Roosting and foraging ecology of eastern pipistrelle (*Perimyotis subflavus*) bats in
SW Nova Scotia

by:

Greg M. Quinn and Hugh G Broders

Department of Biology

Saint Mary's University

Submitted:

14 February 2007

ABSTRACT

Preliminary research in 2001 indicated that there might be a forest-dwelling, breeding population of eastern pipistrelles in SW Nova Scotia (Kejimkujik National Park). Given the paucity of records in the region; it seemed likely that this represented a disjunct actively breeding population. In 2003 a more intensive study on the roosting and foraging ecology in Kejimkujik National Park, NS was initiated. The goal of this study was to gather base line data on aspects of the roosting and foraging ecology of eastern pipistrelles using trapping, radio telemetry and ultrasonic monitoring. Specifically, The objective was to measure the effects of key variables on roosting and foraging behaviour at large (up to 5? Km) and small (10s of meters) scales, and to investigate the factors which best predict the distribution of *Usnea trichodea* Ach., which is used as a roosting medium by reproductive females. Foraging behaviour was investigated using ultrasonic detectors and roosting behaviour was studied by observing radio-tagged individuals, and recording data on their roost sites for comparison to random plots throughout the study area.

INTRODUCTION

The Order *Chiroptera* represents over one quarter of the world's mammalian diversity, second only to *Rodentia* in number of species, but remains one of the least understood among terrestrial mammals: even the taxonomy of the Order remains in a state of flux. Traditionally, our understanding of bats in general has been inhibited by both an inability and a disinclination to study them. Bats are difficult to study given their cryptic, nocturnal nature and their ability to fly, and our treatment of them has been coloured by the popular conception of bats as vile, objectionable pests. Practically speaking, the specialized equipment that allows researchers to effectively study many aspects of bat ecology has only recently been developed, and as a result little is known about even the most common North American species.

In Nova Scotia, anecdotal evidence reports the occurrence of seven different species of bats which include the hoary bat (*Lasiurus cinereus*), red bat (*L. borealis*), silver-haired bat (*Lasionycteris noctivagans*), big brown bat (*Eptesicus fuscus*), little brown bat (*Myotis lucifugus*), northern long-eared bat (*M. septentrionalis*), and eastern pipistrelle (*Perimyotis subflavus*). However, the first systematic study of bat ecology in the province, conducted in 2001, found that only *P. subflavus*, *Myotis septentrionalis*, and *M. lucifugus* were common (Broders *et al*. 2003). Despite being common in many parts of the eastern United States and Mexico, the least understood of these three species is *P. subflavus*.

Taxonomy and Distribution

Kingdom *Animalia*
Phylum *Chordata*
Class *Mammalia*
Order *Chordata*
Family *Vespertilionidae*
Genus *Pipistrellus*
Species *P. subflavus*

The eastern pipistrelle (*Pipistrellus subflavus* F. Cuvier) has traditionally been included in the Genus *Pipistrellus*, but cumulative evidence suggests that *P. subflavus* is not in the same clade as other *Pipistrelli* and should be placed in its own Genus, which has been designated as *Perimyotis* (Hoofer & Van Den Bussche, 2003). While not well defined, the distribution of *P. subflavus* ranges from as far south as Honduras, north through eastern Mexico through the eastern United States, as far west as Texas, Kansas, and Nebraska, continuing up as far as southern Ontario and Massachusetts with a small peripheral population existing in south-western Nova Scotia. A trend of western expansion of range has also been noted for *P. subflavus* (Ammerman, 2005; Armstrong, Adams & Taylor, 2006; Geluso *et al.*, 2005).

Recent findings indicate that the Nova Scotia population may be genetically isolated from the core population in the United States of which the nearest recorded breeding colony was found in Massachusetts by Winchell and Kunz (1996): The eastern pipistrelle is not considered to be a migratory species (Davis, 1966), and there are no records of individuals landing on ships in the Gulf of Maine along likely migratory routes, such as exist for other migratory species that have been known to occur in the region (Carter, 1950; Mackiewicz & Backus, 1956; Peterson, 1970) (Appendix A). Therefore, it is unlikely that genetic flow between this population and those from mainland United States occurs via over-sea routes. Studies in southern New Brunswick found that only *Myotis lucifugus*, and *M. septentrionalis* were common in that area (Broders, Findlay & Zheng, 2004a; Healy, 2002). None of 237 captures in eastern Maine were eastern pipistrelles (Zimmerman & Glanz, 2000), and none were recorded during a systematic survey in Newfoundland (Grindal, 1999). Considering these issues, the Nova Scotia population may be of national importance as a unique, but possibly threatened population.

An ongoing province-wide survey by Lesley Farrow has found that in summer, the Nova Scotia population of *P. subflavus* seems to be concentrated in a triangular geographic area bounded by Halifax on the northeast, Wolfville on the west, and Shelburne on the southeast.

Physical Description

The eastern pipistrelle is typically counted among the smallest North American bats, weighing 4 to 8 grams in much of its range. The dorsal pelage is yellowish brown while the individual hairs being tri-coloured; dark at the base, yellow-brown in the middle, and brown at the tips. The wingspan is approximately 220-225mm (Fujita & Kunz, 1984). The skin of the forearms is distinctively reddish.

They have oblong ears which when held toward their nose, extends slightly beyond the tip of the nostrils.

Hibernation

Perimyotis subflavus is an obligate hibernator, and in southern climates where adequate year-round food supply exists, will still enter torpor during winter in caves and buildings (Briggler & Prather, 2003; Broders, McAlpine & Forbes, 2001; Kurta & Teramino, 1994). In more northern parts of its range, hibernation records are limited to caves (Broders *et al.*, 2001) and in one unusual case, a hydroelectric dam (Kurta *et al.*, 1994).

The Eastern Pipistrelle in Nova Scotia

Previous records of the eastern pipistrelle in the Nova Scotia are very limited. Specimens have been collected in Kejimkujik National Park (Bleakney, 1965), with the most northerly record occurring in Colchester County (Fuller, 1998). Only 10 eastern pipistrelles have been found hibernating in the province. In general, the species was thought to be rare in the province until Broders et al. (2003) found them to be locally abundant in south-western Nova Scotia, though they only constituted 10% of the total recorded activity which was dominated by the two *Myotis* spp.. Recent studies in southern New Brunswick found that only the two *Myotis* species were common in that area (Broders *et al.*, 2004a; Healy, 2002). None of 237 captures in eastern Maine were eastern pipistrelles (Zimmerman *et al.*, 2000), and none have been recorded in Newfoundland (Grindal, 1999).

The ability of a population of eastern pipistrelles to persist in south-western Nova Scotia, which represents the northern limit of its range, may be at least partially attributed to the warm climate in that area relative to the rest of Atlantic Canada. This region is also home to a suite of plant and animal populations which are at the northern range-limit of their species in southern Nova Scotia, and are thought to be disjunct and genetically distinct (Mockford, Snyder & Herman, 1999; Smith, 1999; Standing, Herman & Morrison, 1999) due to a lack of genetic flow and evolutionary pressures unique to the region. This phenomenon has been driven by gradual cooling of the climate over the last

8000 years which has caused the northern range limits of many species to recede to the south. The ocean surrounding the peninsula of Nova Scotia has been a barrier to the southward retreat of some species, which have in turn been forced to adapt to the region's environment or become extirpated.

