

**Roosting and social ecology of the tricolored bat,
Perimyotis subflavus, in Nova Scotia**

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Saint Mary's University, Halifax, Nova Scotia
in Partial Fulfillment of the Requirements for
the Degree of Master of Science in Applied Science.

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**Roosting and social ecology of the tricolored bat, *Perimyotis subflavus*,
in Nova Scotia
by Joseph Poissant**

ABSTRACT

Combinations of abiotic and biotic factors influence the behavior and evolution of a species. Temperate bats are constrained by inhospitable winters, hibernation requirements and interspecific competition for resources, so adaptations must occur to enable those species to remain competitive while maximizing fitness. A small, apparently genetically isolated population of tricolored bats exists in Nova Scotia at the periphery of the species' range and resource requirements of the species were unknown. The objectives of this thesis were to: 1) characterize roost sites in terms of tree and stand level attributes and; 2) to describe the basic social structure of tricolored bats, particularly females, in Nova Scotia. These bats roosted exclusively in *Usnea* lichen, near water, with access to many potentially available roost sites in stands of mostly softwood trees. Females formed closed societies within distinct roosting territories, maintaining an affinity to these territories within and between years.

May, 2009

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"I am against religion because it teaches us to be satisfied with not understanding the world."

-Richard Dawkins

"There is pleasure in the pathless woods,
There is a rapture on the lonely shore,
There is society, where none intrudes,
By the deep Sea, and music in its roar:
I love not Man the less, but Nature more."

-Lord Byron, "By the Deep Sea"

"Adapt or perish, now as ever, is nature's inexorable imperative."

-H. G. Wells

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CHAPTER 1

Roosting and social ecology of the tricolored bat: introduction

Introduction

As anthropogenic changes occur to ecosystems, a characterization of the conditions and resources required to maintain viable populations of species becomes increasingly important for making responsible decisions regarding their conservation (Alagona 2004). If a basic understanding of the needs of species and their interactions with the environment is not understood, the looming threat of the loss of biodiversity becomes all the more real as species are increasingly driven toward extirpation and extinction. Environmental changes can have profound consequences to those species that are highly mobile and may depend on multiple habitat types (e.g., foraging territory, roosting territory, wintering ground). Moose on the mainland of Nova Scotia are experiencing a long term decline in population due to a combination of as yet unexplained factors, possibly including parasites, loss of suitable foraging grounds, competition from deer, a lack of key minerals in the diet and an extensive system of roads reducing the ability to migrate longer distances (Parker 2003). Conversely, bears are being found with increasing regularity in backyards and small towns. Deer are being killed on Nova Scotia roadways at a rate of five per day as of 2003 (Garroway and Broders 2005). It is possible that these effects are being caused by a gradual change to the ranges and territories of these species by a combination of both natural and anthropogenic pressures. However, difficulties in locating and tracking smaller species such as bats and birds may mean that there are discrete losses to biodiversity occurring that are not being realized.

Chiroptera

The order Chiroptera accounts for almost a quarter of all mammals, with more than 1100 described species (Engstrom and Reid 2003). Bats are divided into two suborders, the Micro- and Megachiropterans. Suborder Microchiroptera are distributed globally and through the use of echolocation subsist on a variety of food sources; mainly insects, but also fruit, blood and fish (Whitaker and Findley 1980, Barclay and Brigham 1991, Bonato et al. 2004, Kunz and Fenton 2005). The megachiropterans are limited to the old world, including Europe, Asia, Australia and Africa. These bats subsist only on fruit, do not generally echolocate and include the largest bat species (Stier and Mildenstein 2005). While they are typically cryptic species, bats have successfully evolved to occupy a range of ecotypes worldwide. Many species have broad distributions and large populations (Patten 2004). Some species have adapted to the presence of humans and spend much of their time living in man-made structures (Whitaker 1998, Fellers and Pierson 2002, Willis and Brigham 2004) but this is not the norm. In western North America colonies of both little brown (*Myotis lucifugus*) and big brown bats (*Eptesicus fuscus*) are commonly found roosting in attics and behind the siding of houses and barns (Gitzen et al. 2002, Lausen and Barclay 2006). These buildings provide alternate shelter for individuals that usually roost in trees (Lausen and Barclay 2006, Neubaum et al. 2007). Few tree-dwelling species adapt so readily to human occupation and many species are experiencing population declines (Schulze et al. 2000).

