Fenton et al. 1977; Hirshfeld et al. 1977).

Many bridges in the Willamette National Forest are used as night roosts. The purpose of this investigation was two-fold. First, do bridges used as night roosts have significantly different microclimates, and are these differences reflected in the levels of night roost activity observed at the bridges? I predicted that bats choose bridges that maximize energy savings by maintaining higher roost temperatures, and in which predictable numbers of bats congregate to maximize the benefits of clustering. Second, do *M. lucifugus* and *M. volans* differ in their spatial and temporal use of night roosts in the Willamette National Forest? I predicted that differences in interspecific night roosting patterns occur for *M. lucifugus* and *M. volans* as a result of differences between species in foraging patterns and prey selection, as well as the length of gestation and the timing of parturition.

M. lucifugus is a small (5–9.5 g), insectivorous bat found throughout most of the United States and Canada (Fenton and Barclay 1980; Maser et al. 1984). In Oregon, this species is encountered in all regions (Maser et al. 1984). *M. lucifugus* eats a wide array of aquatic insects with chironomids representing the largest proportion of prey. Foraging activity varies through the night with initial feeding bouts along the edges of streams, rivers, and lakes, and resuming over the open water of lakes as the night progresses. *M. volans* occurs over much of western North America, from coniferous forests to riparian and desert zones (Warner and Czaplewski 1984). This species is widely distributed in Oregon when suitable habitats are available (Maser et al. 1984). The diet of *M. volans* consists primarily of moths (Saunders and Barclay 1992; Warner and Czaplewski 1984; Whitaker et al. 1977). While *M. volans* is slightly larger than *M. lucifugus* (Saunders and Barclay 1992; Warner and Czaplewski 1984), both are characterized by low wing loading and aspect ratios (Saunders and Barclay 1992).

- Study Area Field work was conducted in the Willamette National Forest in Western Oregon during July and August 1993, and May to August 1994. Data were collected at five bridges, all within 6 km of the headquarters for the H.J. Andrews Experimental Forest (44° 12'N, 122° 15'W). Forests in this region are classified as the *Tsuga heterophylla* Zone (Franklin and Dyrness 1973). All the bridges were constructed of a rough aggregate concrete mixture with the underside resembling an “upside-down egg carton” forming several large, individually partitioned recessed chambers.
- Hourly night roost temperatures were measured using thermistor probes and thermometers (Cole-Palmer Instruments, Chicago, Illinois). Hourly readings of ambient temperatures, rainfall levels, relative humidity, and total daily solar radiation were obtained from the meteorological station at H.J. Andrews Experimental Forest Headquarters. Sunrise and sunset times for 44° north latitude were calculated from the 1993–1994 Astronomical Almanac.
- Night roosting bats were counted every 60 minutes using halogen headlamps (Petzel, Inc.) covered with an R25 filter or with a monocular night-vision scope (Javelin Electronics, Inc.). Observers recorded the numbers of bats using the night roost each hour, along with the size and position of individual clusters within the night roost. Bats were periodically captured, using hand nets or a “cluster catcher” attached to an extensible pole, and identified by species, sex, reproductive status, and age (adult or juvenile), along with the time of capture, mass, and forearm length.
- Individual clusters was studied using a closed-circuit television camera (CCTV) operated with lights equipped with Wratten 87 infrared filters (Kodak, Inc.) Arrivals and departures were recorded to the nearest second using an event recorder operated on a Powerbook 140 laptop computer (Apple, Inc.).
- Statistical Analysis Parametric statistics, including linear regression, multiple regression, and analysis of variance (ANOVA), were used for most of the data sets. Log transformations were performed on some data to correct for non-normality (Zar 1984). When assumptions of equal variances were violated, I used the Welch ANOVA Test, which adjusted group means of each level used in the analysis by the reciprocal of the group mean sample variance (JMP Statistical Guide 1994). Differences in sampling periods for 1993 (19 July–26 August) and 1994 (7 May–31 August) meant that some statistical comparisons between the same bridge over both field seasons or between different bridges during the same year were restricted to common sampling periods in the night roosts. Non-parametric statistics, including Kruskal-Wallis tests and the Tukey-Kramer HSD test, were used when nominal variables were involved in an analysis and the violation of normality was suspected (Zar 1984). Chi-square analysis was used to test for differences in species composition at night roost sites, gender composition of bats roosting in clusters or as solitary individuals, and spatial use of night roosts by species.

Night Roost
Microclimates

Nightly mean night roost temperatures were significantly higher than nightly ambient temperatures for 1993–94 (Welch ANOVA, $F = 332.7$, $p < 0.001$, $df = 1$, $n = 131$; Figure 1). A Kruskal-Wallis test for T_d (hourly mean roost temperature minus the hourly ambient temperature) at four of the night roosts indicated a significant difference between bridges ($\chi^2 = 137.2$, $p < 0.001$, $df = 3$). A Tukey-Kramer HSD test indicated that the two larger bridges, Blue River Reservoir Bridge and Quentin Creek Bridge, maintained a higher T_d compared with the smaller bridges, Look-out Bridge and Tidbit Bridge (Figure 2). Multiple regression analysis indicated that night roost temperatures were influenced by roost size, daily solar radiation levels (Langley's) and minutes after sunset ($r^2 = 0.60$, $F = 94.9$, $p < 0.001$, $df = 6$, $n = 367$). Roost size ($F = 34.3$, $p < 0.001$, $df = 4$) and total daily solar radiation ($F = 151.5$, $p < 0.001$, $df = 1$) had a positive effect on night roost temperatures, while minutes after sunset had a significant negative effect ($F = 63.9$, $p < 0.001$, $df = 1$).

A comparison of changes in night roost T_d over the season indicated a significant difference (Welch ANOVA, $F = 18.7$, $p < 0.001$, $df = 6$) in T_d between 15 May and 31 August, with peak night roost T_d occurring between 16 and 31 July. While mean roost temperatures fluctuated over the season, temperature readings from various positions within a single chamber on any given night showed no significant difference.

Night Roost
Microclimates and
Activity Levels

Night roost size significantly affected the number of bats found at a site (Welch ANOVA, $F = 47.6$, $p < 0.001$, $df = 4$). A Tukey-Kramer HSD indicated that the populations at Blue River Bridge were significantly larger than those at Quentin Creek Bridge. Both of these bridges harboured larger populations than the three smaller night roosts. The mean number of bats at the three smaller night roosts did not significantly differ from each other (Figure 3).

Multiple regression analysis was performed to determine the ability of five variables to predict the number of bats observed at different night roosts. The five regressors accounted for 54% of the variation in the model, with roost size (large–small), minutes after sunset, and temperature differential showing a strong positive relationship, and roost size (medium–small) demonstrating a strong negative relationship to the number of bats in night roosts (Table 2). Bridge data from the chambers at Blue River Reservoir indicated that significant differences were found in chamber temperatures (ANOVA, $F = 9.65$, $p < 0.001$, $df = 7$, Figure 4), and that *M. lucifugus* roosted in significantly larger numbers in those chambers that consistently maintained higher temperatures (Welch ANOVA, $F = 67.9$, $p < 0.001$, $df = 7$, Figure 5).

To illustrate the potential impact of roost temperature on night roost energy expenditures for clusters of bats, I constructed a model of night roosting energy budgets based on hypothetical bridges with different temperature regimes. In constructing this model, I used results from previous studies on the metabolic rates and daily energy budgets for bats (Burnett and August 1981; Kunz 1980, Roverud and Chappell 1991). My model assumes a 20% increase or decrease in the temperature-dependent

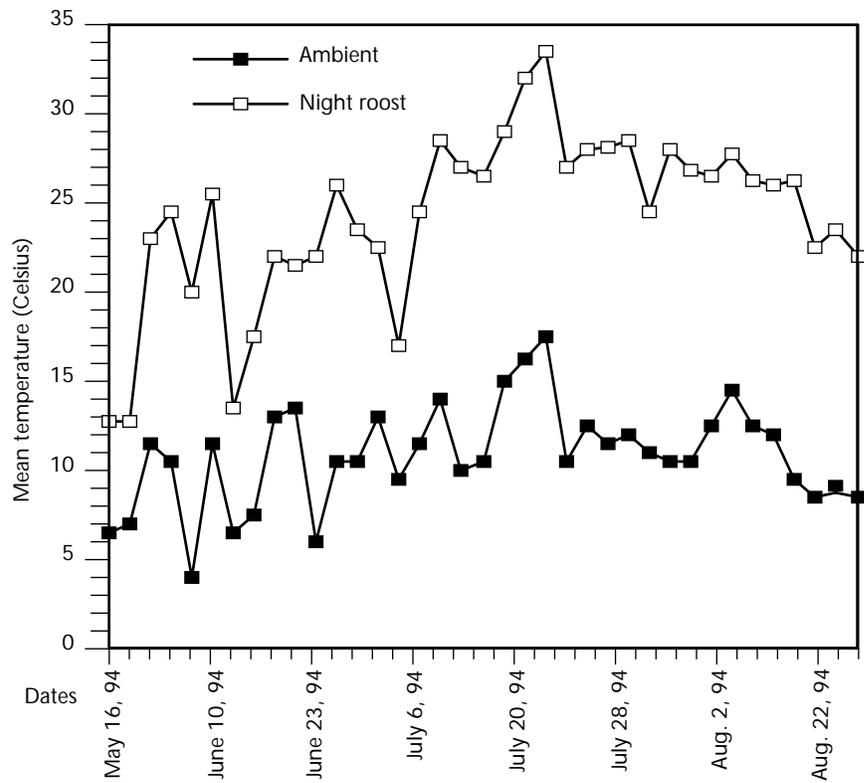


FIGURE 1 Comparison of mean night-time ambient and night roost temperatures (Celsius) at Quentin Creek Bridge for May–August of 1994.

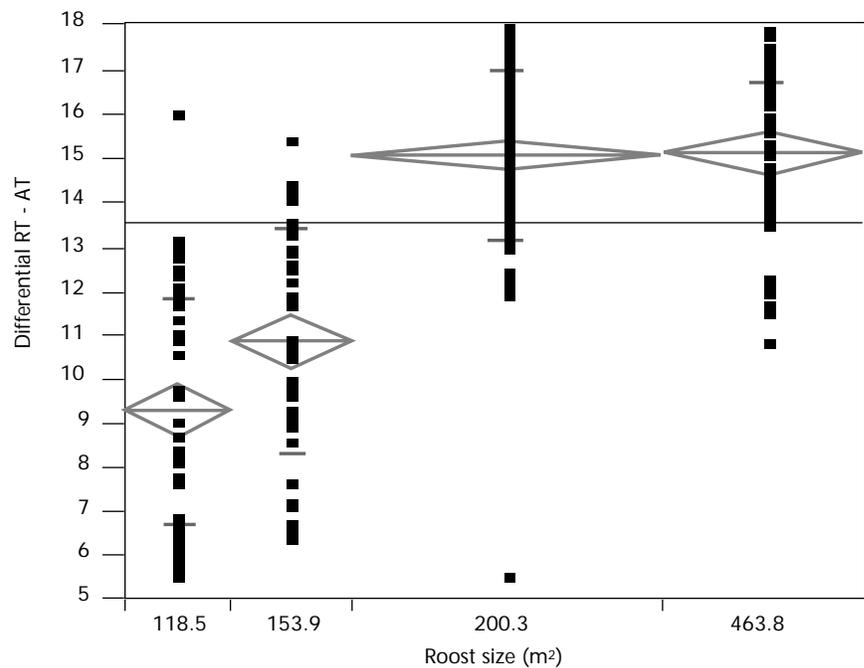


FIGURE 2 Comparison of temperature differential (T_d) by roost size for 1994 (Welch ANOVA, $F = 88.1568$, $p < 0.0001$, $df = 3$, $n = 281$). T_d = night roost temperature (RT)–ambient temperature (AT).