The presence of this population in Nova Scotia offers a unique opportunity to examine how an apparently isolated population adapts to environmental stresses and manages to persist at the limits of its range. Successful reproduction is key for a population to persist, and requires individuals to accrue more food energy than is needed for self maintenance alone, creating greater challenges for reproductive females (Morse, 1980). Females that are solely responsible for birthing and rearing of offspring are often required to seek more optimal foraging and/or roosting habitat than is required by males of the same species (Barclay, 1991). This is evident in many populations of bats where females travel further from winter hibernacula to higher quality habitat for the rearing of young (Barclay, 1991; Barclay, Faure & Farr, 1988; Thomas, 1988). This behaviour is evident in the NS eastern pipistrelles which appear to exhibit sexual segregation in summer habitat (all 22 captures in KNP were female). The necessity of this behaviour would likely be reinforced by the higher energy demands of birthing and rearing twins, as opposed to other Canadian bat species which usually have only one offspring per season (van Zyll De Jong, 1985). It will be essential to the viability of this population to identify and preserve the roosting conditions which allow the eastern pipistrelle to survive and successfully reproduce our region.

The eastern pipistrelle is a non-migratory species (Davis, 1966), and there are no records of individuals landing on ships in the Gulf of Maine along likely migratory routes such as exist for the migratory species that have been known to occur in the region (Carter, 1950; Mackiewicz *et al.*, 1956; Peterson, 1970). Therefore, it is unlikely that genetic flow between this population and those from mainland United States occurs via over-sea routes. Considering these issues, the Nova Scotia population is of national importance, but could also be at increased risk of extirpation.

Roosting Ecology

The conservation of suitable roost trees across the landscape may be crucial to maintain viable local populations of bats (Betts, 1998; Brigham *et al.*, 1997; Campbell, Hallett & O'Connell, 1996; Grindal, 1996). Especially at risk are species where females form maternity colonies in cavity trees, which are becoming increasingly scarce due to intensive forest management (Brigham *et al.*, 1997). (Kunz, 1982) suggested that the destruction of structures suitable for maternity roosts may be the most significant factor contributing to the decline of many species. However, bats which use buildings, foliage, and other roosting structures and are typically thought to be more flexible. The eastern pipistrelle appears to be generalist in its selection of roosting situations, having been found in buildings (Jones & Pagels, 1968; Winchell *et al.*, 1996), foliage of overstory trees (Carter *et al.*, 1999), Spanish moss of understory trees (Menzel *et al.*, 1999; Veilleux, Whitaker & Veilleux, 2003), and rock crevices (Lacki & Hutchinson, 1999). However, to date, only Veilleux et al. (2003) has done a comprehensive study of eastern pipistrelle roosting ecology. They found them to roost exclusively in clumps of foliage in oak (?) trees which formed an umbrella-like structure. Bats did not choose southern exposures for roosting and roost heights relative to the canopy were low. This might suggest that these bats were choosing situations where both low and high temperature extremes could be avoided. Thermoregulatory behaviour in eastern pipistrelles was also noted in a maternity colony inhabiting a barn in Massachusetts (Winchell *et al.*, 1996). This colony tended to move to a cooler position when ambient temperatures rose during the mid-day. While it is often hypothesised that tree-roosting reproductive females will select roosting situations to exploit warmer temperatures, evidence suggests that female eastern pipistrelles may be selecting for situations where temperature extremes are avoided. There is no information available of male roosting ecology.

The Nova Scotia population of eastern pipistrelles demonstrates different roosting behaviour than other records indicate. In KNP, we found that females roost almost exclusively in clumps of *Usnea trichodea* spp. (bony beard lichen) hanging from branches that point northward, and switch trees regularly. It is likely that this situation

allows colonies the warmth of the morning and evening sun, while sheltering them from more direct mid-day sun when ambient temperatures are higher. This behaviour suggests that diurnal thermoregulation is an important energy conservation strategy for the population.

The Nova Scotia population of eastern pipistrelles is at the extreme northern limit of the species' range and the population appears to be small and localized relative to the two sympatric *Myotis* spp. (Broders, Quinn & Forbes, 2003; Rockwell & Broders, 2004). It is possible that roosting behaviour exhibited by individuals in KNP is an adaptation unique to the area that is essential for survival and successful reproduction in the colder Canadian climate. Deviation from this behaviour by reproductive females might have deleterious consequences in terms of over-winter survival if inadequate energy is stored in the summer by either adults, or their offspring.

Temperature is a crucial environmental factor in all stages of a bat's life. Female bats in temperate zones must accumulate enough body fat during summer to rear young and survive winter hibernation. In northerly climes, hibernacula which afford suitable thermal conditions are often limited, and bats are challenged to store adequate energy reserves to survive. This is especially true for bats in their first years, and for reproductive females which allocate much energy in summer to rearing young. It should be expected that in a northern population where temperature is a key limiting factor for survival, less flexibility might be exhibited in roosting behaviour as bats are forced to use only roosts with the optimal conditions. This behaviour, and indeed the conditions, may be unique to the population but if the important roost site selection variables are identified, we will gain important insight into the microclimate requirements for the species in general.

The preservation of adequate roosting conditions requires the preservation of important variables such as *U. trichodea* which also plays an important role in the roosting ecology of other species in Nova Scotia such as the northern and southern flying squirrels and the northern parula. Very little is known about the ecology of lichens in

general and while some have investigated associations of *Usnea* spp. with certain forest and tree conditions such as age and diameter (Arseneau, Ouellet & Sirois, 1998; Boudreault *et al.*, 1993; Gauslaa, Ohlson & Rolstad, 1998; Rolstad & Rolstad, 1999), no clear relationships have been established.

Foraging Ecology

Broders *et al.* (2003) found that nocturnal activity was higher over water bodies, and higher over rivers than lakes. While sampling was conducted on Brier Island, Bon Portage Island, and in Kejimkujik National Park, pipistrelles were only recorded within the park during this study. Rockwell (2004) also found little or no eastern pipistrelle activity in other areas of NS. Despite this, there is likely a localized abundance of males outside of KNP but within a short radius of one or more important hibernacula which have yet to be identified.

Bats select foraging sites based on some combination of prey abundance and physical attributes of the site such as proximity to suitable roosts, wind speed accessibility, and navigability (Grindal, 1996), which are strongly dictated by the physiology of the species. The eastern pipistrelle has a higher aspect ratio than the other two sympatric species of *Myotis* and has higher intensity call with a longer constant frequency segment and lower peak frequency, which is better suited to foraging in lower clutter habitat (Saunders & Barclay, 1992). These characteristics would indicate that the species has evolved to forage in open areas.

In other regions, eastern pipistrelles have been found foraging in open areas such as fields, openings, or over water (Carter *et al.*, 1999; van Zyll De Jong, 1985), and have been observed foraging over the forest canopy. Despite this it was predicted that their activity would be concentrated over the water, and more specifically, over rivers as we found in 2001. We did not rule out foraging niches such as bogs, canopy gaps, and over-canopy, and conducted sampling at representatives of those site types.

Insect prey is generally more abundant over water, but is affected by wind. River corridors would have lower wind speeds and be easier for bats to navigate and forage in than open areas such as lakes (Verboom & Huitema, 1997; Verboom & Spoelstra, 1999) and more cluttered forest environments. The effects of wind on prey are lessened in sheltered areas (Karg and Ryskowski 1985) such as river corridors as opposed to lakes. Species which typically feed over water such as *M. lucifugus* will take advantage of ephemeral concentrations of different prey types as they emerge throughout the season (Belwood & Fenton, 1976). There have been no prior comprehensive studies of foraging behaviour of the eastern pipistrelle although similar prey selection behaviour might be expected over waterways.