Sociality

Although humans are sometimes viewed as the pinnacle of evolution with a highly specialized and advanced social structure (Neuberg and Cottrell 2008), many other species have also demonstrated similar and even more remarkable social behavior. Some insects, while small and typically having limited territories may employ complex social structures. Bees for instance, use chemical cues and the position of the sun to create a dance conveying direction and distance to food from the hive (Tanner and Visscher 2008). They have the ability to relay the position of specific flowers hundreds of meters away to other individuals (Beekman et al. 2005). In addition to bees, ants and termite colonies have individuals with specialized roles (Judd and Fasnacht 2007). Some are workers, clearing new tunnels and removing waste, while others produce and tend to the eggs and developing larvae (Rosset and Chapuisat 2007). What is impressive is the fact that these behaviors all originate in organisms that have very simple central nervous systems (Hoyer et al. 2005). This eusocial behavior is mostly limited to these colonial insects but is shared by a few mammal species including the naked mole rat, *Heterocephalus glaber* (Holmes et al. 2007).

Groups of animals with more developed central nervous systems such as rodents and birds employ behaviors such as alarm calls which alert others in their colony to potential predators (Shelley and Blumstein 2005). These calls are individually distinctive and may serve to identify a specific member of the colony, differentiate their sex and also separate social groups (McCowan and Hooper 2002). While this may put one individual at increased risk of death, it benefits the entire population and research has shown that the more closely related an individual is to the others, the more risk it will expose itself to in

order to protect the population (McCowan and Hooper 2002). The loss of one individual within a large related colony may actually serve to increase inclusive fitness (Grafen 2007) by enabling a greater percentage of the population to survive predation and therefore potentially pass on their genes to more offspring (Lehmann et al. 2007). It is through this sometimes simple but often complex sharing of information that many species thrive and evolve (Perez-Barberia et al. 2007). By coordinating effort and sharing labor among individuals, there is a net gain of energy and resources for the entire group (Burd 1996). This may increase reproductive fitness and give a species the edge it needs to compete with many other species in the same area.

Bat sociality

Bats that have distributions restricted to within 30 degrees of the equator have no need to hibernate over long periods (Arlettaz et al. 2000) but they do employ daily torpor to conserve energy. Their food supply is not limited to insects that experience seasonal population trends as in the northern latitudes and if food is limited they can migrate to areas with higher prey availability (Richter and Cumming 2006). As well, the ability to use alternative food sources including fruit, fish, and pollen and not have to focus on building a reserve of adipose fat tissue for hibernation gives these species the ability to focus on reproduction (Tschapka 2005). Unlike temperate species, their reproduction is also not seasonally limited, and different species will give birth at varying times of the year. For instance, the short-nosed fruit bat, *Cynopterus brachyotis*, gives birth in April and August-October (Bumrungsri et al. 2007), while the Jamaican fruit bat, *Artibeus jamaicensis* and the silky short-tailed bat, *Carollia brevicauda* have shown evidence of lactation in more than 10 months of the year (Estrada and Coates-Estrada 2001),

suggesting they give birth year round without a specific birthing season. The radically different climate in the tropics has therefore given rise to social behavior which is quite different from what would be expected farther north.

Harem-based bat colonies are common in Central America and usually consist of one dominant reproductive male and many females. These bats may roost in cavities (Hodgkison et al. 2003), foliage (Chaverri et al. 2007), caves (Ortega and Maldonado 2006) and even active termite nests (Dechmann et al. 2005). Males that control a harem of females have preferential access to mates, and therefore may have higher reproductive potential. As in birds, males that construct roosts are showcasing an external phenotypic quality that may make them more desirable to females (Dechmann et al. 2005). In this case, reproductive success is a measure of the ability to provide for females; there is not a direct competition between males for creation of shelter but defending a roost against invading males may occur during the reproductive season (Heckel and von Helversen 2002).

