

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

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## ABSTRACT

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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  $40.9 \pm 1.2$  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

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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

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### 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

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#### 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  $40.9 \pm 1.2$  (30–52) cm. Mean roost-tree height was  $25.1 \pm 1.6$  (8–47) m, and mean exit height was  $9.9 \pm 0.9$  (1.4–18) m. Roost trees

were on average  $38.7 \pm 7.1$  (1–147) m away from another tree used as a roost in the same year and  $17.3 \pm 4.5$  (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 =  $40.9 \pm 1.2$  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 =  $33.4 \pm 1.4$  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  $74.2 \pm 7.6$  (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  $\leq 50$  m, only 27% of roost-change distances were that small.

We compared the tendency to change roosts among adult females using a  $3 \times 2$  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  $\geq 10$  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).

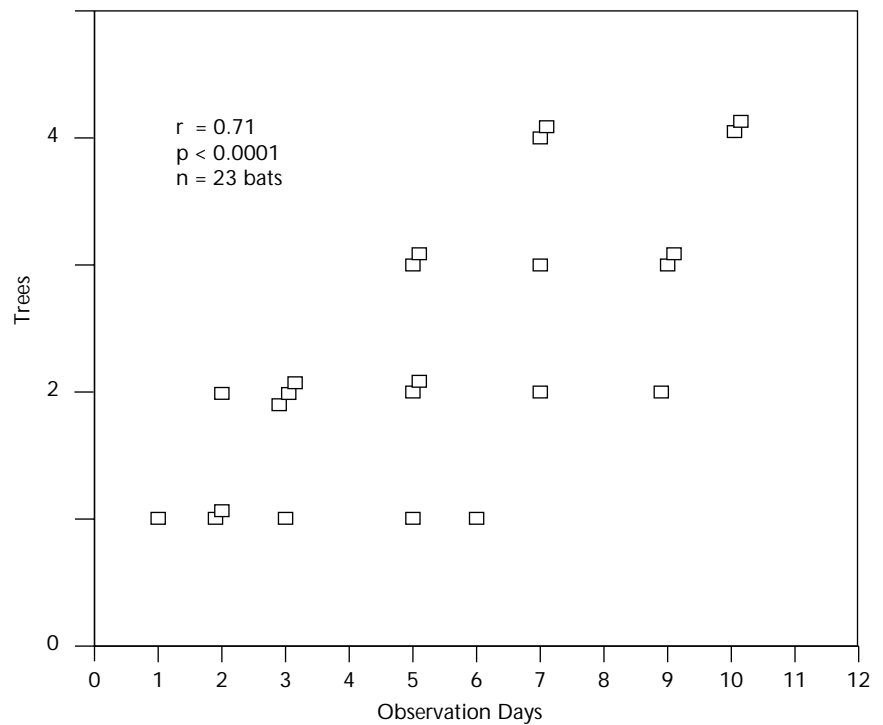
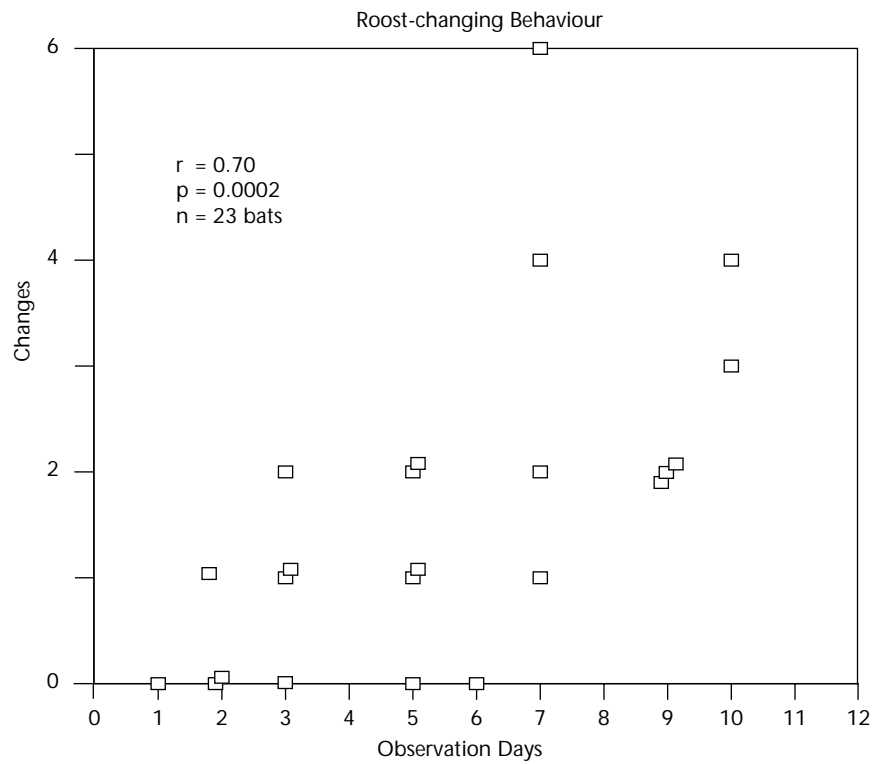