Study Area and Scope

This study was conducted in the eastern portion of Kejimkujik National Park and historic site (44° 23' N 65° 17' W), where a sparse road network allows for transportation of equipment to various sites. The study area also extends to the north and east, outside the park, incorporating privately owned land which is sparsely populated and intensively managed for forestry and farming.

The forest cover of the Park is representative of the Atlantic Uplands forest region, including mixed coniferous and deciduous Acadian forests. The area is marbled with oligotrophic rivers, lakes, fens, and bogs. While much of the forest has been disturbed by past logging, stands of large old growth hemlock (*Tsuga canadensis*) and sugar maple (*Acer sacharum*) -yellow birch (*Betula allegheniensis*) still occur.

The study area is approximately 80 km^2 and was based on the distribution of roost trees that were found in the park (see Appendix A), and the availability of river and lake site replicates for the echolocation monitoring portion of the study. The greater study area for the roosting ecology phase was defined as a 5 km radius circular area encompassing the roost sites. The study area for the foraging portion will largely overlap

that of the roosting study but will be defined by an agglomeration of 5km radius circles centered on echolocation sampling sites. Five km circles were chosen *ad hoc*, to represent the minimum home range for the eastern pipistrelle

The field work for this project spanned two summer seasons lasting from late May until late August for the years 2003 and 2004. Field work was primarily conducted by myself and one to two other research assistants with periodic help from Hugh Broders (my supervisor), and volunteers, when available. Accommodations were located within the study area.

OBJECTIVES

The objectives of this study are:

Roosting ecology:

1)   To determine which variables or groups of variables best differentiate conditions at known roost trees from the conditions at available roost trees across the landscape.

2)   To determine which combinations of a variety of fine-filter and coarse-filter variables best differentiate conditions at known roosting sites from available sites at the landscape-level.

Foraging ecology:

3)   To determine which variables or groups of variables best predict foraging activity at a site as measured by recording of echolocation.

METHODS

To determine roosting and foraging habitat use, a variety of methodologies were employed including trapping bats and insects, radio telemetry, and ultrasonic monitoring.

Trapping was used to assess population structure, reproductive status and to capture animals for radio telemetry. Radio telemetry was used to locate roost trees and opportunistically to gather information on nocturnal activity of radio-tagged bats. Ultrasonic monitoring was used to measure bat activity at different sites so that variables that explain spatial and temporal aspects of eastern pipistrelle activity could be identified. Insects were sampled simultaneously at ultrasonic monitoring sites to provide information on spatial distribution of prey as an independent variable to explain patterns of bat activity.

Roosting Ecology

Free-flying bats were captured over a river site after sunset using various arrangements of 12 meter-long mist nets (30mm mesh size; Avinet, PO Box 1103, Dryden, NY, 13053-1103) in groups of two to four. Mist nets were hoisted on extendable fibreglass poles attached to the bridge and positioned at heights from four to eleven meters above the water to target the high-flying (relative to sympatric species) eastern pipistrelles. Trapping efforts targeting the eastern pipistrelle were made at various river sites where some eastern pipistrelle activity was identified but were unsuccessful. As a result, the majority efforts were focussed at the Eel Weir Bridge site. At this site, a more permanent apparatus was constructed for hoisting nets above the bridge. Three masts were built using 4"X4" lumber, with fibreglass pruning poles attached to the ends, allowing mist nets to be hoisted as high as 12 meters above the surface of the river. Despite the relatively high level of activity at the site, trapping success remained low, at approximately one capture for every 70 mist net hours. Additional simultaneous trapping was conducted opportunistically along nearby forested trails and roads using harp traps (Austbat Research Equipment, Lower Plenty, Victoria, Australia) targeting the two sympatric *Myotis* spp..

From all captured individuals we recorded species, sex, age (young-of-the-year vs. adult), mass (g), forearm length (mm), ear length (mm). We also collected a small

sample of the plagiopatagium from each wing for future genetic and/or stable isotope analyses, a hair sample for potential toxicological analysis and attached a unique (varied color and number combinations) plastic split-ring band (3.1 mm inside diameter; L&M Bird Leg Bands, Inc., PO Box 2943, San Bernardino, CA, 92406, USA) on the forearm (left for females, right for males). The edges of all bands were filed smooth before being used to lessen chance of injury to the animals. We attached ≈0.4g radio transmitters (LB-2N model; Holohil Systems Ltd., Carp, Ontario, Canada) using surgical adhesive (SkinBond, Smith and Nephew United, Inc., Largo, Florida, USA) that permitted us to locate roost trees using a receiver (Advanced Telemetry Systems, Inc., Isanti, MN, U.S.A.) and a folding 3-element Yagi antennae (AF Antronics, Urbana, IL, U.S.A.) which was done on the next day following release, and every day until the transmitter fell off or the battery died. Once the roost tree was identified, binoculars were used to locate the specific roost location on the tree, and detailed notes were taken so that the roost location could be found for further data collection when the bats were absent. We opportunistically observed emergence at roosts to count the number of bats in the colony and record time of emergence for each.

On a day when bats were not using a known roost tree, site-metrics were recorded for a 17.9 m radius circular plot (0.1 ha) centered on the tree. Because of a lack of previous knowledge about the specific roosting behaviour for the eastern pipistrelle, it was necessary to adjust the protocol for these plots over the course of the first season as we learned more about the roosting ecology of this population. Since eastern pipistrelles in KNP in 2003 were found to roost almost exclusively within clumps of bony beard lichen (*Usnea trichodea* Ach.), an index for rating the *U. trichodea* conditions in a tree canopy was developed using a scale of 0-5; zero representing no visible *U. trichodea*, and five representing a tree heavily laden with many hanging clumps of *U. trichodea* throughout the entire crown. A value of two on the scale is used for trees with the some clumps of *U. trichodea* which appear large enough to host a colony of eastern pipistrelles. To maintain consistency, I estimated the Usnea index (UI) for all trees. For the roost tree, the *Usnea Index*, and a variety of other variables were measured. All roost tree heights were measured using a Sunnto clinometer. Canopy closure around the roost tree

was measured one pace from the bole of the roost tree in the four cardinal directions (E, W, N and S) using a densiometer, and an average of these estimates was used. The species and condition of the roost tree were also recorded. Stand conditions were described in terms of species composition, possible disturbance history, slope, and aspect. The total number of deciduous, coniferous, and snags were counted in each plot for each major strata. The number of snags in the plot, and the number of trees as tall as the roost tree within a 5 meter radius were also recorded.

One hundred randomly placed 0.1 ha plots were conducted throughout the study area with a similar protocol as the known roost plots except no specific roost site information will be recorded on the center tree. The center tree for the random plots was the closest tree to the geographic center (as indicated using the GPS unit) with a height greater than six meters. Live or dead trees could be used.

The goal of this part of the study is to learn which variables or groups of variables best explain the difference (if any) between known roost sites and random roost sites using two different scales of analysis. The broader scale aims to determine which combination of a variety of variables ranging from the individual tree-level, to the landscape level best explain the difference between known roost areas (plots), and randomly sampled areas. The finer scale uses a set of variables at the individual tree level to determine which best explain the difference between used trees and those available throughout the study area.