Research on one harem-based cave roosting species, the Jamaican fruit bat, *Artibeus jamaicensis*, demonstrated that some females form a center core in the harem that experiences a higher level of reproduction. These females are ringed by another group of females that serve two purposes; they groom the females within the core and are responsible for expelling females occupying the edge of the harem that may not be as closely related to the colony (Ortega and Maldonado 2006). As well, this species forms large harem groups with subordinate males which have father-son relatedness to the dominant male. While the dominant male sires the most offspring (>65%) subordinates do appear to father offspring as well (>20%). This is another example of inclusive fitness

(Hamilton 1964), where it benefits the dominant male (and therefore the colony) to allow subordinate males to reproduce, as it is passing on his genes to more offspring (Ortega et al. 2003).

Most temperate bats hibernate during the winter. In summer, females form maternity colonies consisting of several to sometimes hundreds or even thousands of individuals (Jones and Suttkus 1973, O'Farrell and Studier 1975, Menzel et al. 2001, Owen et al. 2002, Willis and Brigham 2004). These colonies predominantly consist of females (Kunz 1971, Jones and Suttkus 1973, Kurta 2005). While males may be found, they are usually in small numbers (O'Farrell and Studier 1975). These large summer roosting aggregations conform to a type of sociality known as fission-fusion (Kerth and König 1999, Garroway and Broders 2007, Rhodes 2007). In fission-fusion, on any given day, the colony is subdivided into small, discrete social groups (Willis and Brigham 2004). Although the composition of these groups vary from day-to-day, individuals have preferred associates and these associates roost together more often than expected by chance (Kerth and König 1999, Garroway and Broders 2007). Individuals may form roosting aggregations due to environmental or social circumstances and research suggests that fusion occurs with increased frequency as parturition occurs within the colony (Kerth and König 1999).

Radio telemetry

When radio transmitters were first introduced in the late 1950s, they were primarily used on larger animals, but some collars were small enough to collect data from rodents such as chipmunks (LeMunyan et al. 1959). At the time, transmitter size was limited by the size of transistors, which fueled battery consumption; therefore as transistors became smaller, battery consumption was reduced and smaller batteries could be used (Kenward 1987). The science was still young, so the questions being asked were

predominantly qualitative (Mech et al. 1965, Lance and Watson 1980). Early detractors from the technology argued that this was not good science and so began studies of wild animals versus those in captivity and research into mortality (Mech 1977, Heisey and Fuller 1985).

Transmitter use with bats began in the 1960s (Williams and Williams 1967), but was restricted to larger species such as the fruit-eaters in the tropics (Heithaus and Fleming 1978), which usually have a mass of greater than 50 grams. The large overall size of the transmitter (in excess of 5 to 10g) made them unsuitable for smaller species like the insectivorous bats in Canada to carry without compromising flight dynamics (Aldridge and Brigham 1988). It was not until the 1990s that technology reached a point where transmitters could be affixed to the smallest of bat species in North America (Barclay et al. 1996, Brigham et al. 1997, Crampton and Barclay 1998). Experimental research showed that small bats could only safely carry 5% of its total body mass (Aldridge and Brigham 1988), which equaled approximately 0.35g in the smallest species, before there was a noticeable decrease in flight performance and increase in energy consumption. Since these smaller transmitters have become available, research has been possible and widespread on these cryptic species (Mager and Nelson 2001, Menzel et al. 2001, Willis and Brigham 2003). Data has been collected on the previously unknown behaviors such as fission fusion sociality in small colonies of bats (Kerth and Konig 1999, Willis and Brigham 2004), migratory movement (Hobson and Holland 1995) and landscape usage around hibernacula in the fall (Brack 2006).