FIGURE 1 *Roost-changing behaviour. (Top) The relationship between number of roost changes and number of days that the bat was located. (Bottom) The relationship between number of different trees used and number of days that the bat was located.*

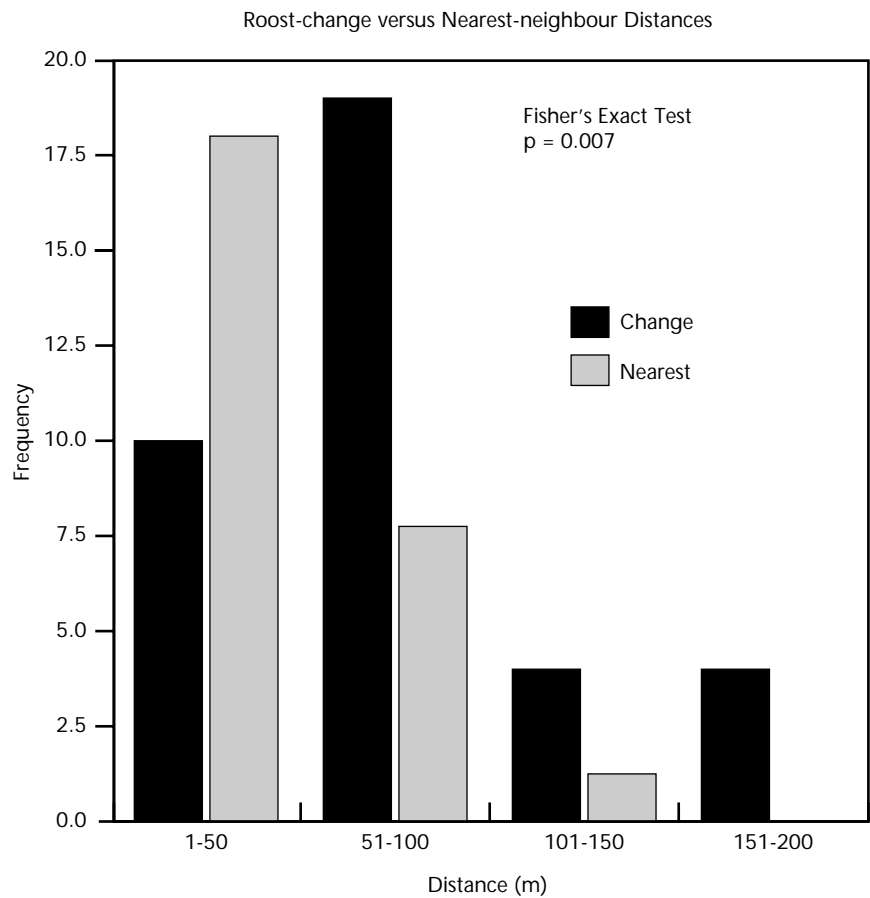


FIGURE 2 *Roost-change distances compared to nearest-neighbour distances within that year. Nearest-neighbour distances were measured only for trees to which Indiana bats were actually radio-tracked in that year.*