For the coarse-scale analysis, roost data from both of the two years were combined and analysed using binomial generalized linear models with a logit link in S-PLUS 2000 (Mathsoft 1999). We used the methods of Hosmer and Lemeshow (2003) for logistic regression to determine which sets of variables best distinguished used plots from the random sample plots, where known roost plots are assigned a value of one and random plots, a zero. Because there are no previous studies which use such modelling to rank variables for the eastern pipistrelle, and this population exhibits different roosting behaviour than existing knowledge would indicate (Veilleux *et al.*, 2003; Whitaker, 1998;

Winchell *et al.*, 1996), a set of variables were derived, some of which are derived *a priori* based on some variables found important to other sympatric species (Broders & Forbes, 2004b; Foster & Kurta, 1999; Grindal, 1999; Lacki & Baker, 2003; Lacki & Schwierjohann, 2001; Sasse & Pekins, 1996), and other *ad hoc* variables relating to *U. trichodea* spp. which were developed as we learned about their behaviour. The spatial variable of 'distance to water' was be measured using Arview GIS 3.2 (ESRI, 2000) in conjunction with G.I.S. forest coverage of the study area. The categorical variables (*ie*. tree species) included in the models were transformed into design variables, which were simplified into two possible outcomes (ie. Softwood = 1, non-softwood = 2) to reduce the number of variables to trim down the estimated standard errors. The variable of crown closure was transformed *ad hoc* to better fit the observation that the mean crown closure at roost sites was 45% above or below-which the chances of finding a roost dropped. As a result, the variable was represented as the absolute value of the distance from 45% crown closure. For example, a crown closure of 30% would be 15% from 45% and would be the scaled the same as a crown closure of 60%.

The seven variables used were:

1) *dtw* -distance to water in meters (lakes or rivers).
2) *nut* - *U. trichodea* conditions in the stand (number of trees with Usnea index greater than two)
3) *tat* - number of trees as tall the roost tree within 5m radius of the roost tree.
4) *cc* - canopy closure
5) *uir* - Usnea index of the roost tree (scale of 1-5 reflecting number of potential roost positions).
6) *lod* - Live or dead. (dead=1, live=0)
7) *psw* - percent softwood of the stand by stem count within the plot.

We synthesised these variables into a set of 25 of a possible 720 models (see Appendix C). We used the small sample variant of the Akaike Information Criterion for overdispersed data (QAIC$_c$) (Akaike, 1973) to rank them. AIC was calculated with the S-PLUS command *extractAIC* in the MASS library (Venables & Ripley, 1997) and AIC$_c$

was calculated on a spreadsheet. The Akaike weights which represent the probability that the i-th model is the best approximating model among all the candidate models, given the data, w_i ; (Burnham and Anderson 2003) was also calculated. For the set of models that make up $\geq 95\%$ of the Akaike weights, we will show the difference between the AIC_c of each model and the AIC_c of the best model (i.e., with the smallest AIC_c ; Δ_i), the model Akaike weight (w_i) and sum of the Akaike weights of the i-th model and all higher ranking models.

To determine which variables best explain the difference between known and random plots, we calculated the variable relative-importance weights for all variables appearing in the 95% confidence set (Burnham and Anderson 2002). This is because while some models may be important, the individual variables which comprise them may not be significant on their own. If a particular variable has importance weight ($\sum w_i$) greater than 0.60, then we considered it important (Broders and Forbes 2004). For all important variables, we presented the model-averaged parameter estimates, estimated unconditional standard errors and relative-importance weights (Burnham and Anderson 2002). Odds ratios were calculated by taking antilogarithm of the parameter estimates.

For the individual tree-level analysis, the variables which best distinguish used roost trees from available trees in the study area were investigated.   Roost trees were compared to the center trees in the random plots using a logistic regression similar to that used in the coarse scale comparison. With the exception of the '*Usnea* Index', the variables for this analysis which were selected *a priori*:

1) *dbh* - diameter at breast height.
2) *tht* – tree height.
3) *sw* - Is the roost tree a conifer (yes=1, no=0).
4) *uir* – *Usnea* index of the tree.

Using combinations of these four variables, seven of a possible 24 models have been constructed and were assessed using the same AIC method described above for the landscape level analysis.

To examine selection of roost-site exposure, we used circular statistics to analyse directional data (Batschelet, 1981). Raleigh's test was used to test for uniformity in the direction that roosts were oriented.

Foraging Ecology

For echolocation sampling, weatherproofed automated ultrasonic detectors (Anabat, Titley Electronics, Ballina, N.S.W., Austrailia) are interfaced with laptop computers through zero-crossing analysis interface modules. The reception areas for all detectors are standardized (Krusic *et al.*, 1996; Larson & Hayes, 2000) at a sensitivity level of ≈ 6. The magnitude of activity at a site is assumed to be represented by the total bytes of echolocation calls recorded for a given species (Broders, 2003). Detectors are always placed so that the cone of reception points along the edge of the opening. On rivers, they are always pointed upstream.

In 2003, the first month of echolocation monitoring involved non-systematic sampling throughout the park and at sites to the north and east of the park. This sampling was done in an effort to learn more about the local distribution of eastern pipistrelles and to identify "hot spots" of activity in the area. In 2001, Broders *et al.* (2003) identified one particular river site in KNP at which 60% of all recorded pipistrelle activity (Broders *et al.* 2003). If other such sites existed in the area, they would be important to identify as they would:

1) Provide additional trapping sites.
2) Offer a better understanding of the distribution of eastern pipistrelle activity across the landscape.

3) Provide replicates of high-activity sites which would help us understand the variables which affect activity.

4) Help to define the study area.

During this period, no other "hot spots" were found in or around the KNP. In fact, very little activity was recorded outside the park. In July, after not identifying any other key foraging sites, we began a system of simultaneous insect trapping and recording, used in systematic randomized block sampling scheme of rivers, lakes, canopy gaps, and forested roads [5 sites for each of 4 different site types (20 sites)* 4 blocks = 80 detector nights (1 detector night represents one entire night of sampling at a given site by an ultrasonic detector)]. To do this required a method to control for the increased bat activity associated with clusters of phototactic insects around the insect light traps. Four ultraviolet light traps were equipped with timers that activate them for three 30-minute periods of the night. Echolocation sequences recorded during the active insect-trapping periods and an additional 15-min buffer period immediately following were removed from analyses so that the effects of the lights on recorded activity would be minimal. By this, we are able to examine the influence of both site type and prey abundance on bat activity at a site (see Appendix E for data summary). Opportunistic sampling was also done at various bog sites as well as over the forest canopy. No eastern pipistrelle activity was recorded at these sites.

This portion of the study was originally designed to be conducted over two field seasons, and a multiple linear regression was to be used to determine which habitat variables best explained high levels of foraging activity. However, only one season of sampling was conducted, and variability both between sites and between sampling nights was very strong, so that standard errors would be too large to divine any sound statistical inference without much larger sample sizes over several seasons. Instead, simple temporal and spatial trends in activity were observed and recorded.

Capture Results

Over the 2003 and 2004 seasons, over 1200 trap-hours (defined as one 6m mist net deployed for one hour or one harp trap deployed for one hour) yielded a total capture of 115 bats, of which only 22 were *P. subflavus.* One of these (a male) was captured at a hibernacula (Hayes Cave), and all others were female and captured at Eel weir bridge in KNP, despite frequent efforts at other locations. Of these 21 individuals, 20 were affixed with radio-transmitters by which there were a total of 60 roost trees located.

Table 1) Capture data including body mass by species and age with standard of deviation and number captured in parentheses.