Mark – recapture techniques

Research into the social structure and roosting ecology of many small (< 15 g) bat species has historically been difficult (Davis and Cockrum 1964, Aldridge and Brigham 1988) due to technological limitations and their cryptic nature. In the last 15 years however, the advent of cost-effective passive integrated transponder (PIT) tagging systems (Gibbons and Andrews 2004, Kunz 2004) have provided a better means of examining behavior by smaller insectivorous bats at multiple scales (Barclay et al. 1996, Menzel et al. 2001, Willis and Brigham 2003;2004, Lacki and Baker 2007, Safi et al. 2007). In the past, banding was the popular marking method for tracking bat movements over extended periods of time and long distances (Allen 1921, Griffin 1945, Trapido and Crowe 1946, Davis and Hitchcock 1965, Hitchcock 1965, Davis 1966, Phillips 1966, Brenner 1974). Banding was first used more than 400 years ago but has only seen widespread use in the last century (Griffin 1936, Hitchcock 1957). Species that fly and have wide dispersal, such as birds and bats, are typically the focus of banding efforts (Trapido and Crowe 1946) but there are inherent drawbacks to banding, specifically the need to physically observe a banded animal or recapture them to identify the individual in question. As well, in bats there are indications that over the long term this method has negative side effects such as patagial membrane scarring and muscle damage that could compromise a bats ability to fly (Hitchcock 1957, Herreid et al. 1960, Baker et al. 2001, Dietz et al. 2006).

PIT tagging alleviates the problems associated with banding, and with the exception of rejection (Harper and Batzli 1996, Gries and Letcher 2002), research has shown that there is no link between PIT tagging and mortality. The tags are

approximately 1 cm long, electronic, coated in a thin layer of biomedical glass and have a life expectancy of greater than 10 years. They are individually packaged in a 12 gauge syringe, ready for use. Passive integrated transponder tags, when injected correctly, provide a safe method to identify bats and other animals to the individual level and represent a means of tracking them over the long term (Hagen 1996, Fischer et al. 2001, Kerth and Reckardt 2003). This is ideal for monitoring the movement and social interactions of individuals within colonies. After initial handling, bats can be manually scanned or move through a remotely deployed antenna to read its uniquely identifying code; this removes the need for recapturing individuals. This lack of subsequent disturbance is crucial for recording movement data of bat species which could be sensitive to repeated capture and handling (Widmaier et al. 1994).

Bats in Nova Scotia

In Nova Scotia, seven bat species have been identified, although only three are commonly found with young during the summer reproductive season (Broders et al. 2003). There are scattered records of the red bat, *Lasiurus borealis*, roosting in the province but data is lacking (Broders et al. 2003). The little brown and northern long-eared (*Myotis septentrionalis*) bats have a province-wide distribution and are thought to have a large population (Broders et al. 2003). These two species are similar in size, with masses from 5 to 11 g and wingspans of 22 to 27 cm (van Zyll de Jong 1985). The northern long eared bat is a forest interior specialist, usually roosting in trees and foraging within the forest and along trails for insects (Broders 2003, Broders et al. 2003). The little brown bat is also insectivorous but forages primarily over water (LaVal et al. 1977) and commonly roosts in both buildings and trees (Jung et al. 1999).

Study species

The tricolored bat, *Perimyotis subflavus*, is considered one of the most common bat species in eastern North America (Barbour and Davis 1969) and is found south to Honduras through eastern Mexico and eastern North America to southern Ontario and east to Nova Scotia (van Zyll de Jong 1985). The tricolored bat forages high over water for insects and also roosts in the forest (van Zyll de Jong 1985). During the summer months, over much of its range the tricolored bat uses dead hardwood foliage for roost sites, including oak (Veilleux et al. 2003). They have also been found in pine (Perry and Thill 2007), Spanish moss (Jones and Pagels 1968), buildings (Whitaker 1998) and caves (Briggler and Prather 2003). It is a small species (female, mass: 5.8 to 7.9 g, wingspan: 22 – 25 cm (Fitch 1966, Farney and Fleharty 1969)) with a dark pelage that is described as tricolored. The hairs are dark near the body, yellowish in the middle and dark again at the tips (Barbour and Davis 1969). This is a distinguishing characteristic from all other bat species found along its range in North America. As there may be variation in the color of the pelage depending on the age of the individual and different species are routinely captured together (juvenile tricolored bats have dark chocolate fur (van Zyll de Jong 1985) similar to *M. lucifugus*), to determine bat species in Nova Scotia, the tragus of a suspect bat is also examined. They vary from the sympatric *M. lucifugus* and *M. septentrionalis*; The tragus is short (~3 mm) and rounded in the tricolored, while in *M. lucifugus* it is slightly longer (4 to 5mm) and in *M. septentrionalis* it is significantly longer (7 mm) and comes to a sharp point .

