

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

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## 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.

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## 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 ( $44^{\circ} 12'N$ ,  $122^{\circ} 15'W$ ). 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  $44^{\circ}$  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 were 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

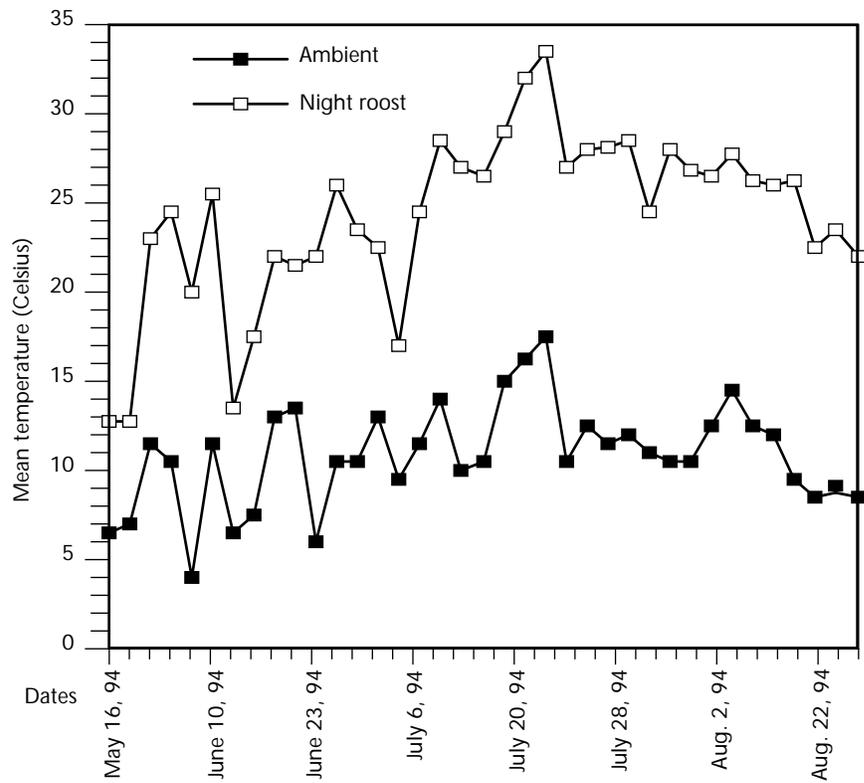


FIGURE 1 Comparison of mean night-time ambient and night roost temperatures (Celsius) at Quentin Creek Bridge for May–August of 1994.