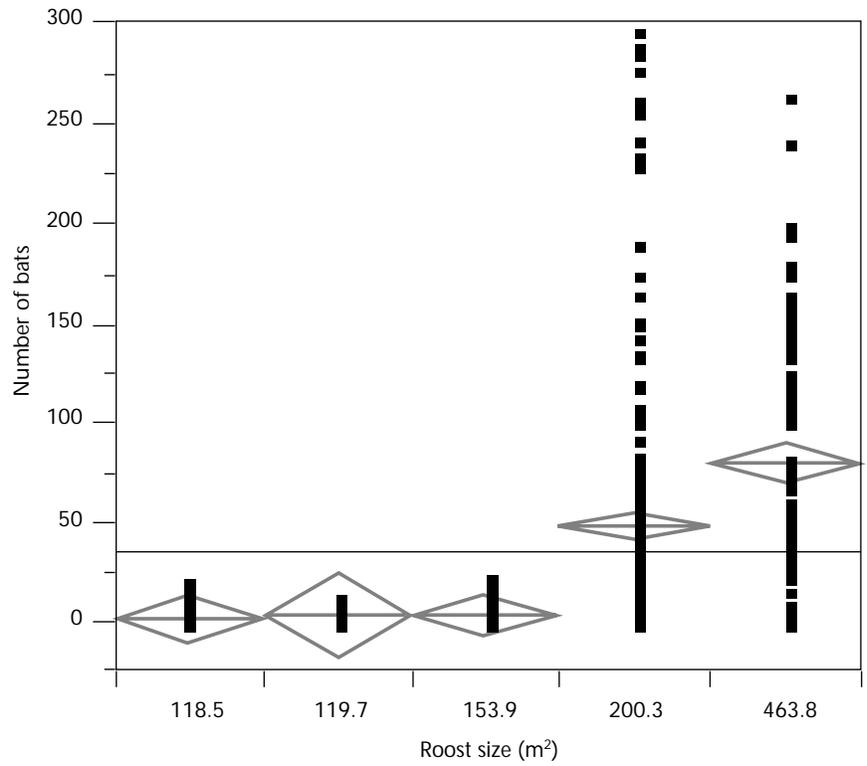


FIGURE 3 *The relationship between roost size and the mean number of bats observed at five night roost sites ($F = 47.6089$, $p < 0.0001$, $df = 4$).*

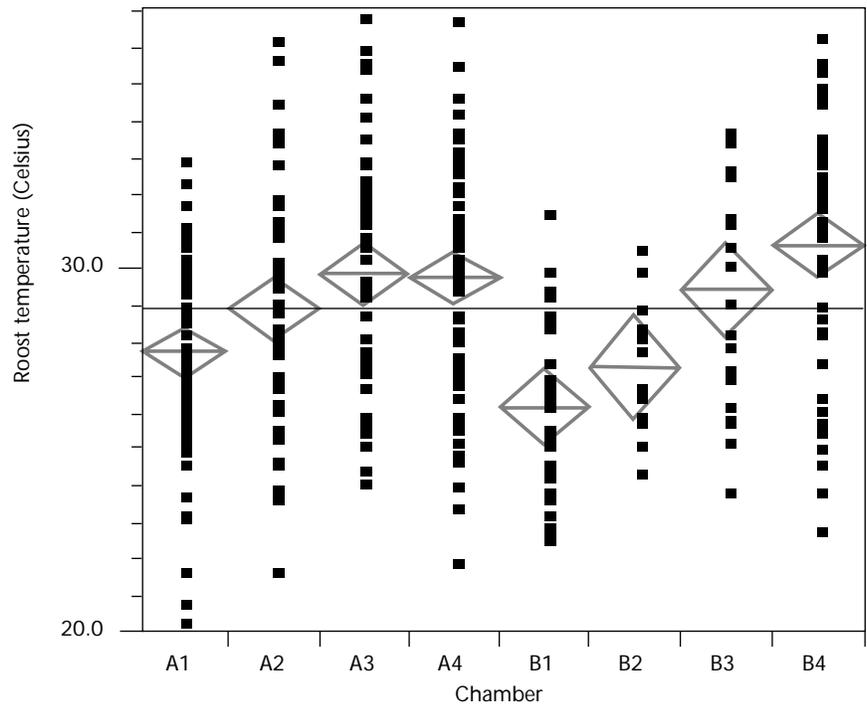


FIGURE 4 *Mean night roost temperatures for the eight individual chambers of the Blue River Reservoir Bridge in 1994 (ANOVA, $F = 9.6484$, $p < 0.0001$, $df = 7$).*

TABLE 1 Summary of species by sex of bats captured at five bridges used as night roosts during 1993–1994.

Species	Males	Females	Total	percent at night roosts
<i>Eptesicus fuscus</i>	6	0	6	1%
<i>Lasionycteris noctivagans</i>	1	0	1	<1%
<i>Myotis californicus</i>	1	1	2	<1%
<i>Myotis lucifugus</i>	29	183	212	51%
<i>Myotis volans</i>	169	10	179	43%
<i>Myotis yumanensis</i>	1	2	3	<1%
<i>Myotis evotis</i>	0	4	4	1%
<i>Corynorhinus townsendii</i>	0	5	5	1%
Total	207	205	412	

TABLE 2 Multiple regression coefficients and levels of significance of five regressors and their ability to estimate the total number of bats (\log_{10}) at night roost sites during 1993–1994. Roost size was treated as a dummy variable.

Variable	Total number of bats (\log_{10})	
	Coefficient	P
Number of minutes after sunset	0.003	<0.0001
Night roost temperature differential	0.048	<0.001
Roost size (large–small)	0.498	<0.0001
Roost size (medium–small)	–0.226	<0.001
Length of night (minutes)	0.001	0.14
Rainfall	–0.088	0.12

metabolic resting rate for each 5°C change in night roost temperature above or below 20°C. This adjustment is based on Roverud and Chappell (1991). As the model illustrates (Figure 6), clusters of bats benefit from being selective in their choice of night roost locations, with bats using warmer night roosts reducing energy expenditures, for the same unit time, when compared with bats in cooler night roosts.

Species and Gender Composition

Eight species of bats were found to use the five bridges as night roosts. There was a significant difference in species representation at the night roosts ($\chi^2 = 81.9$, $p < 0.001$, $df = 7$), with *M. volans* and *M. lucifugus* accounting for approximately 95% of all bats handled (Table 1). Females of these two species dominated night roost populations with *M. volans* ($n = 169$) accounting for 41% and *M. lucifugus* ($n = 183$) 44.4% of all bats captured at the five night roost sites during 1993 and 1994. Male *M. lucifugus* were found in significantly higher numbers at night roosts than male *M. volans* ($\chi^2 = 7.43$, $p < 0.001$, $df = 1$). The roosting patterns of males and females differed significantly in their tendency to form clusters ($\chi^2 = 104.1$, $p < 0.001$, $df = 1$). In all, 99.0% of bats captured in clusters were females ($n = 306$), while solitary roosting bats (Figure 7) were more evenly divided between males ($n = 31$, 47.6%) and females ($n = 34$, 52.3%).

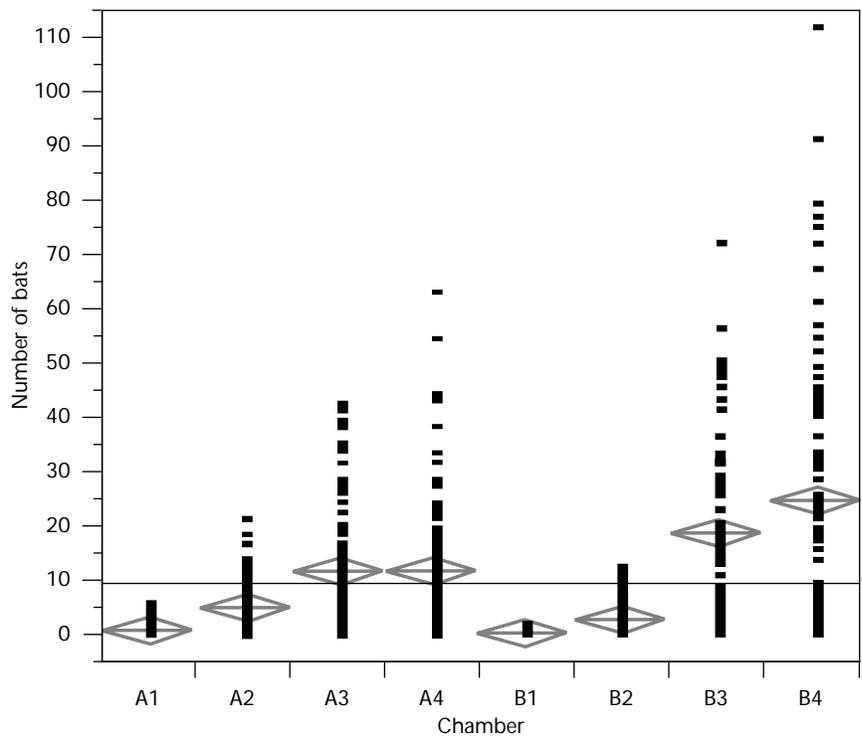


FIGURE 5 The number of bats observed for the eight chambers of the Blue River Bridge for 1994 (Welch's ANOVA, $F = 67.8552$, $p < 0.0001$, $df = 7$).

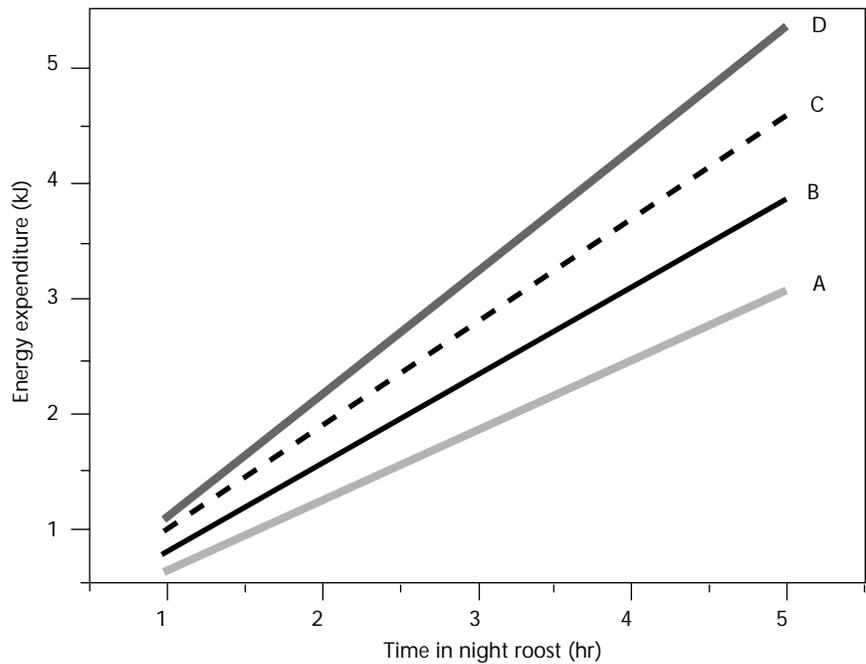


FIGURE 6 The model projects the impact on night roost energy expenditures by time for sites with different temperatures (T_{nr}). Assumptions in the model are that female bats are associated with a cluster and engaged in active body temperature regulation. A ($T_{nr} = 25^{\circ}\text{C}$), B ($T_{nr} = 20^{\circ}\text{C}$), C ($T_{nr} = 15^{\circ}\text{C}$), D ($T_{nr} = 10^{\circ}\text{C}$).