Historically, the tricolored bat was placed in the genus *Pipistrellus* with the western pipistrelle (now *Parastrellus hesperus*) and thirty other species found globally.

However, morphometric irregularities (Menu 1984) spurred genetic research that determined that both North American species were not directly related to the pipistrelle genus and were in fact not even directly related to one another (Hooper and Van den Bussche 2003). Genetic evidence suggests this species is more closely related to the North American *Myotis* species than any other species from the genus *Pipistrellus* (Hooper et al. 2006). As such, the tricolored bat was recently reclassified into its own genus, *Perimyotis* and the common name was changed from the eastern pipistrelle to the tricolored bat (Menu 1984, Hooper et al. 2006).

Using acoustical surveys and trapping in 2001 in Nova Scotia, it was determined that the tricolored bat appears to have a small population that is restricted to the southwest portion of the province (Broders et al. 2003). Due to a lack of long distance migration, it appears that the Nova Scotia population may be disjunct and thus there may be limited gene flow with other populations in North America (Lomolino and Channell 1995, Broders et al. 2003). A concentration of reproductively active female tricoloreds was identified in 2003 in Kejimikujik National Park (Quinn 2003, unpublished data). In 2006 an echolocation study was conducted to determine the extent of this species in southwest Nova Scotia and it was determined that activity dropped off significantly approximately 100 km to the east of the area of highest activity, supporting the prediction that the population was limited in its distribution (Farrow 2007).

The behavioral and morphological distinction of the Nova Scotia population of tricolored bats (Broders et al. 2001, Broders et al. 2003), coupled with the fact that it is monophyletic (Hooper et al. 2006), with a potentially low local population, makes it of special conservation concern. To the north, south and west of Kejimikujik National Park

there are large commercial forestry operations which may have reduced the number of potential summer roost sites. As well, there are several remnant, peripheral populations of other animal species, particularly in the southwest portion of the province, including the southern flying squirrel (Petersen and Stewart 2006), the blanding's turtle (Mockford et al. 2005), and the eastern ribbon snake (Bell et al. 2007). The lack of movement between the populations in Nova Scotia and elsewhere increases the chances of gradual speciation and therefore make these species important pools of genetic material. Through a combination of national and provincial parks, wilderness areas and nature reserves, 169 sites representing approximately 8.2% of Nova Scotia land is protected from development (Anonymous 1999); however the land surrounding these sites is still open to industries such as logging and mining, private development and urban sprawl continues at an alarming rate. It is, therefore, vital to quantify the roosting needs and social behavior of these bats to determine effective management plans to enable the long term sustainability of this important population (Lesica and Allendorf 1995).

Study area

Nova Scotia is on the eastern coast of Canada and effectively operates as an island for many remnant populations of species found there due to the peninsular shape of the province and narrow isthmus of land connecting it with New Brunswick to the north; this makes migration difficult for those species that are spatially segregated from this small connection to the mainland. The province has been extensively logged, with little of the original Acadian forest remaining (Anonymous 1999). The Acadian forest is a transition between the hardwood dominant forests of the northeastern United States and the boreal forests of northern Canada. It is characterized by sugar maple, yellow birch, balsam fir

and red spruce as well as eastern hemlock, red and white pine and American beech. Other trees include white birch, red maple and red oak. Logging, agriculture and urban development in Nova Scotia has created patchy stands of varying ages; it is not uncommon to find a pure stand of young white spruce bounded by mid-successional hardwoods. There is little continuity in the forest structure of the province although conifers (particularly spruce) are chiefly planted by logging companies from Saint Margaret's Bay in the east to Yarmouth in the west. The climate in Nova Scotia is described as a maritime climate, with the thermal properties of the ocean keeping Nova Scotia warmer than inland North America in the winter but cooler in the summer (Davis and Browne 1996). The average annual temperature is 5 to 7 Celsius with precipitation recorded between 122 and 189 days of the year (Davis and Browne 1996).