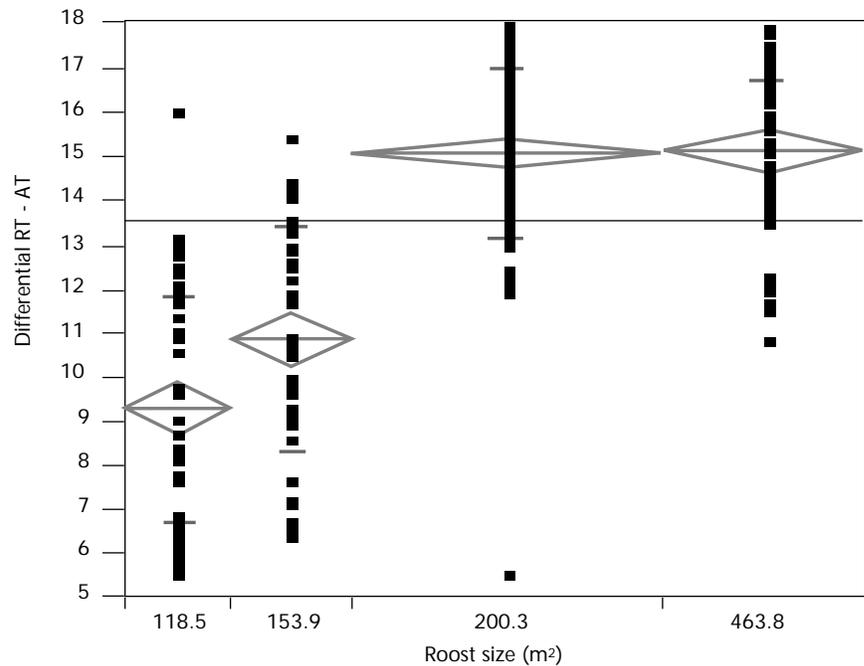


FIGURE 2 Comparison of temperature differential ( $T_d$ ) by roost size for 1994 (Welch ANOVA,  $F = 88.1568$ ,  $p < 0.0001$ ,  $df = 3$ ,  $n = 281$ ).  $T_d$  = night roost temperature (RT)–ambient temperature (AT).

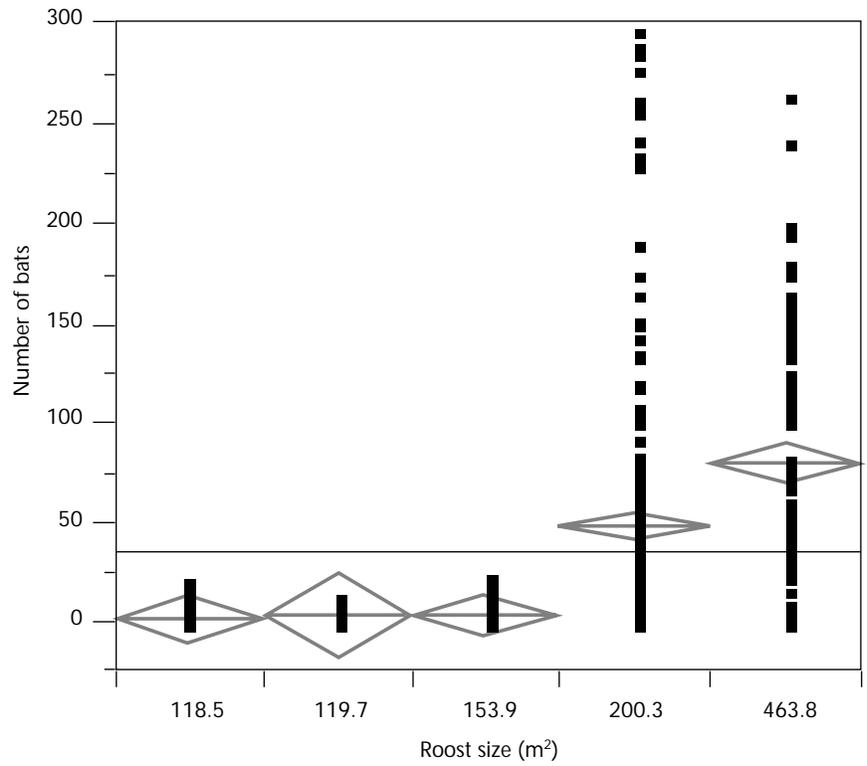


FIGURE 3 The relationship between roost size and the mean number of bats observed at five night roost sites ( $F = 47.6089$ ,  $p < 0.0001$ ,  $df = 4$ ).