Species	Adult (g)	Juvenile (g)	Second Year (g)	Total (g)
M. lucifugus	8.7 ± 1.4 (44)	6.9 ± 0.9 (9)	7.44 ± 1.0 (5)	8.3 ± 1.5 (58)
M. septentrionalis	7.7 ± 0.8 (25)	7.2 ± 0.8 (7)	6.7 ± 0.1 (3)	7.5 ± 0.8 (35)
P. subflavus	8.4 ± 1.4 (14)	5.9 (1)	7.2 ± 0.4 (7)	7.9 ± 1.3 (22)
All Species	8.3 ± 1.3 (83)	6.9 ± 0.9 (17)	7.2 ± 0.7 (15)	8.0 ± 1.3 (115)

Roosting Ecology

For the eastern pipistrelle a total of 64 roost trees were found for seven distinct colonies. Distance of roosts from the capture point varied from 0.3 – 5 km. In general, eastern pipistrelles showed roost area fidelity but switched trees regularly. They were colonial roosters (3-15 individuals per colony while reproductive) and primarily in softwoods in clumps of *Usnea trichodea* on small diameter branches pointing in a northward direction. The average number of days a roost tree was used was 2.3 (1.5 SD); the average height of the roost tree was 16.5m (2.9 SD); the average diameter at breast height was 24.5 (6.9 SD); the average height of the roost site was 10.3 (2.7 SD); the average crown closure around the roost trees was 45% (15.1 SD); the average estimated basal area was 20.1 m^2/ha (7.6 SD). Of the 64 roost trees only ten were in deciduous trees and only four roost locations were not in clumps of *Usnea trichodea* and these were not during the reproductive period.

Stand level landscape analysis:

The model which best explained the difference between the conditions at known roost plots and those at random roost plots at the coarse scale contained the variables: percent softwood, number of trees as tall as within five meters of the roost, the usnea index of the roost tree, and the distance to the nearest water body (Table 2). This model had a much higher weight than the other models in the 95% confidence set combined which would suggest that relative to other models tested, this model explains roost site selection very well.

Table 2) Akaike weights for the 95% confidence set of models for roost site selection.

Rank	Variables in the logistic models	Δ_i	w_i	$\sum w_i$
1	psw+tat+uir+dtw	0.000	0.365	0.646
2	tat+cc+psw+uir+dtw	1.225	0.198	0.178
3	nut+psw+dtw+tat+uir	1.898	0.141	0.100
4	dtw+psw+uir	3.540	0.062	0.075

Of all variables included in the 95% confidence set of models, only four of the six are important according to our 0.6 importance weight criterion (Table 3). These variables are: percent softwood of within the plot (positive relationship), the usnea index of the roost tree (strongly positive relationship), the distance to the nearest body of water (negative relationship), and the number of trees as tall as the roost tree within five meters (negative relationship). The importance weights for these four are much higher than the fifth most important variable on the list, and are those that comprise the best fitted model in Table 2.

Table 3) Multi-model inference showing the relative importance of the variables included in the 95% confidence set of models (with the increments that were used to scale the variable in parentheses). Only the top four variables have greater than 0.6 importance weights ($\sum w_i$) and are deemed important.

Rank	Variable (increments)	Importance Weight ($Nw_{i\,i}$)	MA PE	EU SE	Odds Ratio (CI 95%)
1	*psw*- percent softwood of stand (10)	**1.000**	0.052	0.025	1.690(1.640,1.739)
1	*uir*- *Usnea* index of roost tree (1)	**1.000**	2.230	0.516	9.304(8.292,10.316)
1	*dtw* -distance to nearest water (200m)	**1.000**	-0.006	0.003	0.310(0.304,0.316)
4	tat- trees as tall as roost tree (2)	**0.925**	-0.687	0.390	0.253(-0.511,1.018)
5	cc- crown closure (10% from 45)	0.178	-0.008	0.017	0.927(0.894,0.960)
6	Nut- number of *Usnea* trees in plot (5 trees)	0.100	0.001	0.006	1.007(0.995,1.019)
		y-intercept	-2.579	1.750	0.076(-3.355,3.506)

<u>Tree level landscape analysis:</u>

At the smaller scale of the individual roost tree, the model which best explains the difference between used trees and available trees is that containing the three variables: *Usnea* index of the tree (uir), live or dead condition (lod), and whether the center tree is conifer or deciduous (sw) (Table 4). While there are several models within the 95% confidence set for this analysis, the top model has more than twice the weight as the second most important model. It should be noted, however that the second model is a single variable which is not included in the top ranked model.

Table 4) Akaike weights for the 95% confidence set for roost tree selection.

Rank	Model	Δ_i	w_i	$\sum w_i$
1	sw+lod+uir	0	0.317	0.317
2	ht	1.44702	0.154	0.154
3	ht+uir+sw+lod	1.54589	0.146	0.146
4	lod+uir+ht	1.87919	0.124	0.124
5	lod	2.77371	0.079	0.079
6	ht+sw+uir	3.22709	0.063	0.063
7	sw	3.2681	0.062	0.062
8	sw+uir	3.53958	0.054	0.054

Of all the variables that occur in the models comprising the 95% confidence set, only three of the four are deemed important. These are the usnea index of the roost tree *uir* (positive) , whether the roost tree is alive *lod* (positive), and whether or not it is a conifer or a deciduous tree *sw* (weakly positive) (Table 5). The moderate odds ratios which indicate the nature of the variable's relationship with roosting occurrence, and the presence of so many models in the 95% confidence set with a fairly gradual spread in Akaike weights would suggest that the models used to explain habitat use at the stand scale are likely more useful than these models applied to the individual tree scale.

Table 5) Multi-model inference showing the relative importance of the variables included in the 95% confidence set of models (with the increments that were used to scale the variable in parentheses). Only the top three variables have greater than 0.6 importance weights ($\sum w_i$) and are deemed important.

Rank	Variable	Imp.Weight (Nw_{ii})	MAPE	EUSE	Odds Ratio (CI 95%)
1	*Usnea* (1)	**0.704938**	0.322566	0.212859	1.381(-1.325,4.087)
2	**Live or Dead tree (y/n)**	**0.666966**	0.133142	0.113967	1.142(-1.097,3.382)
3	**Softwood? (y/n)**	**0.642867**	0.05418	0.099389	1.056(-1.013,3.125)
4	Tree height (3m)	0.487516	0.018356	0.031565	1.057(-1.014,3.128)
	y-intercept		-2.74773	0.371954	1.381(-1.325,4.087)

Coarse Scale Landscape Comparison:

    All of the roosting colonies were located to the northwest of Eel Weir Bridge where all of the pipistrelles were captured. The landscape composition of this area was compared to the greater area which is equal to a 5km radius around Eel Weir Bridge. This radius was chosen as it was the furthest distance from the capture point at which a colony was found so that it was assumed that a bat could travel that distance to roost in any direction. What we hoped to determine is why they only use one particular direction. The analysis was done using GIS and the variables chosen were limited to those that could be compared using the available spatial data. The variables used were the proportion of water in the used area vs the unused area, and the proportion of mature softwood in the used area vs the unused area. What we found was that there was much more water in the used portion of the landscape compared to the available landscape. Contrary to what we predicted, there was a slightly greater proportion of mature softwood in the available landscape than the used landscape.
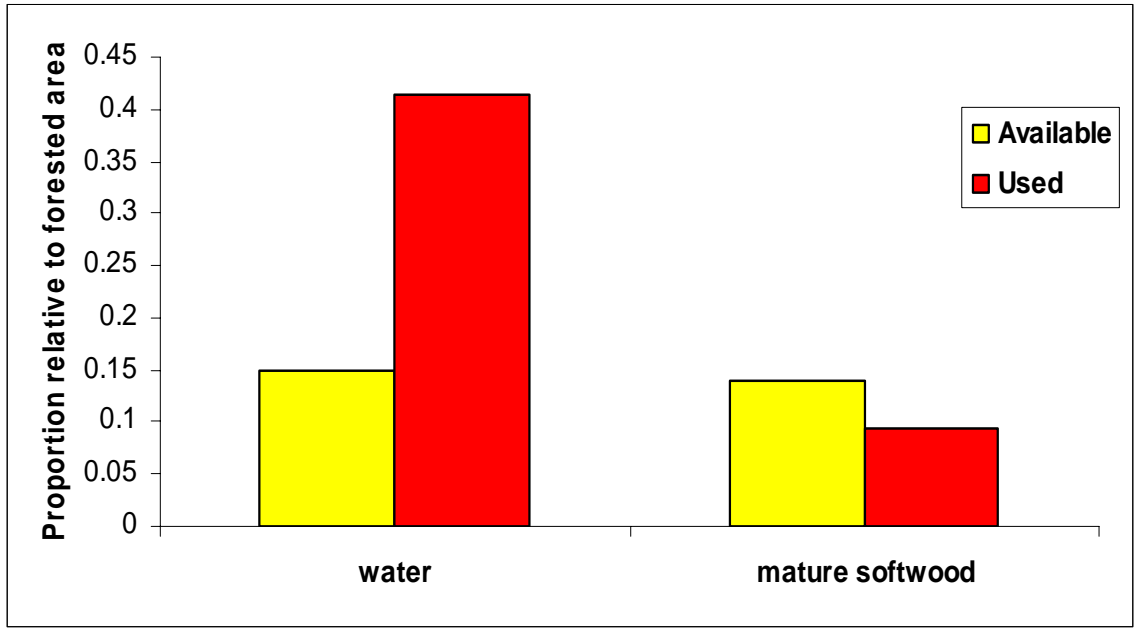
Figure 1) A comparison of two landscape variables within the used and available portions of the study area.

Roost orientation:

Bats were found to roost within a very small range of exposures, limited to the NNW side of the tree without exception.

Table 6) Circular statistical values for roost orientation.

Mean Angle	339.947
Mean Vector	0.851
Ang. S.D.	31.245
Ang. Var.	976.272
Circ. S.D.	32.511
Circ. Var.	1056.962
95%CL (±)	11.045
Count	47.000
Rayleigh's Z	34.062
Prob(Z)	0.000
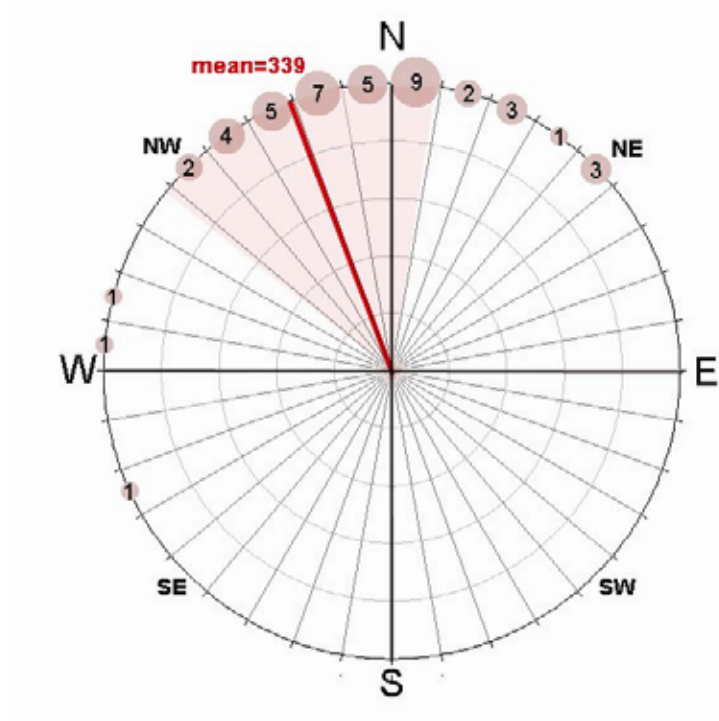
Figure 2) A graphical display of roosting orientation including the mean and standard deviation in pink.

Foraging Behavior

Non-systematic ultrasonic surveys:

We recorded 16,400 echolocation sequences over 48 detector nights at 28 different sites. Low levels of eastern pipistrelle activity were found at river and lake sites to the north and east of KNP. Haphazard sampling of water sites in the area did not identify any new areas of high eastern pipistrelle activity outside of KNP. None of the sites sampled have comparable activity levels to the Eel Weir river site within the park at which eastern pipistrelle activity is relatively very high. In general, there are greater levels of eastern pipistrelle activity within the park than in areas sampled outside. Also, only one eastern pipistrelle sequence was recorded over the forest canopy, and none were recorded over bogs.

In the randomized block portion of the survey, 31,000 files were recorded over 80 detector nights. The magnitude of activity of *P. subflavus*, as determined by ultrasonic surveys, was about 10% of the magnitude of activity of *Myotis* spp. Seventy percent of *P. subflavus* activity was recorded over rivers, 94% over rivers and lakes combined (see Figure 3). Sixty percent of total eastern pipistrelle activity was recorded at one site (Eel Weir river) which was also where we captured 38% of the total insect biomass collected. A further 21% of eastern pipistrelle activity was recorded at two lake sites. However, bat activity at a given site was not highly correlated with prey availability (correlation coefficients of 0.37 for *Myotis spp.* and 0.43 for eastern pipistrelle). Also, on 01 July 2003, 10 m above the river at Eel Weir we recorded 7 echolocation sequences that were attributable to either big brown bat or silver-haired bat.
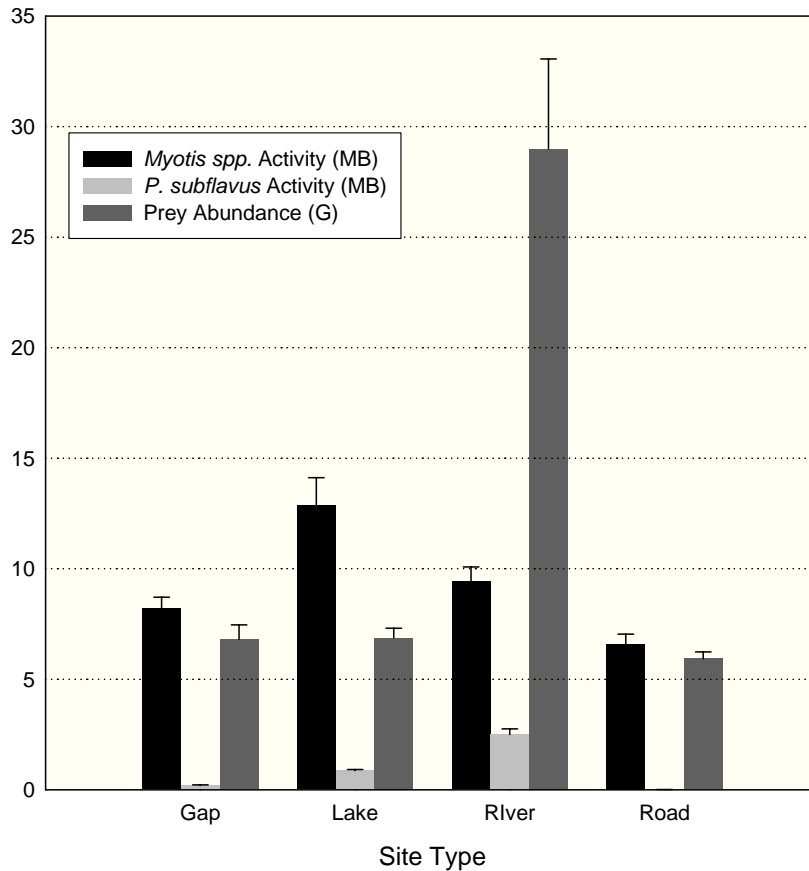
Figure 3). Summary of bat activity (in megabytes; See Broders 2003) and prey abundance (grams) for each of the four site-types.