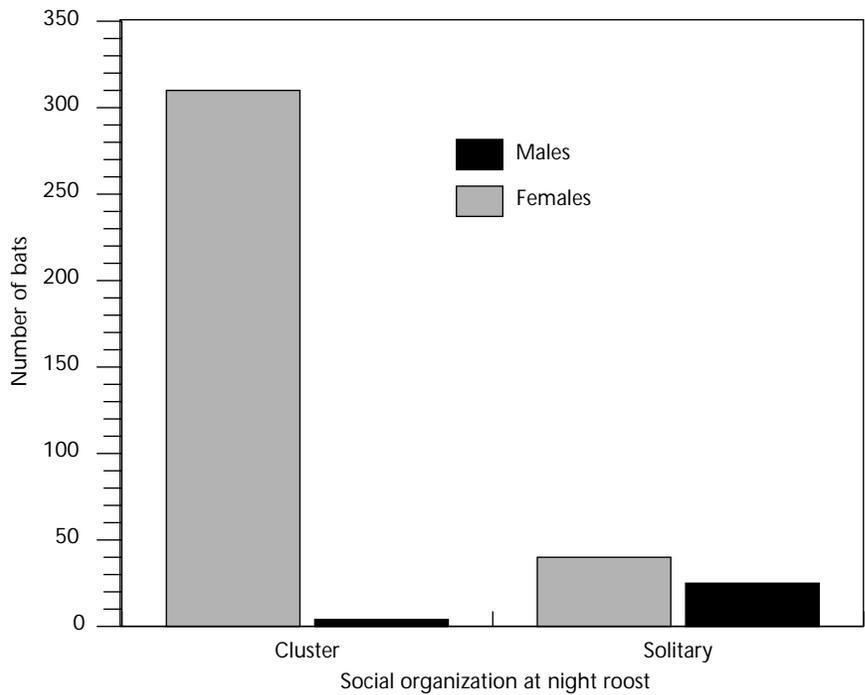


FIGURE 7 *Distribution of males and females captured at night roosts based on their association with clusters or as solitary individuals.*

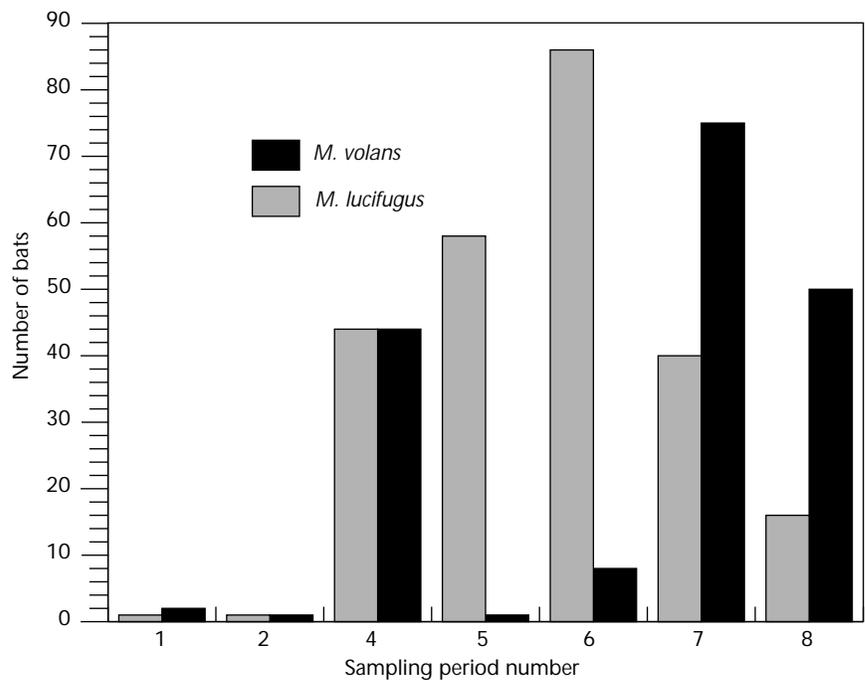


FIGURE 8 *Summary of the distribution of M. lucifugus and M. volans at night roosts during sampling periods covering 1 May to 30 August for 1993-1994. Sampling period # are as follows: #1 (1 May 1-15 May); #2 (16 May-31 May); #3 (1 June-15 June); #4 (16 June-30 June); #5 (1 July-15 July); #6 (16 July-31 July); #7 (1 August-15 August); #8 (16 August-31 August).*

I found significant differences in the capture rates of different species in the various sampling periods using the combined data for 1993–1994 ($\chi^2 = 184.6$, $p < 0.001$, $df = 6$). The largest numbers of *M. lucifugus* ($n = 206$) at night roosts occurred during July, with 58% of the females ($n = 74$) being pregnant or lactating. *M. volans* ($n = 169$) populations reached their maximum levels during the month of August, with 68% of the females ($n = 70$) being pregnant or lactating (Figure 8). A comparison of captures at the five bridges showed significant differences in the distribution of *M. volans* and *M. lucifugus* ($\chi^2 = 219.2$, $p < 0.001$, $df = 4$), with 94.8% ($n = 153$) of captures at the Blue River Reservoir Bridge being *M. lucifugus*. In contrast, *M. volans* accounted for 71.8% ($n = 238$) of bats captured at the four bridges located over streams (Figure 9).

Temporal Differences

Examination of temporal data indicated significant differences (Student's $t = 2.27$, $df = 32$, $p < 0.05$) in the number of minutes after sunset at which the maximum number of bats were observed at Quentin Creek Bridge ($\bar{X} \pm SE = 461.5 \pm 17.1$) and Blue River Reservoir Bridge (396.4 ± 21.7). Linear regression plots for the number of bats by minutes after sunset for two night roosts showed different patterns of occupancy. Quentin Creek Bridge, occupied primarily by *M. volans*, followed a linear fit indicating a steady increase in night roost activity through the night and into the late hours of the early morning. The bridge at Blue River Reservoir, where the population was dominated by *M. lucifugus*, conformed to a 2^o polynomial fit, with bat activity increasing rapidly, peaking around 375 minutes after sunset, followed by a rapid decline well before sunrise (Figure 10).

I monitored 12 clusters from formation to complete dispersal between 6 July and 25 August. These cluster analyses were made at two sites, the Blue River Reservoir Bridge and the Quentin Creek Bridge. Clusters observed at these two night roosts differed significantly in mean number of minutes after sunset when the clusters initially formed (Student's t , $t = 4.15$, $df = 9$, $p < 0.01$), the mean number of minutes clusters remained intact (Student's t , $t = 4.90$, $df = 9$, $p < 0.001$), and the time the last bat departed from the cluster (Student's t , $t = 2.29$, $df = 9$, $p = 0.05$; Table 3).

DISCUSSION

My results confirmed the work of previous studies (Anthony et al. 1981; Barclay 1982), which found that a significant portion of the nightly time budget for bats was taken up by night roosting. Given the importance of night roosting in the daily energy budget of some species of bats (Burnett and August 1981), locating warm, stable night roosts should be a high priority during a bat's nightly period of activity. Bridges that maintained higher temperatures over the course of the evening supported significantly larger numbers of bats compared to smaller, cooler bridges. Higher night roost temperatures translate into low metabolic rates for bats and a concurrent decrease in daily energy expenditures. Aggregating in night roosts further enhances these thermal savings by reducing metabolic rates for individual bats within a cluster (Burnett and August 1981; Kurta 1985; Roverud and Chappell 1991).

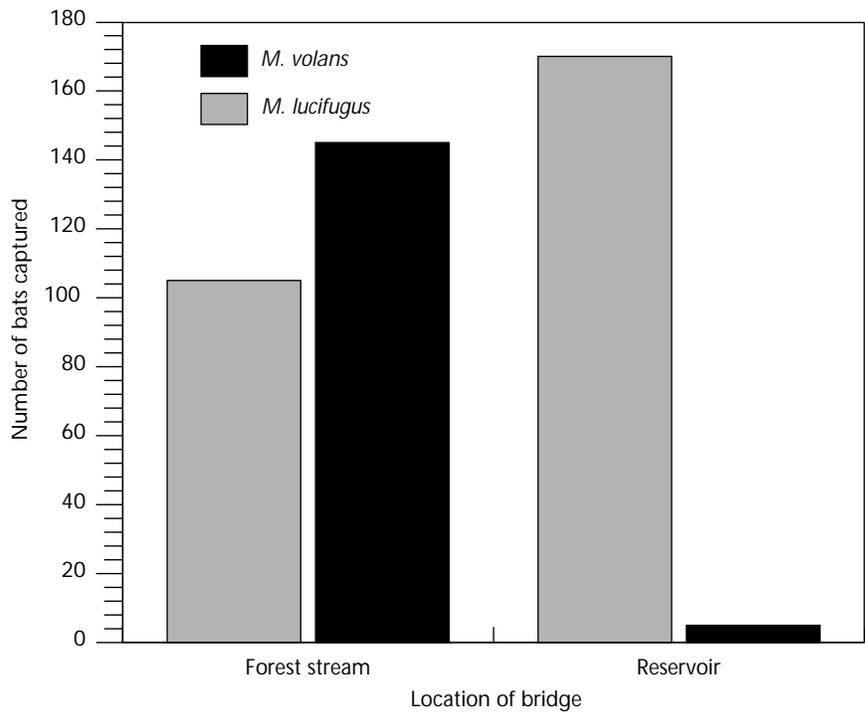


FIGURE 9 Distribution of *M. volans* and *M. lucifugus* at night roosts located over streams and the reservoir.

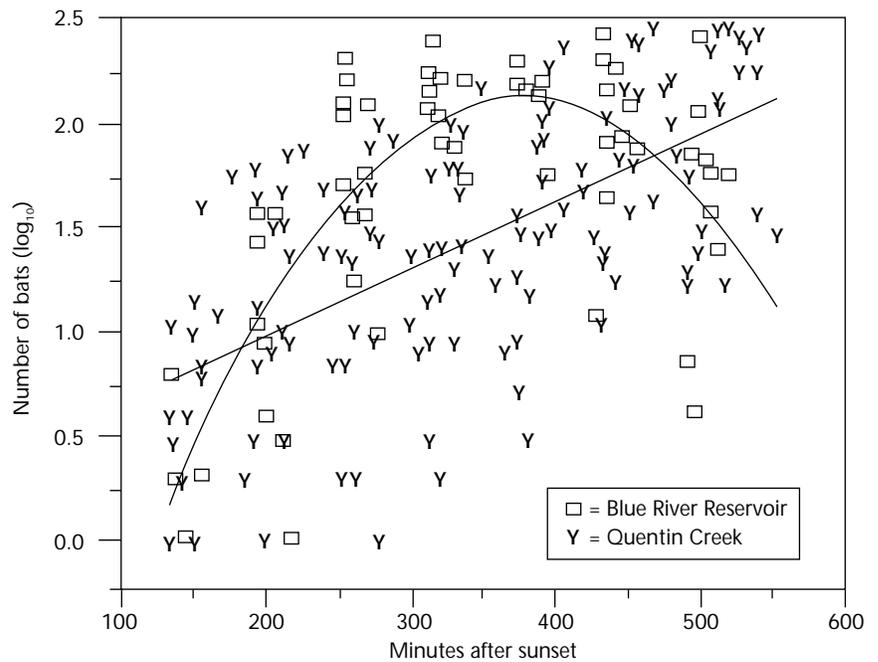


FIGURE 10 Linear regression of the number of bats (\log_{10}) by minutes after sunset for 1993-1994. The parabolic curve (polynomial fit -2 degrees) represents data points for Blue River Reservoir Bridge ($r^2 = 0.71$, $F = 98.9$, $p < 0.0001$, $df = 84$) and the linear fit ($r^2 = 0.39$, $F = 90.3$, $p < 0.0001$, $df = 141$) represents the data for Quentin Creek Bridge.