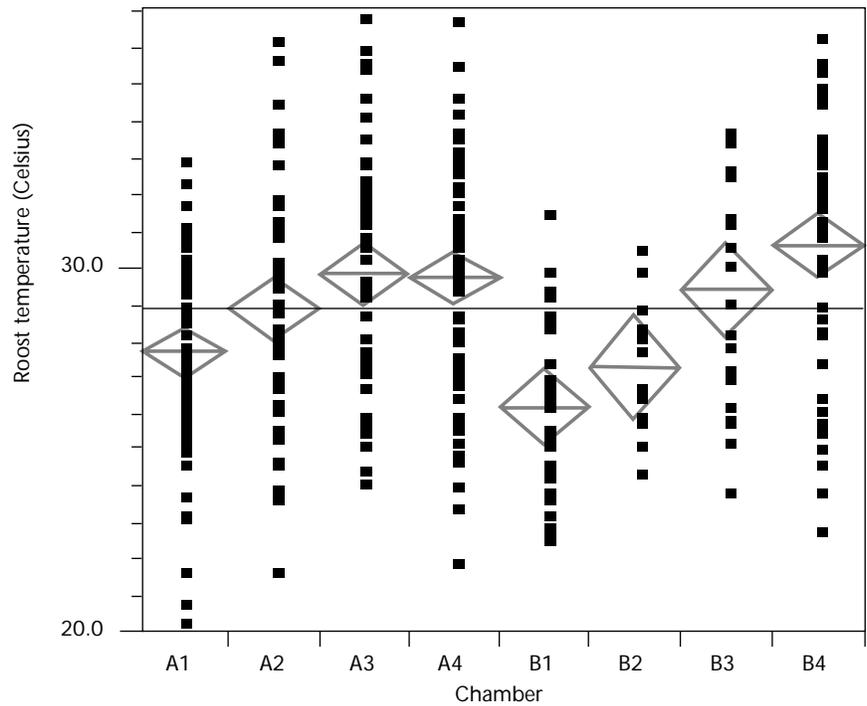


FIGURE 4 Mean night roost temperatures for the eight individual chambers of the Blue River Reservoir Bridge in 1994 (ANOVA,  $F = 9.6484$ ,  $p < 0.0001$ ,  $df = 7$ ).

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%).

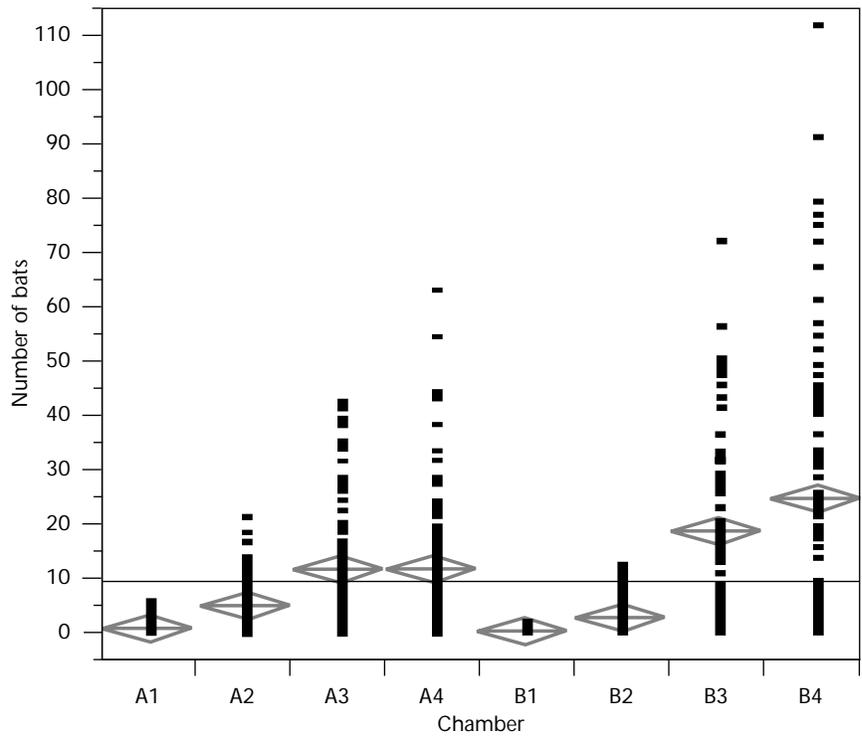


FIGURE 5 The number of bats observed for the eight chambers of the Blue River Bridge for 1994 (Welch's ANOVA,  $F = 67.8552$ ,  $p < 0.0001$ ,  $df = 7$ ).