Activity over the night:

Nightly activity patterns show greatest activity was early in the night at river and gap sites, while activity at lake sites was more consistent through the night (Figure 4.).
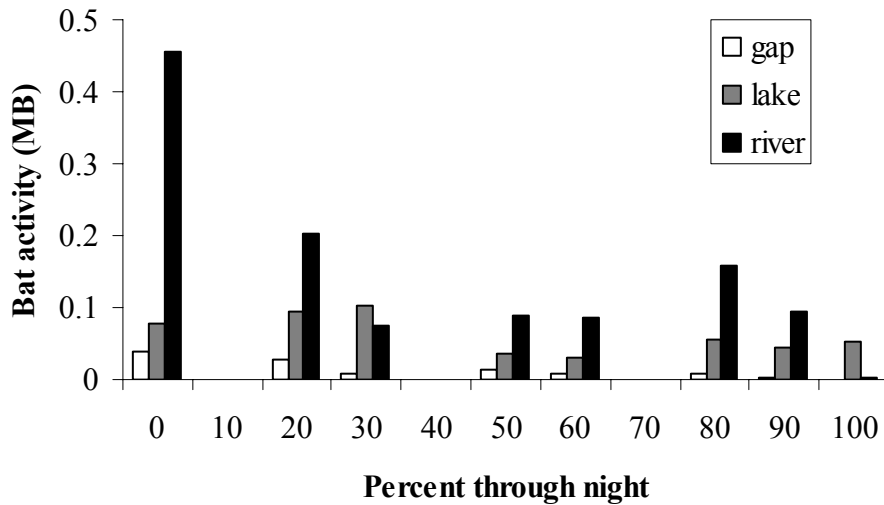

Figure 4). Activity levels for *P.subflavus* in Megabytes by percent through night at gaps, lakes, and rivers. Insect trapping took place during periods 10, 40, and 70 which have been removed.

REFERENCES

Akaike, H., ed. (1973) *Information theory as an extension of the maximum likelihood principle.*, pp 267-281. Akademiai Kiado, Budapest.

Ammerman, L.K. (2005) Noteworthy records of the eastern pipistrelle, Perimyotis subflavus, and silver-haired bat, Lasionycteris noctivagans, (Chiroptera : Vespertilionidae) from the Chisos Mountains, Texas. *Texas Journal of Science*, **57**, 202-207.

Armstrong, D.M., Adams, R.A., & Taylor, K.E. (2006) New records of the eastern pipistrelle (Pipistrellus subflavus) in Colorado. *Western North American Naturalist*, **66**, 268-269.

Arseneau, M.J., Ouellet, J.P., & Sirois, L. (1998) Fruticose arboreal lichen biomass accumulation in an old-growth balsam fir forest. *Canadian Journal of Botany-Revue Canadienne De Botanique*, **76**, 1669-1676.

Barclay, R.M.R. (1991) Population structure of temperate zone insectivorous bats in relation to foraging behavior and energy demand. *Journal of Animal Ecology*, **60**, 165-178.

Barclay, R.M.R., Faure, P.A., & Farr, D.R. (1988) Roosting behavior and roost-selection by migrating silver-haired bats (*Lasionycteris noctivagans*). *Journal of Mammalogy*, **69**, 821-825.

Beazley, K. & Cardinal, N. (2004) A systematic approach for selecting focal species for conservation in the forests of Nova Scotia and Maine. *Environmental Conservation*, **31**, 91-101.

Belwood, J.J. & Fenton, M.B. (1976) Variation in the diet of *Myotis lucifugus* (Chiroptera: Vespertilionidae). *Canadian Journal of Zoology*, **54**, 1674-1678.

Betts, B.J. (1998) Roosts used by maternity colonies of silver-haired bats in northeastern Oregon. *Journal of Mammalogy*, **79**, 643-650.

Bleakney, J.S. (1965) First specimens of the eastern pipistrelle from Nova Scotia. *Journal of Mammalogy*, **46**, 528-529.

Boudreault, C., Bergeron, Y., Gauthier, S., & Drapeau, P. (1993) Bryophyte and lichen communities in mature to old-growth stands in eastern boreal forests of Canada. *Canadian Journal of Forest Research*.

Briggler, J.T. & Prather, J.W. (2003) Seasonal use and selection of caves by the eastern pipistrelle bat (*Pipistrelleus subflavus*). *American Midland Naturalist*, **149**, 406-412.

Brigham, R.M., Vonhof, M.J., Barclay, R.M.R., & Gwilliam, J.C. (1997) Roosting behavior and roost-site preferences of forest-dwelling california bats (*Myotis californicus*). *Journal of Mammalogy*, **78**, 1230-1239.

Broders, H.G. (2003) Another quantitative measure of bat species activity and sampling intensity considerations for the design of ultrasonic monitoring studies. *Acta Chiropterologica*, **5**, 235-241.

Broders, H.G., Findlay, C.S., & Zheng, L. (2004a) The effects of clutter on echolocation call structure of *Myotis septentrionalis* and *M. lucifugus*. *Journal of Mammalogy*, **85**, 273-281.

Broders, H.G. & Forbes, G.J. (2004b) Interspecific and intersexual variation in roost-site selection of northern long-eared and little brown bats in the greater Fundy National Park Ecosystem. *Journal of Wildlife Management*, **68**, 602-610.

Broders, H.G., McAlpine, D.F., & Forbes, G.J. (2001) Status of the eastern pipistrelle (Pipistrellus subflavus) (Chiroptera : Vespertilionidae) in New Brunswick. *Northeastern Naturalist*, **8**, 331-336.

Broders, H.G., Quinn, G.M., & Forbes, G.J. (2003) Species status, and the spatial and temporal patterns of activity of bats in southwest Nova Scotia, Canada. *Northeastern Naturalist*, **10**, 383-398.

Campbell, L.A., Hallett, J.G., & O'Connell, M.A. (1996) Conservation of bats in managed forests: Use of roosts by *Lasionycteris noctivagans*. *Journal of Mammalogy*, **77**, 976-985.

Carter, T.C., Menzel, M.A., Chapman, B.R., & Miller, K.V. (1999) Summer foraging and roosting behavior of an eastern pipistrelle, *Pipistrellus subflavus*. *Bat Research News*, **40**, 5-6.

Carter, T.D. (1950) On the migration of the Red Bat, *Lasiurus borealis borealis*. *Journal of Mammalogy*, **31**, 349-350.

Davis, W.H. (1966) Population dynamics of the bat *Pipistrellus subflavus*. *Journal of Mammalogy*, **47**, 383-396.

ESRI (2000) ESRI ArcView GIS. Environmental Systems Researc Institute Inc., Redlands CA, USA.