TABLE 3 Table shows the $\bar{X} \pm SE$ for the number of minutes after sunset for the start of a cluster, the $\bar{X} \pm SE$ of minutes for the duration of clusters and the $\bar{X} \pm SE$ minutes after sunset of the last departure for the clusters observed at Blue River Reservoir Bridge and Quentin Creek Bridge.

Roost name	n ^a	Start of cluster minutes after sunset	Duration of cluster total minutes	Last departure minutes after sunset
Blue River	7	215.96 ± 33.41	268.14 ± 17.20	345 ± 47.14
Quentin	4	446.0 ± 44.20	122.00 ± 23.78	524.50 ± 62.36

^a n = number of individual clusters analyzed.

Calculations of daily energy budgets indicate that a bat's energy expenditure during night roosting can be influenced by within-site variables, including roost temperature, duration of stay, and the decision to join a cluster (Burnett and August 1981; Kurta et al. 1989). While it appears that the bridges examined in this study fulfilled one of the requirements of a suitable night roost, namely, maintaining a temperature higher than ambient, bats that choose warmer bridges may achieve some savings in their daily energy expenditure. Night roosts that consistently maintain cooler temperatures can be expected to increase a bat's daily energy expenditure compared with warm locations as a result of increased metabolic resting rates (Roverud and Chappell 1991). The significantly higher number of bats at Blue River Reservoir and Quentin Creek Bridge indicated that bats using these night roosts may be minimizing the night roost energy component of their daily energy budget. Within each night roost site, further savings in energy can be achieved by using chambers with the highest temperatures. These metabolic savings can be further increased by clustering. Studies comparing resting metabolic rates of bats roosting alone versus that of bats associated with clusters (Kurta and Kunz 1988; Kurta 1985; Roverud and Chappell 1991) documented a significant reduction in metabolic rates for the latter group resulting from increased insulation and a corresponding reduction in thermal conductance.

The predominance of females at night roosts and their tendency to associate with clusters of other females as the season progressed is likely a response to the increased energy demands incurred during the later stages of pregnancy (Kurta et al. 1989). The correlation between peak occupancy rates and an increase in the number of females positively identified as pregnant for *M. lucifugus* and *M. volans* indicated that night roost populations were highest towards the later stages of pregnancy. The largest night roost populations for *M. volans* and *M. lucifugus* occurred during periods when the night roost temperatures were at their maximum. Other studies have shown a strong correlation between high roost temperatures and a corresponding decrease in the length of gestation periods resulting from accelerated fetal development (Racey 1982). The importance of these night roosts to pregnant females is further supported by studies showing that during the later stages of pregnancy, female bats may lose their ability to remain homeothermic (Studier et al. 1973) and experience a decrease in foraging success because of increased wing loading imposed by a growing fetus (Barclay 1989; Kalcounis and Brigham 1995; Kunz 1974). In combination, all of these factors make it evident that taking refuge in a warm

night roost is an effective strategy for pregnant females. Predictions based on the model I have presented, along with direct observations during this study, support the idea that pregnant females are selective in their choice of night roost with differing microclimates. Selection should be less critical for non-reproductive females.

Despite the apparent benefits of clustering on daily energy expenditures, adult males in almost all cases roosted alone. It has been suggested that solitary roosting and the use of torpor are strategies employed by male bats in the temperate regions to achieve reduced energy expenditures (Williams and Findley 1979). Unlike pregnant females, males are able to regularly enter torpor because they are not committed to maintaining the high metabolic rates and increased energy demands documented for pregnant and lactating females (Kurta et al. 1989; Tuttle 1976; Williams and Findley 1979). Because males are not bound by the energetic demands of pregnancy and lactation (Kurta et al. 1989; Racey 1982), the cost of roosting alone may be less than those incurred by associating with clusters, such as an increase in the risk of transmission of diseases or ectoparasites (Brown and Brown 1986) or increased levels of aggression. Despite their tendency to roost alone, males likely achieve some energetic savings by taking up residence at bridges. The appearance of males at the night roost may serve a secondary function. According to Trivers (1972), in mating systems where males provide no parental care, female reproductive success depends upon their ability to exploit resources as contrasted with male reproductive success, which is measured by their ability to gain access to females. The presence of adult males at night roosts may increase their reproductive success by allowing earlier access to females who become sexually receptive once the young are weaned.

Although warmer bridges supported greater numbers of bats compared with cooler sites, foraging areas and prey selection may be influenced by differences in night roost activity levels for the two species. Dietary differences exist between *M. volans* and *M. lucifugus* in this region (Whitaker et al. 1977). Dipterans account for 51.7% of the diet of *M. lucifugus* in western Oregon, with aquatic insects, such as chironomids, the most common prey item. In contrast, 87.2% of the diet of *M. volans* consists of moths (Whitaker et al. 1977).

Despite its preference for chironomids, *M. lucifugus* is opportunistic and eats a wide range of prey, often feeding in swarms of insects (Belwood and Fenton 1976; Anthony and Kunz 1977). The large, open area of slow-moving water at the reservoir, the high levels of feeding activity observed in the early evening at the bridge, and the predominance of *M. lucifugus* at this night roost suggested a spatial link between night roost sites and foraging areas. The bridge at Blue River Reservoir appeared to provide an ideal location for *M. lucifugus* because of its consistently high night roost temperatures and presumably greater prey availability. The lower numbers of *M. lucifugus* at the four other bridges spanning swift-moving streams may have been the result of several factors, including reduced levels of prey items, a more cluttered foraging habitat with less open water (Saunders and Barclay 1992), and areas where water noise could reduce bat feeding activity (von Frenckell and Barclay 1987). All of these factors, in combination, may have reduced the amount of suitable foraging habitat surrounding these bridges for *M. lucifugus* as compared

with the reservoir. The consequence of these factors could be a reduced capacity for supporting large numbers of *M. lucifugus* at bridges surrounded by a greater amount of forest canopy.

In contrast to the distribution of *M. lucifugus*, *M. volans* occurred in significantly higher numbers at night roosts over streams, but rarely at the Blue River Reservoir Bridge. Previous studies of foraging patterns for *M. volans* indicated that feeding occurs high in the forest canopy and along the edges of cliffs (Fenton and Bell 1979; Saunders and Barclay 1992; Whitaker et al. 1977). The restriction of *M. volans* to certain bridges suggests that the bats' preferred prey were more readily available around bridges located in the forest canopy as compared with the habitat surrounding the reservoir. The role of dietary differences and its influence on night roosting patterns for *M. lucifugus* and *M. volans* needs to be confirmed by investigating foraging patterns and diet.

A second potential influence on activity levels at night roosts may be the types and locations of day roosts selected by *M. lucifugus* and *M. volans*. If selecting a night roost with more favourable thermal conditions means travelling farther from the day roost, the savings achieved from a warmer night roost may be negated by increased commuting costs. A study of energy demands for pregnant and lactating *M. lucifugus* indicated that day roosting required over twice the energy when compared to night roosting (Kurta et al. 1989). This data would suggest that selection of a suitable day roost site may be an overriding consideration in terms of energy budgets when compared to selecting a thermally superior night roost. Operating under this scenario, a bat could be expected to trade-off higher energy expenditures by using a cooler night roost, provided that this site was in close proximity to a stable, thermally superior day roost. Analysis of day roost selection by *M. volans* is currently underway (P. Ormsbee, pers. comm.), and should provide information about the spatial relationship between night and day roost sites.

Differences in temporal activity patterns in *M. lucifugus* and *M. volans* may indicate that the social organization observed at night roosts serves different functions for these species. *M. lucifugus* arrived at their night roosts earlier after sunset, remained for significantly longer and left earlier, presumably to engage in a second feeding bout. Barclay (1991) found that aquatic insects, such as chironomids, a major component of the diet in *M. lucifugus*, are an ephemeral food source that emerge briefly in the early evening. The rapid increase in bats at the reservoir night roost may indicate that bats were responding to dwindling food supplies (Anthony et al. 1981). The benefits of group foraging become even more critical in *M. lucifugus*, which has a bimodal feeding pattern (Anthony and Kunz 1977) because the second feeding period occurs when prey levels are depressed (Barclay 1991). When faced with increasingly scarce prey resources, using the "collective ears" of many bats during foraging trips may serve to increase foraging success. Besides the energetic benefits of clustering, these aggregations may fulfil a secondary function by allowing cohorts to "cue in" on other bats at the night roost and improve their feeding success (Brown 1988; Krebs and Davies 1989).

This temporal pattern of activity at night roosts contrasts sharply with that of *M. volans*. *M. volans* arrived at their night roost later in the evening, stayed significantly less time and often left during or after the

morning twilight period. Combining these observations with evidence that *M. volans* is capable of flying at cooler temperatures (O'Farrell and Bradley 1977; Schowalter 1980) and forages for a substantial portion of the night (Warner 1985), suggests that this species devotes a greater percentage of its nightly time budget to foraging and less to night roosting. By aggregating at night roosts shortly before sunrise and synchronizing their departures to day roosts, aggregations of *M. volans* at bridges may serve an anti-predatory function by diluting the impact of potential predators, such as owls and hawks, on groups of bats returning to day roosts (Fenton et al. 1994; Krebs and Davies 1989).

Seasonal differences in night roost populations of *M. lucifugus* and *M. volans* likely reflect the reproductive ecology of the two species. The gradual increase in pregnant *M. lucifugus* at night roosts during June and July, the rapid decline in their numbers, and the appearance of lactating females in August, probably signals the onset of parturition during late July and August (Anthony et al. 1981; Barclay 1982). These dates of parturition are later than those observed in other studies (Anthony and Kunz 1977; Barclay and Cash 1985), and could be the consequence of lower day-time ambient temperatures in this region and the use of natural structures as maternity roosts, sites that perhaps produce less favourable temperature conditions than artificial roosts. The significant decline in *M. volans* at night roosts during July and the reappearance of large numbers of lactating females in August suggests that some births occurred during their absence from night roosts in July. The presence of pregnant and lactating females at night roosts well into mid-August supports other studies that indicate births in *M. volans* may occur throughout the summer (Warner and Czaplewski 1984).

In conclusion, higher levels of night roost activity were found at bridges that sustained higher temperatures throughout the evening. It appears that not all bridges are created equal, with larger structures absorbing greater amounts of solar radiation and retaining heat for longer periods of time over the course of the evening. Differential use of warmer night roosts reflects the fact that these sites reduce energy expenditures for bats when foraging success declines or declining ambient temperature inhibits flight. I found that the highest levels of night roost activity correspond to times with the largest proportion of pregnant females in the population of both species. Females of both species enhance energy savings by associating in clusters, while males avoid clustering. I attribute spatial and temporal differences in *M. lucifugus* and *M. volans* observed in this study to differences in foraging strategies, prey selection, reproductive biology, and the role of social groupings at night roosts.

Several important aspects concerning the management and monitoring of bat populations have emerged from this study. First, bridges do provide valuable night roosting habitats for many species of bats. This fact is useful to wildlife biologists who wish to obtain easy access to large numbers of bats. Given the distinct differences in seasonal, spatial, and temporal patterns of night roost activity by *M. lucifugus* and *M. volans*, wildlife biologists should be able to accurately schedule surveys at selected bridge sites to determine the presence and variety of species in an area, as well as the reproductive status of night roost populations. Second, this study has yielded information on the types of bridges and the conditions preferred

as night roost sites for several species of bats. Design and construction of any new bridges could be carried out in such a way to enhance the availability of additional night roost sites. While I have shown that bridges can serve as valuable night roost sites, additional research is needed to locate and quantify the importance of natural night roosts to a community of bats.