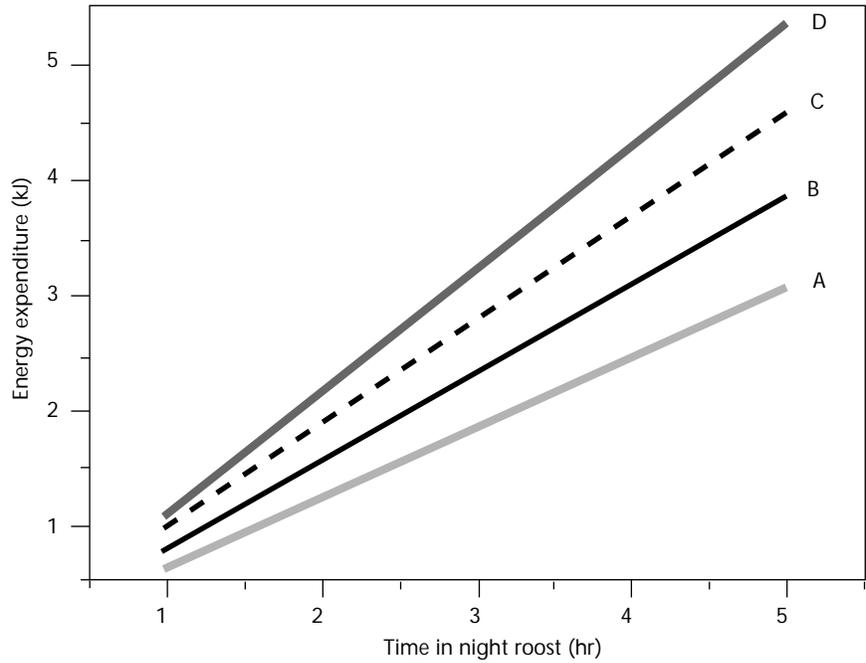


FIGURE 6 The model projects the impact on night roost energy expenditures by time for sites with different temperatures ( $T_{nr}$ ). Assumptions in the model are that female bats are associated with a cluster and engaged in active body temperature regulation. A ( $T_{nr} = 25^{\circ}\text{C}$ ), B (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

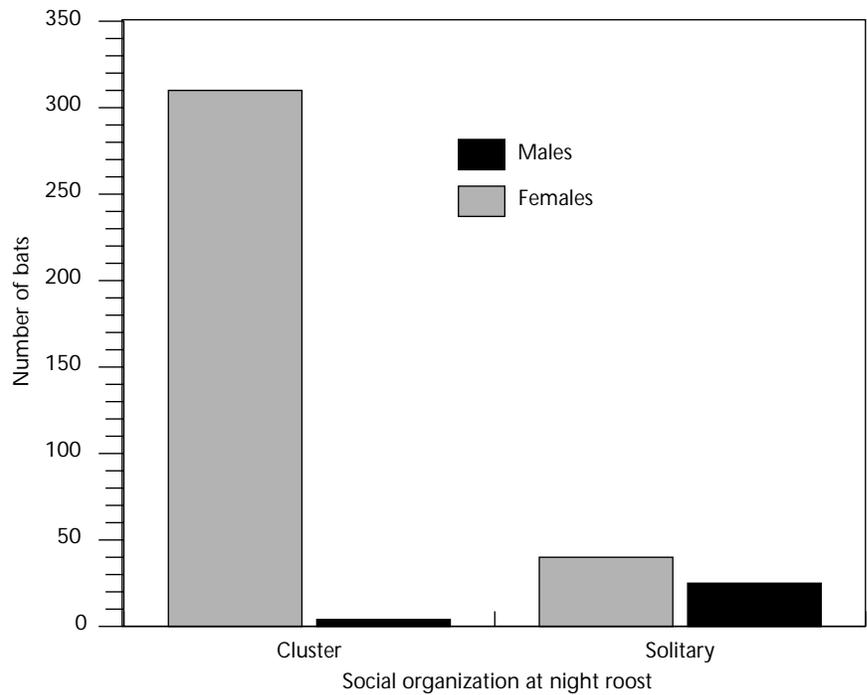


FIGURE 7 *Distribution of males and females captured at night roosts based on their association with clusters or as solitary individuals.*