Foster, R.W. & Kurta, A. (1999) Roosting ecology of the northern bat (Myotis septentrionalis) and comparisons with the endangered Indiana bat (Myotis sodalis). *Journal of Mammalogy*, **80**, 659-672.

Fujita, M.S. & Kunz, T.H. (1984) *Pipistrellus subflavus*.

Fuller, S. (1998). Atlas of rare, threatened and infrequent fauna of Nova Scotia.

Gauslaa, Y., Ohlson, M., & Rolstad, J. (1998) Fine-scale distribution of the epiphytic lichen Usnea longissima on two even-aged neighbouring Picea abies trees. *Journal of Vegetation Science*, **9**, 95-102.

Geluso, K., Mollhagen, T.R., Tigner, J.M., & Bogan, M.A. (2005) Westward expansion of the eastern pipistrelle (Pipistrellus subflavus) in the United States, including new records from New Mexico, South Dakota, and Texas. *Western North American Naturalist*, **65**, 405-409.

Grindal, S.D. (1996). Habitat use by bats in fragmented forests. In *Bats and Forests Symposium* (eds R.M.R. Barclay & R.M. Brigham), pp. 260-272. British Columbia Ministry of Forests, Victoria, Canada.

Grindal, S.D. (1999) Habitat use by bats, *Myotis* spp., in Western Newfoundland. *The Canadian Field-Naturalist*, **113**, 258-263.

Healy, M.J. (2002) *Abundance of bat species during autumn in Fredericton, New Brunswick*, University of New Brunswick.

Hoofer, S.R. & Van Den Bussche, R.A. (2003) Molecular phylogenetics of the chiropteran family Vespertillionidae. *Acta Chiropterologica*, **5, supplement**, 1-63.

Jones, C. & Pagels, J. (1968) Notes on a population of *Pipistrellus subflavus* in southern Louisiana. *Journal of Mammalogy*, **49**, 134-139.

Krusic, R.A., Yamasaki, M., Neefus, C.D., & Pekins, P.J. (1996) Bat habitat use in White Mountain National Forest. *Journal of Wildlife Management*, **60**, 625-631.

Kunz, T.H. (1982). Roosting ecology. In *Ecology of bats* (ed K. TH), pp. 1-56. Plenum Press, New York.

Kurta, A. & Teramino, J.A. (1994) A Novel Hibernaculum and Noteworthy Records of the Indiana Bat and Eastern Pipistrelle (Chiroptera: Vespertilionidae). *American Midland Naturalist*, **132**, 410-415.

Lacki, M.J. & Baker, M.D. (2003) A prospective power analysis and review of habitat characteristics used in studies of tree-roosting bats. *Acta Chiropterologica*, **5**, 199-208.

Lacki, M.J. & Hutchinson, J.T. (1999) Communities of bats (Chiroptera) in the Grayson Lake Region, northeastern Kentucky.:*Journal of the Kentucky Academy of Science*, **60**, 9-14.

Lacki, M.J. & Schwierjohann, J.H. (2001) Day-roost characteristics of northern bats in mixed mesophytic forest. *Journal of Wildlife Management*, **65**, 482-488.

Larson, D.J. & Hayes, J.P. (2000) Variability in sensitivity of Anabat II bat detectors and a method of calibration. *Acta Chiropterologica*, **2**, 209-213.

Mackiewicz, J. & Backus, R.H. (1956) Oceanic records of *Lasionycteris noctivagans* and *Lasiurus borealis*. *Journal of Mammalogy*, **37**, 442-443.

Menzel, M.A., Krishon, D.M., Carter, T.C., & Laerm, J. (1999) Notes on tree roost characteristics of the northern yellow bat (*Lasiurus intermedius*), the Seminole bat (*L. seminolus*), the evening bat (*Nycticeius humeralis*), and the eastern pipistrelle (*Pipistrellus subflavus*). *Florida-Scientist*, **62**, 185-193.

Mockford, S.W., Snyder, M., & Herman, T.B. (1999) A preliminary examination of genetic variation in a peripheral population of Blanding's turtle, *Emydoidea blandingii*. *Molecular Ecology*, **8**, 323-327.

Morse, D.H. (1980) *Behavioral mechanisms in ecology* Harvard University Press, Cambridge, MA, U.S.A.

Peterson, R.L. (1970) Another Red Bat, *Lasiurus borealis*, taken aboard ship off the coast of Nova Scotia. *Canadian Field-Naturalist*, **84**, 401.

Rockwell, L. & Broders, H.G. (2004) *The summer range and distribution of Nova Scotia bats*, Saint Mary's, Halifax.

Rolstad, J. & Rolstad, E. (1999) Does tree age predict the occurrence and abundance of *Usnea longissima* in multi-aged submontane *Picea abies* stands? *The Lichenologist*, **31**, 613-625.

Sasse, D.B. & Pekins, P.J. (1996). Summer roosting ecology of northern long-eared bats (*Myotis septentrionalis*) in the White Mountain National Forest. In *Bats and Forests Symposium* (eds R.M.R. Barclay & R.M. Brigham), pp. 91-101. British Columbia Ministry of Forests, Victoria, Canada.

Saunders, M.B. & Barclay, R.M.R. (1992) Ecomorphology of insectivorous bats: a test of predictions using two morphologically similar species. *Ecology*, **73**, 1335-1345.

Smith, K. (1999) COSEWIC Status report on Northern Ribbon Snake (*Thamnophis sauritus septentrionalis*). *Prepared for COSEWIC*.

Standing, K.L., Herman, T.B., & Morrison, I.P. (1999) Nesting ecology of Blanding's turtle (*Emydoidea blandingii*) in Nova Scotia, the northeastern limit of the species' range. *Canadian Journal of Zoology*, **77**, 1609-1614.

Thomas, D.W. (1988) The distribution of bats in different ages of douglas-fir forests. *Journal of Wildlife Management*, **52**, 619-626.

van Zyll De Jong, C.G. (1985) *Handbook of Canadian Mammals: Bats* National Museums of Canada, Ottawa, Canada.

Veilleux, J.P., Whitaker, J.O., & Veilleux, S.L. (2003) Tree-roosting ecology of reproductive female eastern pipistrelles, Pipistrellus subflavus, in Indiana. *Journal of Mammalogy*, **84**, 1068-1075.

Venables, W.N. & Ripley, B.D. (1997) *Modern applied statistics with S-Plus (second edition)* Springer Verlag, New York, U.S.A.

Verboom, B. & Huitema, H. (1997) The importance of linear landscape elements for the pipistrelle *Pipistrellus pipistrellus* and the serotine bat *Eptesicus serotinus*. *Landscape Ecology*, **12**, 117-125.

Verboom, B. & Spoelstra, K. (1999) Effects of food abundance and wind on the use of treelines by two insectivorous bats, *Pipistrellus pipistrellus* and *Eptesicus serotinus. Canadian Journal of Zoology*, **77**, 1393-1401.

Whitaker, J.O. (1998) Life history and roost switching in six summer colonies of eastern pipistrelles in buildings. *Journal of Mammalogy*, **79**, 651-659.

Winchell, J.M. & Kunz, T.H. (1996) Day-roosting activity budgets of the eastern pipistrelle bat, *Pipistrellus subflavus* (Chiroptera: Vespertilionidae). *Canadian Journal of Zoology*, **74**, 431-441.

Zimmerman, G.S. & Glanz, W.E. (2000) Habitat use by bats in eastern Maine. *Journal of Wildlife Management*, **64**, 1032-1040.

Batschelet, 1981 E. Batschelet, Circular Statistics in Biology, Academic Press, London (1981).