ACKNOWLEDGEMENTS

I would like to thank Brock Fenton for his moral and financial backing for this research in fulfilment of my Master's Thesis at York University. I am grateful to Bridget Stutchbury and Dawn Bazley for their critical feedback and insights as members of my thesis committee. I also want to thank Pat Ormsbee, of the Willamette National Forest for her support of my work and for securing funding from her agency that made this project possible. I want to acknowledge the long hours and hard work put in by the devoted members of the bat crew: A. Hart, M. Yoder, J. Fittipaldi, M. Rowan, J. Humphreys, A. Black, C. Barnes, R. Tallmadge, S. Thorin, K. Baker, and J. Ott. A special thanks to the staff at H.J. Andrews Experimental Forest for allowing us to use their facilities during the course of this work. I would like to express my appreciation to Dr. Larry Irvin for acting as my statistical consultant. Finally, this project would not have come about if not for the support, devotion, and extra-human tolerance of my wife (significant other for the politically correct), Anne Todd, and my two sons, Todd and Cody Perlmeter. If possible, I would gladly issue my "Master of Science" to my deserving family. This research was funded by the National Sciences and Engineering Research Council of Canada (NSERCC) and the Willamette National Forest.

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Night Roost Sampling: A Window on the Forest Bat Community in Northern California

E. D. PIERSON, W. E. RAINEY, AND R. M. MILLER

ABSTRACT

Surveys of night roosts in anthropogenic features, particularly concrete bridges, offer an efficient, but species-selective method for examining the bat community in forested landscapes. In the upper Sacramento River canyon some species (*Antrozous pallidus*, *Eptesicus fuscus*, *Myotis volans*, *Corynorhinus townsendii*) were captured more frequently per person-hour of sampling in night roosts than by mist netting over water, while others (e.g., *Myotis californicus*, *Myotis ciliolabrum*, *Lasiurus* sp., *Lasionycteris noctivagans*, *Euderma maculatum*) never used these sites. Protected, but open-bridge night roosts remain warmer than ambient through most of the night over the summer. Recaptures of *Myotis yumanensis* and small numbers of *A. pallidus*, *E. fuscus*, and *M. volans* indicated fidelity to night roosts through four years of survey. Capture at aggregated night roosts permits long-term monitoring without disturbance to maternity roosts. For species that roost in trees by day, particularly in areas of timber harvest, bridge night roosts may persist longer than day roosts, and offer continuing access to marked populations that switch among day roosts.

INTRODUCTION

Many bat species use night roosting sites, which are separate from day roosts and likely serve both physiological and sociobiological functions (Barclay 1982; Kunz 1982; Lewis 1994). Kunz (1982) discussed four night roost types: resting places, feeding perches (used by sallying predators), feeding roosts (sites where food is consumed), and calling roosts (used for mating displays). For North American temperate-zone bats, the best-characterized night roosts are aggregated resting places. For many species, prey ingestion rates exceed digestion rates. In night roosts bats can digest food between foraging bouts without the energetic costs of returning to the day roost. Sites selected as night roosts generally maintain night-time temperatures greater than ambient, offering thermoregulatory benefits (Anthony et al. 1981; Barclay 1982).

Anthony et al. (1981) noted that for *Myotis lucifugus* in the north-eastern United States, night roost sites are less exposed than day roosts.

The opposite appears to be true in parts of the western U.S., where identified night roosts are typically in environmentally buffered, but exposed locations—e.g., inside entrances of abandoned mines, on ceilings of old buildings, and under bridges (Barbour and Davis 1969; Lewis 1994; O’Shea and Vaughan 1977). Bridges (complex structures with high thermal inertia often close to water) are widely used as both day and night roosts (Constantine 1961; Cross and Clayton 1995; Davis and Cockrum 1963; Frazee and Wilkins 1990; Hayward 1970; Hirshfield et al. 1977; Kunz 1982; Lewis 1994).

Assessing species diversity and relative abundance of a forest bat assemblage presents tactical challenges. Recent research using radio-telemetry shows that in forested landscapes in western North America, most bat species (including those best known from studies on building roosts) roost by day in trees (Brigham 1991; Crampton 1994; Grindal 1994; Kalcounis 1994; Morrell et al. 1994; Rainey et al. 1993; Rainey and Pierson 1995; this volume). Tree roosts are generally located in cavities or under bark, often over 10 m above the ground. Given the dispersion of these cryptic roosting sites, and evidence that even in mesic habitats many species travel substantial distances to drink and forage near surface water (Thomas 1988), sampling bat communities typically involves intercepting animals during their nightly activity cycle. Common inventory methods are mist netting near ground level along flyways or areas of concentrated foraging (i.e., near water), monitoring echolocation calls, or locating roosts (Cross 1986; Kunz and Kurta 1988; Thomas and LaVal 1988). Given the differential detectability of species by different methods, some combination is usually required to obtain an overview. This paper examines the efficiency and selectivity of night roost surveys, particularly of bridges, as one approach to sampling species diversity and relative abundance in areas transected by roads.

STUDY AREA

This study was conducted from 1991 to 1995 in northern California (Siskiyou and Shasta counties), along 60 km of the upper Sacramento River (approximately 41°N lat., 122°E long.), between Lakehead and Dunsmuir, from 320 m to 730 m elevation. Within this dissected, high-relief portion of the drainage basin, the habitat is primarily montane hardwood/conifer, dominated by ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), and black oak (*Quercus kelloggii*) (Mayer and Laudenslayer 1988). At lower elevations, grey pine (*Pinus sabiniana*) and Pacific madrone (*Arbutus menziesii*) become common. On the higher slopes (approximately 1800 m elevation), Jeffrey pine (*Pinus jeffreyi*), incense cedar (*Libocedrus decurrens*), red fir (*Abies magnifica*), and white fir (*Abies concolor*) are also common.

The primary historical and current land use is timber production. The resulting landscape is a complex, largely anthropogenic, mosaic dominated by regenerating timber stands of varied ages. Limited development is concentrated along the major transportation corridor (both a railroad and four-lane, interstate highway) paralleling the river in the canyon floor.

Site Selection In July 1991 a railroad accident released a tank-car load of metam sodium, a soil fumigant, into the Sacramento River above Dunsmuir, killing most macroscopic life in the river up to 60 km south of the spill site (Calif. Dept. Fish and Game 1993). Sampling sites used for this analysis were selected in the context of a larger study examining the impacts of this spill on bat populations. All were located within a few hundred metres of the river.

METHODS

- Night Roost Sampling Bridges, abandoned buildings, and other possible night roost sites (generally on public lands) within 500 m of the Sacramento River in the study section, were examined for evidence of bats (e.g., guano, urine stains, or roosting bats). Bridges included overcrossings along the interstate highway and older bridges on nearby secondary or abandoned roads.
- After initial surveys in the summer of 1991 and the spring of 1992, nine bridges, which were consistently used as night roosts, were selected for monitoring, conducted primarily between June and September. These sites were approached at night (generally between 23:00 and 2:00 h), and roosting animals were captured in rectangular-frame hand nets mounted on telescoping painters' poles. Temporary fabric curtains were used to reduce escape at one large *M. yumanensis* night roost under an abandoned bridge and, once contained, bats were captured with hand nets and a harp trap.
- To compare ambient with night roost temperatures, a miniature digital temperature logger with an internal thermistor (Onset Computer Model ST1B08; equilibration time 15 minutes, maximum error 0.5°C, sampling interval 30 minutes) was attached to the concrete in a night roost site on an interstate highway bridge crossing a secondary road. A second logger simultaneously recorded ambient in shade nearby.
- Mist Netting Mist nets were set on sectional poles over open water (sites chosen for depth <1.5 m and low surface turbulence). Nets typically spanned the width of the river or tributary streams near their confluence with the river. Nets were opened after local sunset and closely tended until midnight. The sample treated here includes 47 nights of netting at 15 stations along the 60-km section. Stations were typically sampled no more than once per year; five stations were sampled in all five years. Net area deployed each night (overall mean = 173 m²) varied with both site constraints (e.g., narrow, sub-canopy streams) and personnel available to extract bats.
- Handling of Animals In both mist netting and night roost surveys, after identification and measurement, most species were fitted with 2.8- or 3.5-mm, numbered, lipped, metal forearm bands (British Mammal Society or Lambournes' Ltd). Because of concerns about band effects, *Lasiurus* sp., *Corynorhinus townsendii* and species <4.0 g body weight were typically not marked. Consistent with the findings of Herd and Fenton (1983), morphological overlap in co-occurring *M. yumanensis* and *M. lucifugus* left specific identification of some individuals unresolved.

Sampling Effort

To compare efficiency of capture by mist netting at foraging areas and hand netting at night roosts, effort was evaluated by examining the number of bats captured per person hour. To standardize the estimates, it was assumed that mist netting required four persons (although the actual crew was frequently larger), and night roost sampling required two persons (although occasionally the surveys were conducted by one). For mist netting, time was calculated as the actual number of hours that the nets were open, plus 3 hours per netting station per night for set up and disassembly (although setting nets over a 30-m wide, swift river frequently took longer), and night roost sampling was estimated to take 20 minutes for capture, plus 10 minutes for preparation, per site. For two night roosts that harboured large aggregations, we used actual site preparation and capture times.

RESULTS

Structural and Environmental Features of Night Roosts

The predominant bridge designs in the study area on highways or secondary roads were either concrete girder or the more recent concrete box girder. There were two types of concrete girder bridges. The older one, found in all those abandoned to vehicular traffic and a few active bridges, had only longitudinal girders extending below the bridge deck (Figure 1 of Davis and Cockrum 1963). The more common type had both longitudinal and transverse girders, producing (as noted by Lewis 1994) a grid of open, rectangular, concrete cells extending from the underside of the bridge. Box girder bridges have an enclosed, flat underside that offers little or no sheltered vertical surface to which bats might cling.

Thirteen of the 16 concrete girder bridges examined were repeatedly used as night roosts by at least small numbers of bats. Of the three not used, one was brightly lit. Five of the girder bridges harbouring night roosts were abandoned to traffic, one was on a lightly travelled frontage road, and seven were on the interstate highway over intersecting roads. Bats using the latter had almost continuous heavy vehicular traffic overhead, and moderate to almost no traffic beneath. Night roosting was found in one of 11 box girder bridges; in this instance adjoining portions of the north and south interstate lanes had created a 2-m-wide crevice that harboured the bats.

Although some accessible expansion-joint crevices were present, night roost sites were always on open surfaces in areas protected from wind and rain. Bats were in ventral contact with the vertical sides of the girders at the bridge deck junction, often in a corner. In the case of interstate highway overcrossings, occupied sites were separated from the secondary road by support columns. Bats selected sites that were 2–6 m above the ground, typically favouring the highest possible roosting sites. Figure 1 illustrates thermal buffering provided by the concrete girder structure at one of the interstate bridge roosts (Soda Creek) during July 1995. While the monthly mean bridge roost temperature varies 4°C daily and does not drop below 23°C, ambient temperature varies more than 16°C. For at least late June through September, the roost had a positive temperature differential all night (>10°C from midnight to dawn; all data not shown).