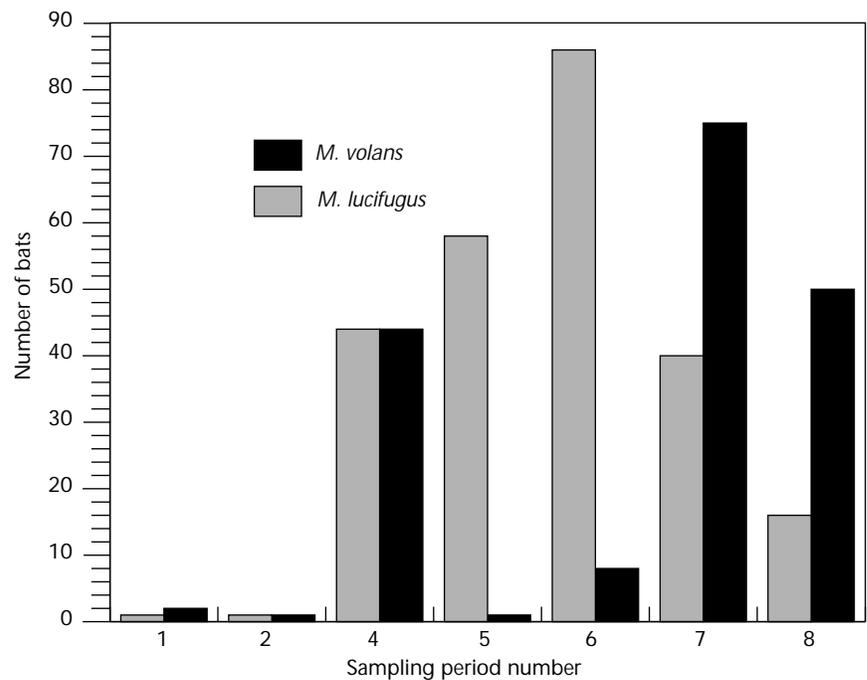


FIGURE 8 *Summary of the distribution of M. lucifugus and M. volans at night roosts during sampling periods covering 1 May to 30 August for 1993-1994. Sampling period # are as follows: #1 (1 May 1-15 May); #2 (16 May-31 May); #3 (1 June-15 June); #4 (16 June-30 June); #5 (1 July-15 July); #6 (16 July-31 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 ( $396.4 \pm 21.7$ ). 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° 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

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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).