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

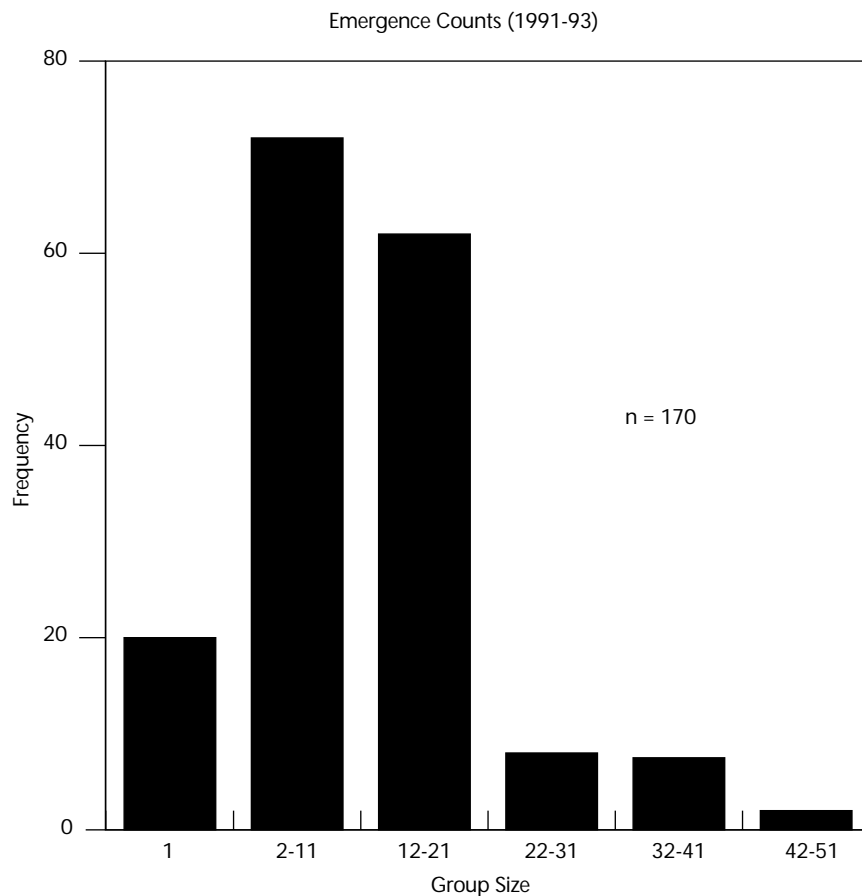


FIGURE 3 Histogram showing frequency of roost population sizes.