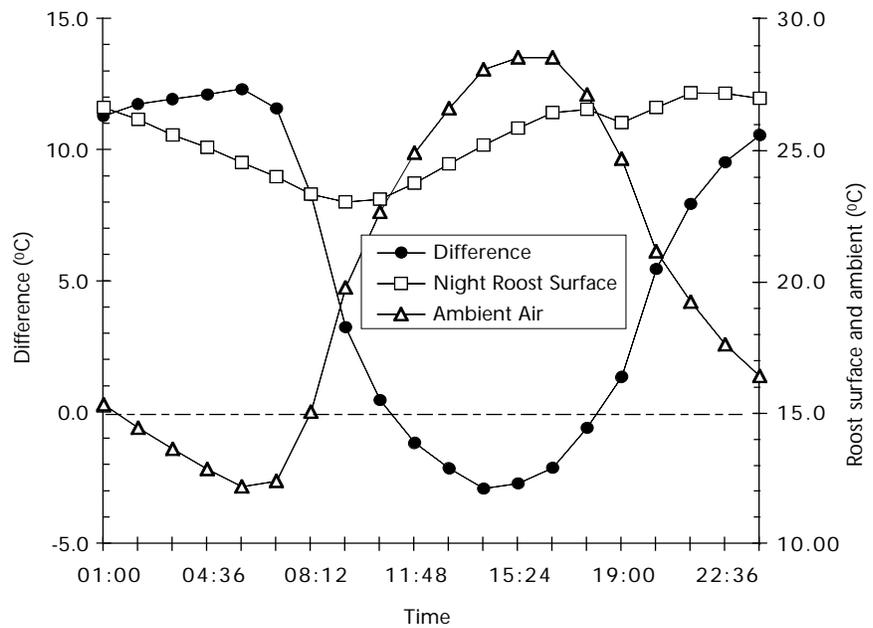


FIGURE 1 Daily cycle of ambient and surface night roost temperatures, and the differential (roost-ambient) at the Soda Creek interstate highway bridge roost, plotting monthly means for July 1995.

Only one building, an abandoned house, was identified as a night roost, with bats using several sites, most reliably the attic. A number of tributary streams reached the Sacramento River via large-diameter, concrete-lined tunnels up to several hundred metres long. Bats were not observed night roosting in these relatively cool sites.

Species Diversity,
Relative Abundance,
and Capture
Efficiency

In this study, 17 species of bats were documented as occurring along the upper Sacramento River (Table 1). Fifteen were netted over water; nine of these were also captured at night roosts; two were detected only acoustically (*Eumops perotis*) or acoustically and visually (*Euderma maculatum*). Eight of the 17 species (47%) were never observed at night roosts.

Although 4.5 times as many person hours were expended on mist netting, some species (*M. yumanensis*, *Antrozous pallidus*, *Eptesicus fuscus*, and *Myotis volans*) were captured more times at night roosts than in mist nets (Figure 2). Table 2 lists the five most commonly observed species by both methods. Only two, *M. yumanensis* and *M. lucifugus*, appear on both lists, with *M. yumanensis* being the most frequent by either method. Two of the species most commonly observed in mist nets (*Lasionycteris noctivagans* and *Myotis californicus*) were never observed in bridge night roosts. *C. townsendii*, which was very rare by both sampling methods, being taken only once in a mist net and found at only one night roost site, was known from five day roosts, including two maternity sites (an abandoned train tunnel and an abandoned mine) within the study area. These roosts were located by day roost surveys.

Table 3 gives the relative abundance of six species that were sampled by both mist netting and night roost surveys. Three species, *A. pallidus*, *C. townsendii*, and *M. yumanensis*, were excluded from this comparison because they were selectively targeted for focal studies at particular night

TABLE 1 Primary detection methods for 17 bat species observed along the upper Sacramento River drainage.

	Mist nets	Night roosts	Acoustic
<i>Antrozous pallidus</i>	×	×	
<i>Corynorhinus townsendii</i>	×	×	
<i>Eptesicus fuscus</i>	×	×	
<i>Euderma maculatum</i>			× ^a
<i>Eumops perotis</i>			× ^a
<i>Lasionycteris noctivagans</i>	×		
<i>Lasiurus blossevillii</i>	×		
<i>Lasiurus cinereus</i>	×		
<i>Myotis californicus</i>	×		
<i>Myotis ciliolabrum</i>	×		
<i>Myotis evotis</i>	×	×	
<i>Myotis thysanodes</i>	×	×	
<i>Myotis lucifugus</i>	×	×	
<i>Myotis volans</i>	×	×	
<i>Myotis yumanensis</i>	×	×	
<i>Pipistrellus hesperus</i>	×		
<i>Tadarida brasiliensis</i>	×	×	

^a Species which could be identified acoustically with certainty.

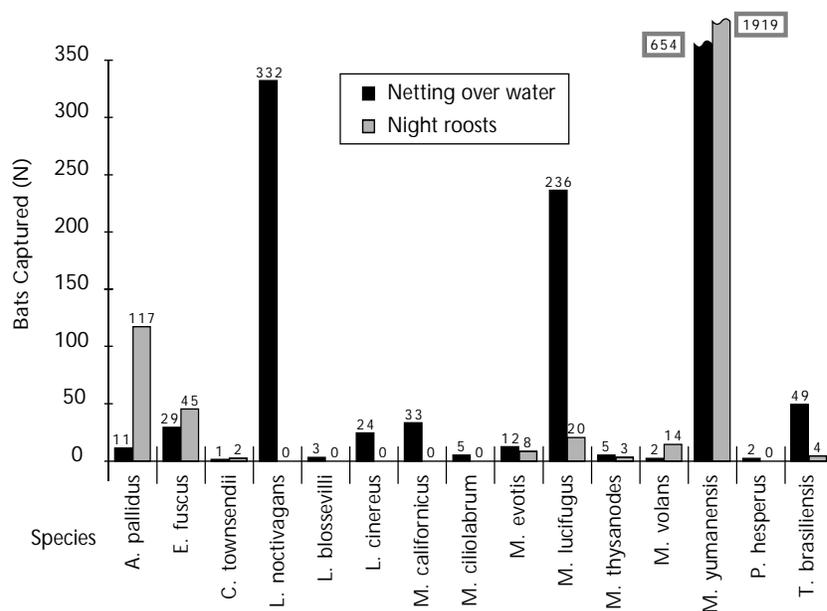


FIGURE 2 Total number of bat captures by species in mist nets and night roosts along the upper Sacramento River (1991–1995).

roosts. Four species, *E. fuscus*, *Myotis evotis*, *Myotis thysanodes*, and *M. volans*, were relatively more abundant in the night roost surveys, whereas *M. lucifugus* and *T. brasiliensis* were relatively more abundant in the mist netting surveys.

Pooling data across sites and nights, catch/unit effort was 6.9 times greater at night roosts than by mist net. Eleven bats were captured per

TABLE 2 Five species most frequently observed in mist nets and night roosts, listed in order of abundance.

Mist nets	Night roosts
<i>Myotis yumanensis</i>	<i>Myotis yumanensis</i>
<i>Lasionycteris noctivagans</i>	<i>Antrozous pallidus</i>
<i>Myotis lucifugus</i>	<i>Eptesicus fuscus</i>
<i>Tadarida brasiliensis</i>	<i>Myotis lucifugus</i>
<i>Myotis californicus</i>	<i>Myotis volans</i>

TABLE 3 Relative abundance of bats species captured randomly in mist nets and at night roosts.

Species	Nets		Night roosts	
	Ratio	n	Ratio	n
<i>E. fuscus</i>	0.087	29	0.479	45
<i>M. evotis</i>	0.036	12	0.085	8
<i>M. lucifugus</i>	0.709	236	0.213	20
<i>M. thysanodes</i>	0.015	5	0.032	3
<i>M. volans</i>	0.006	2	0.149	14
<i>T. brasiliensis</i>	0.147	49	0.043	4
Totals	1.000	333	1.000	94

person hour at night roosts (2134 bats for 194 hours) versus only 1.7 in mist nets (1399 bats for 780 hours). Depending on the time of night, season, weather, and species, capture success in night roosts varied. When warm and alert the bats could fly as the hand net approached them; when torpid they could be quite slow to drop into a net.

Species Distribution
Among Night Roost
Sites

Three bridges, all abandoned or little used, housed substantial night roosting aggregations (one of >30 *A. pallidus*, two of 250–450 *M. yumanensis*; Table 4). Two other abandoned bridges, not monitored on a regular basis, had smaller (<100) *M. yumanensis* aggregations. All these aggregations were comprised primarily of adult females, and after mid-summer, volant young (although the *A. pallidus* roost included adult males).

Although none of the interstate highway structures supported large, colonial night roosts, they yielded greater diversity. The number of species found under a particular bridge varied from one to six. Also, the likelihood of encountering particular species varied. *M. yumanensis* was the species most commonly encountered. *E. fuscus* was found under all the interstate highway bridges, and some of the older ones. *M. volans* was found under more than half the bridges. Although *A. pallidus* was found primarily at one colonial night roost, individuals were occasionally found at four other bridges. By contrast, *M. lucifugus* and *M. thysanodes* were found under only two bridges. One of the *M. thysanodes* sites was only a few hundred metres from a building day roost.

The small numbers found simultaneously under the interstate bridges (generally 1–10, with up to 25 *M. yumanensis*) often included several species

TABLE 4 Distribution of bat species among night roost sites.

	Species									Total no. species
	<i>A. pallidus</i>	<i>C. townsendii</i>	<i>E. fuscus</i>	<i>M. evotis</i>	<i>M. thysanodes</i>	<i>M. lucifugus</i>	<i>M. volans</i>	<i>M. yumanensis</i>	<i>T. brasiliensis</i>	
<i>Interstate Highway Bridge</i>										
Castle Ck. I-5			×	×			×	×		4
Conant I-5	×		×	×			×			4
Flume Ck. I-5			×	×	×		×	×		5
Panorama Way I-5			×							1
Sims I-5	×		×			×	×	×		5
Soda Ck. I-5	×		×	×	×		×	×		6
<i>Abandoned or Access Road Bridge</i>										
Boulder Ck.			×			×		C		3
Gibson Rd.	C							×	×	3
Shotgun Ck.	×		×				×	C		4
<i>Building</i>										
La Moine House		×						×		2
Total no. sites	5	1	8	4	2	2	6	8	1	

× = individuals or small groups; C = colonial night roosts.

that typically roosted separately. Individuals captured at these sites included adults of both sexes, plus volant, and occasionally non-volant, young.

C. townsendii was found night roosting only in the attic of one abandoned house. Although this site never contained more than a few individuals at any one time, the species could typically be found there.

Recapture Rates and Site Fidelity

The overall recapture rate was markedly higher at night roost sites than in mist nets. Of the 1399 mist net captures only 58 (4.2%) had been previously banded; whereas 638 of 2134 night roosts captures (29.9%) were recaptures.

Recaptures for the three species most commonly encountered in night roosts, *A. pallidus*, *E. fuscus*, and *M. yumanensis*, show substantial year-to-year roost fidelity. This is best documented for *M. yumanensis* at the Shotgun Creek night roost, which was sampled once per year (in late August), 1991–1995. With the exception of the first year, when about 25% of the animals were captured, over 90% of the animals present were captured in each survey. From a total of 608 recaptures at the site, 506 (83%) were originally banded there, and the proportion increased each year (Figure 3). Figure 4 shows the distribution of intervals between initial capture at this site and recapture events there.

For 93 banded *A. pallidus*, all 18 individuals recaptured at night roosts had been originally captured there or in nets less than 100 m away. Three individuals were caught three times; for two of them there was at least 10 months between each recapture event. While virtually all year-to-year night roost recaptures of *M. yumanensis* were female, an adult male *A. pallidus* was recaptured two years after initial capture.