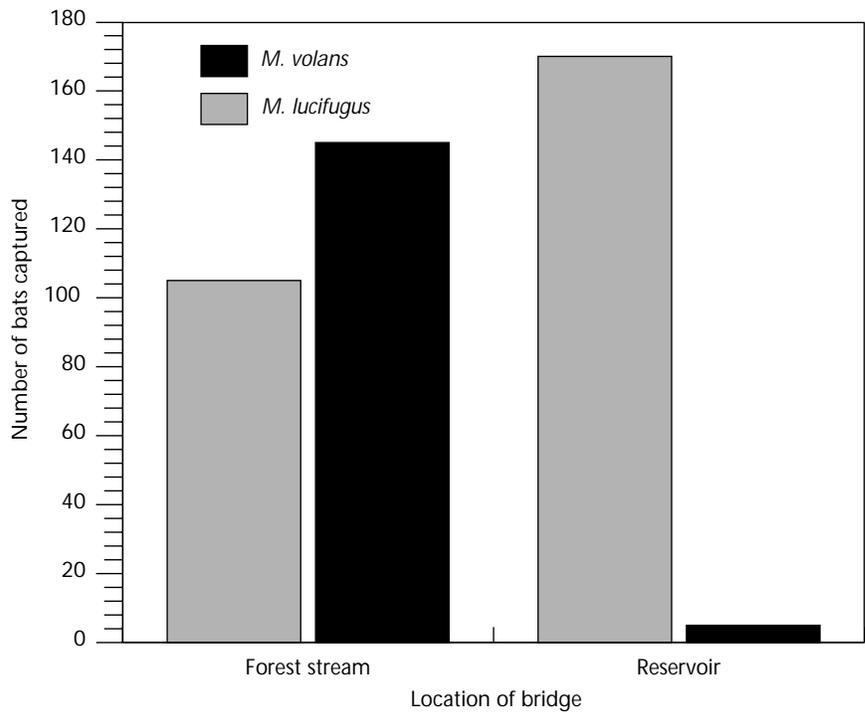


FIGURE 9 Distribution of *M. volans* and *M. lucifugus* at night roosts located over streams and the reservoir.

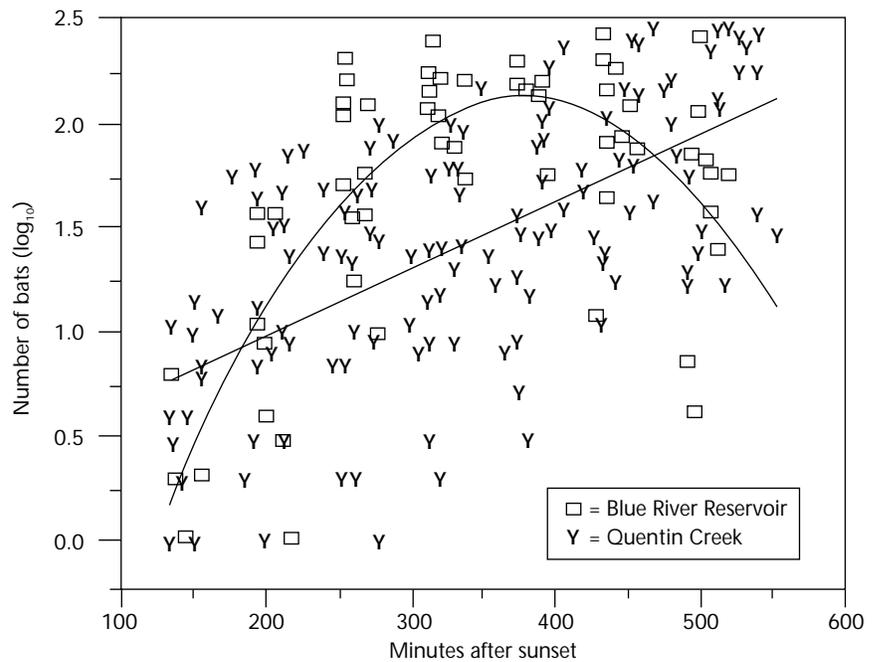


FIGURE 10 Linear regression of the number of bats ( $\log_{10}$ ) by minutes after sunset for 1993-1994. The parabolic curve (polynomial fit -2 degrees) represents data points for Blue River Reservoir Bridge ( $r^2 = 0.71$ ,  $F = 98.9$ ,  $p < 0.0001$ ,  $df = 84$ ) and the linear fit ( $r^2 = 0.39$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

<sup>a</sup> 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

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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.

#### LITERATURE CITED

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- Anthony, E.L.P. and T.H. Kunz. 1977. Feeding strategies of the little brown bat, *Myotis lucifugus*, in southern New Hampshire. *Ecology* 58:775-86.
- Anthony, E.L.P., H.M. Stack, and T.H. Kunz. 1981. Night roosting and the nocturnal time budget of the little brown bat, *Myotis lucifugus*: Effects of reproductive status, prey density, and environmental conditions. *Oecologia* 51:151-56.
- Barclay, R.M.R. 1982. Night roosting behavior of the little brown bat, *Myotis lucifugus*. *J. Mammal.* 63:464-74.
- . 1989. The effects of reproductive condition on the foraging behaviour of the female hoary bats, *Lasiurus cinereus*. *Behav. Ecol. Sociobiol.* 24:31-37.
- . 1991. Population structure of temperate zone insectivorous bats in relation to foraging behaviour and energy demand. *J. Anim. Ecol.* 60:165-78.