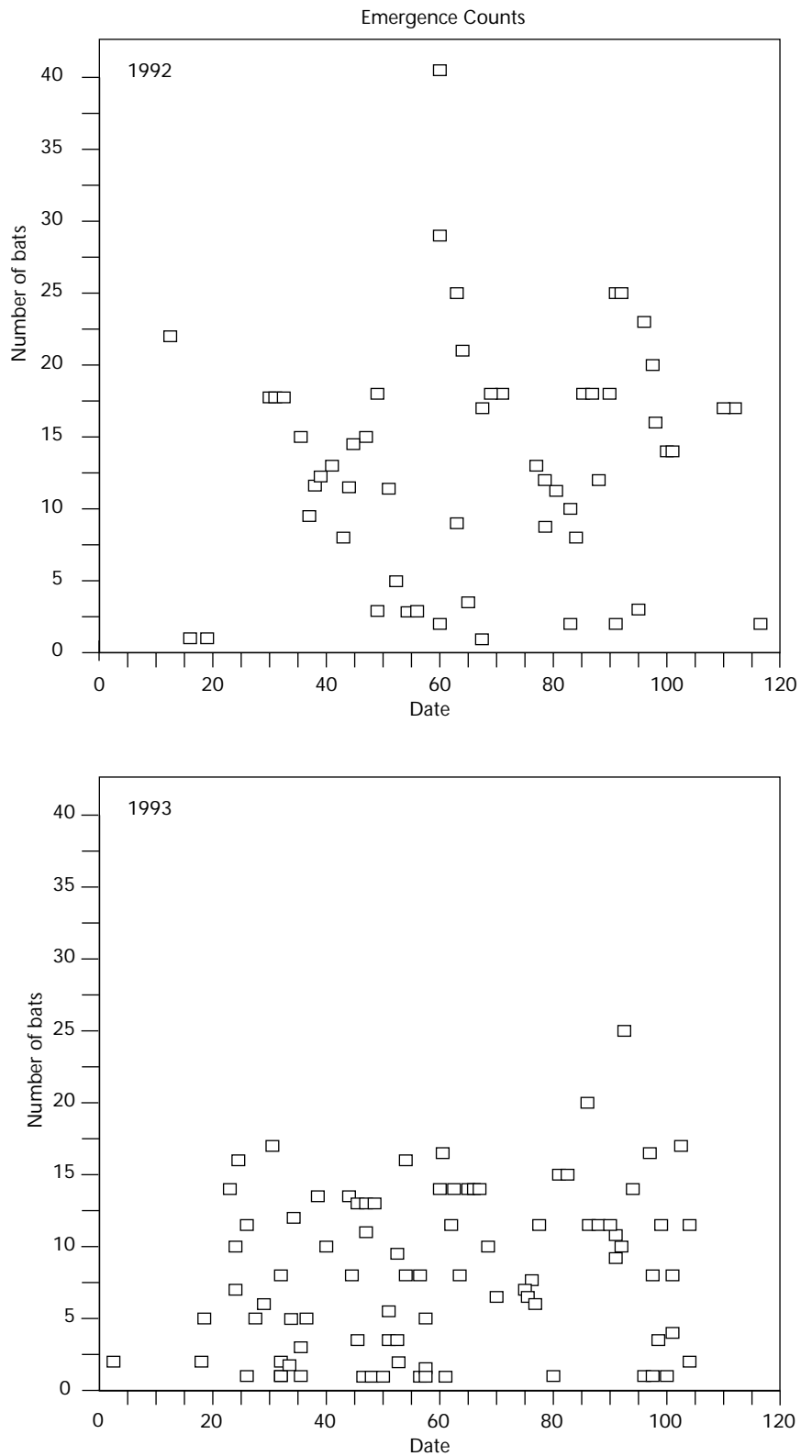


FIGURE 4 Emergence counts by date in 1992 and 1993. Dates are numbered sequentially beginning with 1 May as day 1. Day 78 is 17 July, the first date on which volant juveniles were recorded.

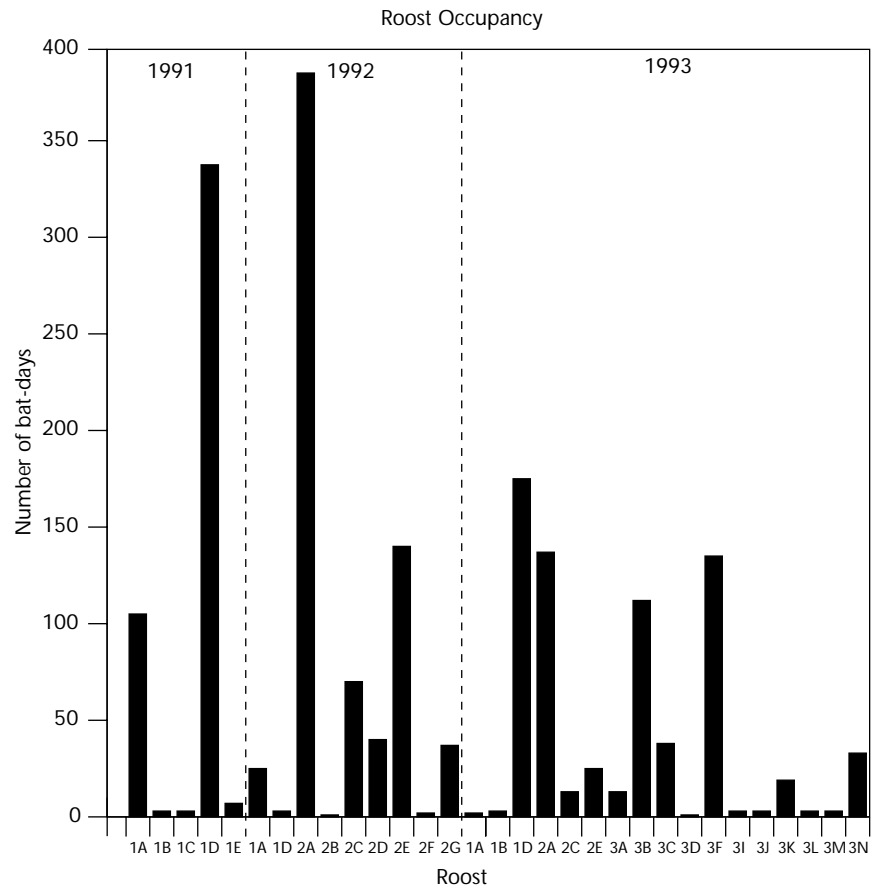


FIGURE 5 Number of bat-days for each roost tree in each year. Code names for each roost consisted of a number representing the year of discovery (1–3 for 1991–93), and a letter assigned in order of its discovery in that year. Roosts 3E, 3G, and 3H were used by adult males and were not included.

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  $35^\circ\text{C}$  were harmful to Indiana bats, 14 of our bats (82%) achieved a  $T_b$  greater than  $35^\circ\text{C}$  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  $35^\circ\text{C}$  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 ( $8^\circ\text{C}$ ) night—a situation often leading to torpor in insectivorous bats. The highest  $T_b$  recorded in either year was  $40.3^\circ\text{C}$ , at sunset on a day when air temperature ( $T_a$ ) external to the roost was only  $22^\circ\text{C}$ . The highest  $T_a$  was  $33^\circ\text{C}$ , and it corresponded to a  $T_b$  of  $37.7^\circ\text{C}$ .

## 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.

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