For *E. fuscus*, night roosting aggregations larger than presumed mother-young pairs were not observed and many individuals, including all of the

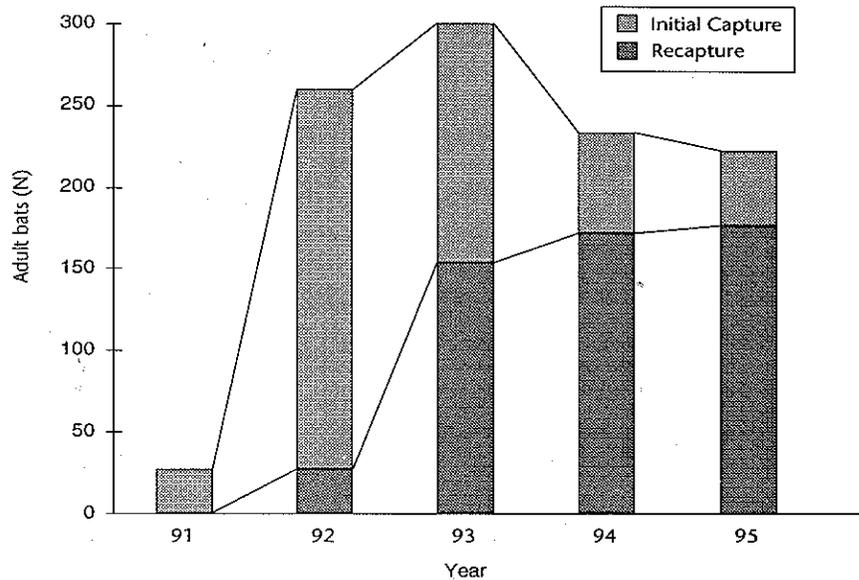


FIGURE 3 Number of adult female *M. yumanensis* initially captured and recaptured at Shotgun Creek bridge night roost, 1991 through 1995.

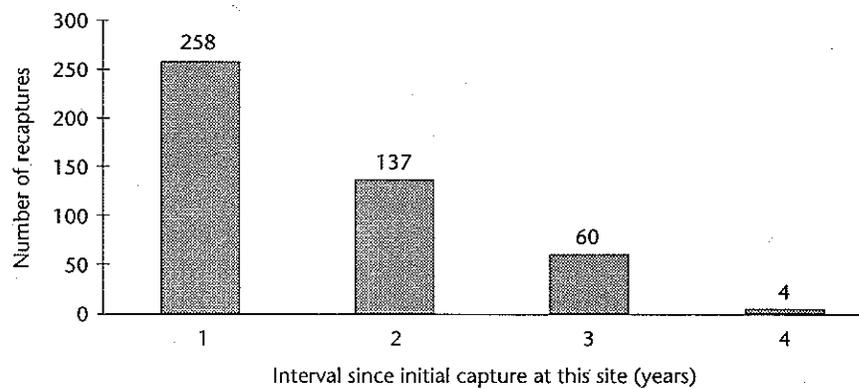


FIGURE 4 Distribution of intervals in years between initial capture at Shotgun Creek bridge night roost and any subsequent recapture there for *Myotis* sp., 1991-1995.

males captured, were solitary. Five out of 43 banded *E. fuscus* were recaptured in night roosts. Three were recaptured at the same bridge, one at a different bridge (4.4 km away), and one had originally been captured in a net 1.8 km away. One adult male was captured four times between 1992 and 1995 at the same bridge night roost. A single adult female *M. volans* was recaptured two years later at the same interstate highway bridge.

DISCUSSION

Function of Night Roosts and Role of Bridge Structure

All night roosts in this study were located close to the Sacramento River, identified by netting, radio-tracking, and diet analyses as a major foraging corridor for the bat community in this drainage basin (unpub. obs.). This

is consistent with the role of night roosts as resting places for digestion between foraging bouts, although they may also have additional sociobiological functions (Kunz 1982; Lewis 1994).

The observation that concrete girder bridges were used as night roosts and unmodified box girder bridges were not, parallels Lewis's findings (1994) for *A. pallidus* in Oregon, and suggests that bridge structure plays an important role in roost selection. Occupied sites offer vertical surfaces with enough texture for bats to cling to and maintain ventral contact. Although we did not measure relevant parameters, the "cells" typically selected in the gridwork of longitudinal and transverse girders beneath the bridge deck appear well buffered against wind, and partially isolated from the sporadic lights and sound of vehicles passing under the bridge. Bats clearly accommodate to the episodic, subjectively intense, partly audible (to humans) vibration transmitted through the structure from traffic on the bridge deck above. Occupied sites have ready flight access, but are sufficiently high to protect torpid bats from all terrestrial predators. Our temperature data suggest the large, insulated area of the bridge deck and the thermal inertia of these massive structures offer substantial passive thermal buffering, even to solitary night roosting bats.

Notably, the only bridges that harboured substantial aggregations, including large numbers of mother-young pairs (deduced by differing pelage colour), were abandoned or little used. All these bridges crossed streams rather than roads, so there was no vehicular traffic beneath. A physical feature of older concrete bridges that might make them suitable for bats, especially less dextrous young, is more irregular surface texture generated by rougher casting forms, weathering, and efflorescence. In seeking explanations for larger aggregations on older bridges, we should not ignore, however, the role of history for colonies of long-lived animals showing high site fidelity. A potentially important difference between the interstate bridges with low bat numbers and the abandoned bridges is that the latter have been part of the landscape for 50 years longer.

Species Diversity and Relative Abundance

Night roost captures offered relatively efficient access to a subset of the species identified by contemporaneous mist netting and acoustic surveys in a forested area. No species were captured only in night roosts, but some, particularly *A. pallidus*, *E. fuscus*, and *M. volans*, were most readily detected there. Other species were under-represented, e.g., both net captures and acoustic monitoring indicated that *T. brasiliensis* was locally common, yet only scattered individuals were captured at night roosts. Day roost surveys indicated that *C. townsendii* is likely more common in the area than revealed by netting or night roost surveys.

Certainly bridge design, alternative habitat, climate, and season influence what, if any, bat species might be found night roosting along highways elsewhere. For example, we never observed *M. californicus* in a bridge night roost, but it uses them in Oregon (M. Perkins, pers. comm.). Night roosting *E. fuscus* in this study were typically scattered individuals, yet we have observed aggregations (over 75 individuals) at a number of other bridge night roosts in California (unpubl. obs.). Although some studies have suggested that *T. brasiliensis* does not generally night roost in localities separate from the day roost (Krutzsch 1955; Hirshfield et al.

1977), we have observed a night roost of several thousand *T. brasiliensis* in a lava tube about 17 km northeast of the current survey area.

Bridge night roosting does appear to be widespread for *A. pallidus* and *M. yumanensis* (Barbour and Davis 1969; Cross and Clayton 1995; Lewis 1994, pers. obs.), and may be a reasonable indicator of the presence/absence of these species in an area. By contrast, we know of no references to night roosting in structures by the tree and cliff roosting species absent from night roosts in our study area (i.e., *E. maculatum*, *E. perotis*, *L. noctivagans*, *Lasiurus blossevillii*, *Lasiurus cinereus*, and *Pipistrellus hesperus*).

Site Fidelity

Although site fidelity to maternity roosts has been well documented for a number of species (see Kunz 1982 for a review), little evidence has accumulated for night roosts, particularly those that are geographically separate from day roosts. Kunz (1982) states that bats are opportunistic in their choice of night roosts, thus implying that site fidelity would be low. Lewis (1994) has recently reported night-to-night and year-to-year fidelity to night roosts in a two-year study of *A. pallidus*. In the present study, year-to-year night roost fidelity for *A. pallidus*, *E. fuscus*, *M. volans*, and *M. yumanensis* was observed over varied periods up to four years.

The decreasing proportion of unbanded adult *M. yumanensis* (Figure 3) with each year after 1992 suggests that a single late-season, mass capture per year in a night roost is sufficient to band a large proportion of young (i.e., most individuals in the population are present in the night roost after midnight on an arbitrarily chosen night in August) and that movement of adults from other unmarked night roosts (known to occur within a few km) is infrequent.

Advantages and Limitations of Bridge Roost Surveys

The comparative ease with which night roosts, especially bridges, can be identified and sampled has not been explicitly acknowledged in the literature. The method is simple, requiring only hand nets and lights. Bats are not tangled in nets, so handling time, and presumably stress, is generally lower than for netting. The association of night roosts with roads typically allows convenient access. Also, when roads follow rivers, bridge surveys can provide a distributed series of sampling stations along an altitudinal habitat transect.

The evidence of within-year and between-year fidelity to night roosts for several species means that night roost aggregations offer a convenient alternative to more disturbance-sensitive maternity roosts for long-term monitoring of many aspects of reproduction and demography. In a forested setting, where day roosts may be both relatively inaccessible (i.e., over 10 m high inside a tree cavity) and occupied for short intervals, night roosts could offer the best opportunity for following a population over time. Particularly in landscape with extensive, ongoing timber harvest, bridge night roost sites probably persist over longer intervals than do day roosts.

The primary limitation of the bridge roost surveys is that they only sample a subset of the species present in the community (in this study, nine of 17). Adequate bat community inventory requires a combination of techniques. Also, fortunately, some areas still lack both roads and bridges.

ACKNOWLEDGEMENTS

We would like to thank M. Colberg, J. Miller, J. Siperek, P. Pridmore, and a number of short-term volunteers who assisted in surveys. We also thank California Department of Transportation, Southern Pacific Corporation, and other landowners for temporary access for surveys. Bat capture was conducted under a memorandum of understanding with California Department of Fish and Game (DFG). Most of the field research was supported by the DFG Cantara Program.

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Does Competition for Roosts Influence Bat Distribution in a Managed Forest?

J. MARK PERKINS

ABSTRACT

Previous studies disagree regarding the mechanism that determines distributions of nearctic bat species. Many papers suggest that competition for foraging areas is important and is dictated by morphological characters or roost diversity. Here, I present evidence that suggests that local bat distribution, diversity, and population size in managed forests are related to interspecific competition for limited roost sites, and to intraspecific division by sex that depends on local population numbers.

INTRODUCTION

Findley (1993) summarized relationships between bat morphology, diet, and ecological niches to define a bat community in attribute space. Using work of Findley and Wilson (1982), Findley and Black (1983), and Aldridge and Rautenbach (1987), Findley states “. . . it is possible to have a reasonable amount of confidence in the ability of morphology to provide an insight into the feeding and foraging of insectivorous bats. Bat reproduction, occurrence, and abundance are related to food abundance, and in that sense food is clearly limiting to animals.” Humphrey (1975), however, found a strong correlation between the diversity of physical structure and the diversity and richness of colonial bats. Perkins (1993) reported that the distribution of bat species in a nearctic managed forest is not random, and speculated that forest bat distribution is a result of roost availability, insect concentrations, or competition between species resulting in displacement. Perkins and Peterson (1995) concluded that the distribution of reproductive female bats in a managed forest was affected by availability of roosts. In areas where harvest of large, older trees was highest, statistical analysis indicated a significant over-representation of the largest bat species. In areas where timber harvest was non-existent or minimal, the only competition exhibited at foraging sites was between the three species that forage exclusively or primarily on moths (*Corynorhinus townsendii*, *Myotis thysanodes*, *Myotis volans*). In contrast, Bell (1980) reported no foraging competition between paired bat species at concentrated insect patches in similar forested and Great Basin habitat.

Here, I examine data regarding male and female distribution, prey, and roost selection in a managed forest. I hypothesized that (1) the males forage separately from females of the same species; and (2) the determinant of the presence of any paired species at foraging sites is not solely foraging competition, but also involves roost availability.

STUDY SITE

My study area is in northeastern Oregon on the Wallowa-Whitman National Forest (44° 44' to 46° 00'N, 116° 30' to 117° 45'W; Figure 1). I sampled 140 sites distributed arbitrarily throughout four ranger districts: Hells Canyon National Recreation Area, Wallowa Valley Ranger District, Eagle Cap Ranger District, and Pine Creek Ranger District. Over 486,000 ha (1.2 million acres) of public and private forest and canyons comprise the study area. Ponderosa pine (*Pinus ponderosa*), western larch (*Larix occidentalis*), Douglas-fir (*Pseudotsuga menziesii*), and white fir (*Abies grandis*) are the dominant tree species. I divided the study area into three habitat blocks, based on vegetation and management practices: Forest, Forest/Canyon Edge, and Canyon. Roost habitat surrounding Forest sample sites is limited to trees, snags, stumps, and a few buildings. This habitat comprises the largest area, had the most sample sites, and has had the greatest timber harvest in past decades. Roost habitat in the Forest/Canyon area included trees, snags, stumps, cliffs, talus, mines, and buildings. This was the second-largest sample area, had fewer sample sites, and the least impact in terms of timber harvest. Canyon habitat is not considered in this analysis.