- Barclay, R.M.R. and K.J. Cash. 1985. A non-commensal maternity roost of the little brown bat (*Myotis lucifugus*). *J. Mammal.* 66:782–83.
- Belwood, J.J. and M.B. Fenton. 1976. Variation in the diet of *Myotis lucifugus* (Chiroptera: Vespertilionidae). *Can. J. Zool.* 54:1674–78.
- Brown, C.R. 1988. Enhanced foraging efficiency through information centers: a benefit of colonality in cliff swallows. *Ecology* 69:602–13.
- Brown, C.R. and M.B. Brown. 1986. Ectoparasitism as a cost of colonality in cliff swallows. *Ecology* 67:1206–18.
- Burnett, C.D. and P.V. August. 1981. Time and energy budgets for day-roosting in a maternity colony of *Myotis lucifugus*. *J. Mammal.* 62:758–66.
- Fenton, M.B., N.G.H. Boyle, T.M. Harrison, and D.J. Oxley. 1977. Activity patterns, habitat use, and prey selection by some African insectivorous bats. *Biotropica* 9:73–85.
- Fenton, M.B. and G.P. Bell. 1979. Echolocation and feeding behaviour in four species of *Myotis* (Chiroptera: Vespertilionidae). *Can. J. Zool.* 57:1271–77.
- Fenton, M.B. and R.M.R. Barclay. 1980. *Myotis lucifugus*. *Mammalian Species* 142:1–8.
- Fenton, M.B., I.L. Rautenbach, S.E. Smith, C.M. Swanepoel, J. Grosell, and J. van Jaarsveld. 1994. Raptors and bats: threats and opportunities. *Anim. Behav.* 48:9–18.
- Franklin, J.F. and C.T. Dyrness. 1973. Natural vegetation of Oregon and Washington. U.S. Forest Service Gen. Tech. Rep., PNW–8.
- Hirshfield, J.R., Z.C. Nelson, and W.G. Bradley. 1977. Night roosting behavior in four species of desert bats. *SW Nat.* 22:427–33.
- Howell, D.J. 1979. Flock foraging in nectar-feeding bats: advantages to the bats and the host plants. *Amer. Nat.* 114:23–49.
- JMP Statistics and Graphics Guide. 1994. SAS Institute Inc., Cary, N.C.
- Kalcounis, M.C. and R.M. Brigham. 1995. Intraspecific variation in wing loading affects habitat use by little brown bats (*Myotis lucifugus*). *Can. J. Zool.* 73:89–95.
- Krebs, J.R. and N.B. Davies (editors). 1989. *An Introduction to Behavioural Ecology*. Blackwell Scientific Publications, Oxford, U.K.
- Krebs, J.R. and A. Kacelnik. 1991. Decision-making. In *Behavioural Ecology: An Evolutionary Approach*. J.R. Krebs and N.B. Davies (editors), pp. 105–36. Blackwell Scientific Publications, London, U.K.
- Kunz, T.H. 1974. Feeding ecology of a temperate insectivorous bat (*Myotis velifer*). *Ecology* 55:693–711.
- . 1980. Daily energy budgets of free-living bats. In *Proceedings of the Fifth International Bat Research Conference* (D.E. Wilson and A.L. Gardner, editors), pp. 369–92. Texas Tech. Press, Lubbock, Texas.