I have recorded by capture or audible call signatures 13 species from the study area. Four of these species were not considered due to their low capture rates (*Lasiurus cinereus*, *Euderma maculatum*, *Corynorhinus townsendii*, and *Myotis yumanensis*).

MATERIALS AND METHODS

I sampled Forest and Forest/Canyon sites by setting mist nets over open water. Mist netting occurred from 1 June to 1 September 1984–1994. Netting periods lasted at least two hours after sunset. Bats were identified to species, sexed, aged, weighed, and morphological measurements were taken.

To test for division of foraging sites by sex, I used the chi-square test (Williams 1993). *Lasionycteris noctivagans* data are from Perkins and Cross (1992). To test for independence of distribution at foraging sites I paired each possible group of species and applied Fisher's exact test. Netability varies among species. To minimize this bias, I assigned a value for each species at each site as either present (1) or absent (0).

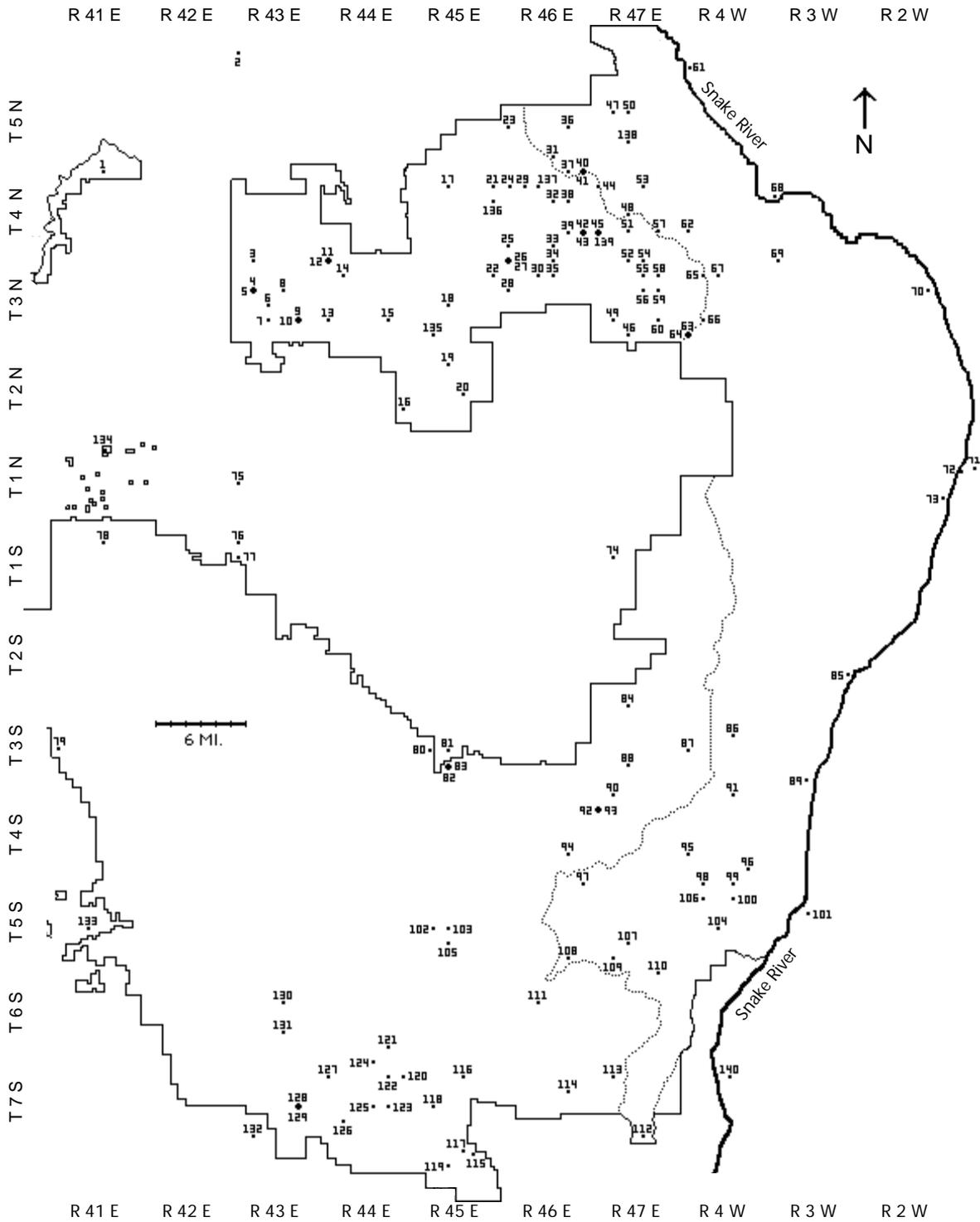


FIGURE 1 Study area, WWNF, Oregon, U.S.A. Thin line indicates forest boundary. East of the broken line is the HCNRA. Small dots represent single sample sites to nearest section. Large dots show two sites within section.

Chi-square analysis of exclusivity in male and reproductive female foraging patterns resulted in statistically significant separation between the sexes for all eight species for both portions of the study area, regardless of timber impacts (Table 1). However, Fisher's exact test indicates that when reproductive status is not considered, paired *M. californicus*, *M. ciliolabrum*, and *M. thysanodes* in both habitats had no foraging separation between the sexes. *M. californicus*, *M. ciliolabrum*, and *M. thysanodes* were the species that I captured the least of the eight considered. In the Forest/Canyon habitat, *M. evotis* and *M. lucifugus* also had no significant segregation by sex.

If we divide the bats into morphological sizes based on forearm length, skull size, and mass, we get a large bat group (*E. fuscus*, *L. noctivagans*), a middle-sized group (*M. evotis*, *M. volans*, *M. thysanodes*), and a small group (*M. lucifugus*, *M. ciliolabrum*, and *M. californicus*). The occurrence of large and small species together at sites was less than expected by chance in 67% (32 of 48) of the cases. Middle-sized bats and small bats were less frequently associated than expected in 73% (35 of 48) of cases.

In terms of foraging "style," gleaners (*M. evotis*, *M. thysanodes*) show competitive exclusion for both sexes. Forest and clearing aerial-insectivores (*E. fuscus*, *L. noctivagans*, *M. californicus*, *M. ciliolabrum*, and *M. volans*) produced mixed results indicating lower competition. In pairs of these species, 58% of cases indicated significant avoidance (29 of 50). *M. lucifugus* is the only water-surface forager, but significantly avoided other species in 68% of cases (19 of 28).

There was a slight difference in frequency of significant avoidance between the two habitats (when I excluded same species/different sex pairs). In the Forest habitat, competition was indicated in 70% of cases (74 of 105), while in the Forest/Canyon habitat competition occurred in 60% of cases (63 of 105).

DISCUSSION

My results indicate that the long-held assumption that sexes forage in separate areas is valid, particularly for the larger species, and those which form larger colonies outside of human structures. The lack of foraging habitat segregation by sex in the small and less numerous bat species (*M. californicus*, *M. ciliolabrum*, *M. lucifugus*, and *M. thysanodes*) suggests that prey biomass is not a critical factor in determining distribution or foraging sites when numbers of resident individuals are low.

Analysis of species pairs by sex seems to validate the concept of competition for foraging areas as a factor influencing distribution (Findley 1993). If one takes into account prey species and foraging techniques, it is difficult to imagine how *L. noctivagans* or *E. fuscus*, who forage at tree-top level at dusk, compete with *M. lucifugus*, *M. californicus*, or *M. ciliolabrum*, who forage low over meadows, water, in clearings, or under canopies in riparian zones. Whitaker et al. (1977) demonstrated that diets of

M. californicus and *M. lucifugus* only overlap with the middle-sized and large bat species in consumption of Diptera and Lepidoptera. *M. lucifugus* and *M. californicus* consume (by volume) mostly Diptera, while for large and middle-sized bats, Diptera make up less than 10% of consumed volume. Lepidoptera seem to be the prey common to all bat species represented on the study area. Prey analysis indicates that the small bat species eat less Lepidoptera by volume by at least a factor of two when compared with the larger bat species. Dietary competition is most likely to occur in consumption of lepidopterans: *L. noctivagans* (32% of prey volume), *E. fuscus* (21% of prey volume), *M. evotis* (46% of prey volume), *M. thysanodes* (46% of prey volume), and *M. volans* (78% of prey volume) (Whitaker et al. 1977; Whitaker et al. 1981). However, if prey competition is important, why is there inconsistent evidence of foraging competition between *E. fuscus* and *M. volans*, and between *L. noctivagans* and *M. volans*?

A close inspection of roosting behaviour provides the most likely answer. *E. fuscus*, *L. noctivagans*, and *M. volans* females all prefer abandoned woodpecker holes as maternity roosts, while males of these three species generally use crevices (Barclay 1985; Vonhof 1994; Kalcounis 1994; P. Ormsbee, pers. comm.). If roost availability is the determining factor in the significant differences in paired bat distributions, then female *L. noctivagans*, *E. fuscus*, and *M. volans* should rarely occur together. Indeed, my data suggest that this is the case. Other bat species of both sexes seem to rely mostly on crevices in cliffs and trees, or exfoliating bark, in the absence of human structures (Perkins 1993; Kalcounis 1994; P. Ormsbee, pers. comm.). If we assume that roosts adequate for *M. californicus* are also adequate for other crevice-roosting bats, I would expect that "might makes right," and the larger and more aggressive bat species out-compete the smaller and the less aggressive species.

Differences in the distribution of bats between the two habitats in the study area can be attributed to the greater harvest of trees in the Forest habitat. As well, in the Forest/Canyon habitat, alternate roost sites such as cliffs, caves, and human structures are more abundant than in the Forest habitat, thereby lessening competition. Perkins and Peterson (1995) noted potential foraging competition only among reproductive females of three bat species that are moth strategists (*M. thysanodes*, *M. volans*, and *C. townsendii*), and only in the Forest/Canyon habitat. Other significant differences noted in Tables 1 and 2 could be attributed to foraging interactions, but results here, and those of Perkins (1993), Perkins and Peterson (1995), Humphrey (1975), and Bell (1980) all agree that bat distribution is more likely dependent upon roost availability and interspecific competition for roosts rather than dietary competition. Sexual segregation in foraging areas occurs in most species, and may be correlated with local population densities of a given species.

IMPLICATIONS

If competition for roosts and roost availability is important in determining the distribution and success of bat species in nearctic forests, several questions arise:

1. Are present harvest practices especially harmful to smaller and less aggressive bat species?
2. Will future harvest practices result in lower population densities?
3. If competition for roosts is reducing populations of small and less aggressive species in the summer, what are the effects for species that depend on forest tree-roosts for hibernation?

ACKNOWLEDGEMENTS

I wish to thank the following individuals for their help in the field: Joshua Peterson, Andrew Perkins, B.J. Perkins, Travis Ash, Steve Farley, Holly Klocke, Paul Cryan, and Laurel Reuben. Monetary support was by various contracts with the Wallowa-Whitman National Forest and the Oregon Department of Fish and Wildlife. I also wish to thank R. Anderson, S. Monnell, and K. Martin, the biological staff for the Forest's north zone, for their encouragement and expedition of the projects.

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