- . 1982. Roosting ecology of bats. In Ecology of Bats, T.H. Kunz (editor), pp. 1–55. Plenum Press, New York, N.Y.
- Kurta, A. 1985. External insulation available to a non-nesting mammal, the little brown bat (*Myotis lucifugus*). *Comp. Biochem. Physiol.* 82:413–20.
- Kurta, A. and T.H. Kunz. 1988. Roosting metabolic rate and body temperature of male little brown bats (*Myotis lucifugus*) in summer. *J. Mammal.* 69:645–51.
- Kurta, A., G.P. Bell, K.A. Nagy, and T.H. Kunz. 1989. Energetics of pregnancy and lactation in free ranging little brown bats (*Myotis lucifugus*). *Physiol. Zool.* 62:804–18.
- Maser, C., B.R. Mate, J.F. Franklin, and C.T. Dryness. 1984. Natural History of the Oregon Coast Mammals. Pacific Northwest Forest and Range Experiment Station. U.S. Dept. Agric. Forest Service, Gen. Tech. Rep., PNW-133:1–496.
- O'Farrell, M.J. and W.G. Bradley. 1977. Comparative thermal relationships of flight for some bats in the southwestern United States. *Comp. Biochem. Physiol.* 58A:223–27.
- O'Shea, T.J. and T.A. Vaughan. 1977. Nocturnal and seasonal activities of the pallid bat, *Antrozous pallidus*. *J. Mammal.* 58:269–84.
- Racey, P.A. 1982. Ecology of bat reproduction. In Ecology of Bats (T.H. Kunz, editor). Plenum Press, New York, N.Y.
- Roverud, R.C. and M.A. Chappell. 1991. Energetic and thermoregulatory aspects of clustering behavior in the neotropical bat *Noctilio albigentris*. *Physiol. Zool.* 64:1527–41.
- Saunders, M.B. and R.M.R. Barclay. 1992. Ecomorphology of insectivorous bats: a test of predictions using two morphologically similar species. *Ecology* 73:1335–45.
- Schowalter, D.B. 1980. Swarming, reproduction, and early hibernation of *Myotis lucifugus* and *Myotis volans* in Alberta, Canada. *J. Mammal.* 61:350–54.
- Studier, E.H., V.L. Lysengen, and M.J. O'Farrell. 1973. Biology of *Myotis thysanodes* and *M. lucifugus* (Chiroptera: Vespertilionidae) II. Bioenergetics of pregnancy and lactation. *Comp. Biochem. Physiol.* 44A:467–71.
- Trivers, R.L. 1972. Parental investment and sexual selection. In *Sexual Selection and The Descent of Man*, B. Campbell (editor). Aldine, Chicago, Ill., pp. 136–79.
- Trune, D.R. and C.N. Slobodchikoff. 1976. Social effects of roosting on the metabolism of the pallid bat (*Antrozous pallidus*). *J. Mammal.* 57:656–63.
- Tuttle, M.D. 1976. Population ecology of the gray bat (*Myotis grisescens*): philopatry, timing and patterns of movement, weight loss during migration, and seasonal adaptive strategies. *Occas. Papers, Mus. Nat. Hist., University of Kansas*, 54:1–38.

- Vaughan, T.A. 1976. Nocturnal behavior of the African false vampire bat (*Cardioderma cor*). *J. Mammal.* 57:227-48.
- von Frenckell, B. and R.M.R. Barclay. 1987. Bat activity over calm and turbulent water. *Can. J. Zool.* 65:219-22.
- Warner, R.M. 1985. Interspecific and temporal dietary variation in an Arizona bat community. *J. Mammal.* 66:45-51.
- Warner, R.M. and N.J. Czaplewski. 1984. *Myotis volans*. *Mammalian Species* 224:1-4.
- Whitaker, J.O., Jr., C. Maser, and L.E. Keller. 1977. Food habits of bats in Western Oregon. *NW Science* 51:46-55.
- Wilkinson, G.S. 1992. Information transfer at evening bat colonies. *Anim. Behav.* 44:501-18.
- Williams, D.F. and J.S. Findley. 1979. Sexual size dimorphism in vespertilionid bats. *Amer. Midl. Natur.* 102:113-26.
- Zar, J.H. 1984. *Biostatistical Analysis*. Prentice Hall Inc., Englewood Cliffs, N.J.