Kejimikujik National Park is a 400 km² protected area established in 1969. The area is characterized by mixed upland and lowland regions, an extensive system of small rivers and lakes and glacial topography with drumlins running in a roughly north-south orientation. The Mersey River enters Kejimikujik Lake from the east and drains to the south. Due to extensive logging in the period before inception, the park has a patchwork of mixed forest, with young white pine in the south, spruce bogs in the lowland regions around the lakes, mixed softwood and hardwood in the west with pure stands of red maple and yellow birch in the upland regions. There are several remnant old growth stands of eastern hemlock in the north of the park and yellow birch and red maple in the west.

The question

The goal of this thesis was to better understand the roosting ecology and social structure of the tricolored bat in Nova Scotia. The objectives of this study were therefore:

- 1) Chapter 2: to locate and characterize roost sites and trees in terms of tree and stand level attributes via a modeling study and;
- 2) Chapter 3: to describe the basic social structure of tricolored bats, particularly females in Nova Scotia

Chapters 2 and 3 are written as standalone manuscripts formatted for publication. In both of these chapters I have included data collected in 2003 & 2004 by a previous MSc student, Greg Quinn. He will be an author when these papers are published but I played the primary role in both the compilation of the chapters and the statistical analysis.

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CHAPTER 2

Use of lichen as a roosting substrate by *Perimyotis subflavus*, the tricolored bat, in Nova Scotia

Abstract

An apparently disjunct population of tricolored bats (*Perimyotis subflavus*) exists in southwest Nova Scotia. During the summers of 2003-2004 and 2007-2008 we trapped bats in mist nets set at a bridge over the Mersey River in Kejimikujik National Park. In total we captured 44 tricolored bats (43 female and 1 male) and fitted 32 females and the single male with transmitters and tracked them to their roost sites daily. Characteristics of roost sites were compared to those of potentially available roost sites using an *a priori* selected candidate set of models and ranked using AIC_c for model selection. In total we found 99 unique roost trees in 9 spatially distinct (8 female, 1 male) roosting areas. On average, bats spent 2.6 days in a roost tree. While conspecifics from other parts of the species range typically roost in tree foliage, maternity colonies of tricolored bats in Nova Scotia roosted exclusively in *Usnea trichodea* lichen, typically in conifers (of which 91% were spruce; *Picea* spp.) that were on average 212 m from water. Only 4% of the 300 random trees from the landscape contained *Usnea trichodea*. These trees were a mixture of softwood and hardwood (58% and 42%, respectively), and were, on average, 550 m from water.

Introduction

Animals select and use resources in ways that maximize survival and reproduction (Krebs 2001). For bats, roosts offer refuge from adverse abiotic conditions (e.g., precipitation, temperature; Callahan et al. 1997, Willis and Brigham 2007), or protection from predators (Riskin and Pybus 1998) and are places where information transfer and socialization likely occur (Kerth and Reckardt 2003). Thus roost site characteristics and location are likely a function of complex interactions between weather, site microclimate, physiology, sociality (e.g., territoriality) and the proximity to other resources (e.g., prey and water) (Vonhof and Barclay 1996, Kerth et al. 2003). Therefore, roost selection is an important consideration for ecological studies of bat biology. In temperate zones, bats exploit a wide range of sites for roosting including buildings (Whitaker 1998, Neubaum et al. 2007), caves and crevices (Hurst and Lacki 1999, Rancourt et al. 2005), and tree cavities (Kurta et al. 1993, Crampton and Barclay 1998, Menzel et al. 2001, Perry and Thill 2007b). The females of many forest roosting species form female-biased maternity colonies in the summer to give birth and raise young. Urban expansion and anthropogenic activities such as logging and agriculture have decreased the availability of natural summer roosting sites used by many forest bats and may have contributed to increased use of buildings (Ritzi et al. 2005, Neubaum et al. 2007). Loss of such suitable sites is likely to have consequences for reproductive success and colony dynamics.

Bat species that are year-round residents in temperate areas have fairly similar life histories. Typically the year can be divided into two separate periods: winter, which begins with migration, usually to a underground site (cave or abandoned mine), to mate and store fat for the 8 months of hibernation, and summer; which begins in late spring

when females return to their maternity colonies, to which they exhibit strong affinity (Jaberg and Blant 2003, Kerth et al. 2003, Willis et al. 2003, Veilleux et al. 2004). The tricolored bat (*Perimyotis subflavus*) is a typical temperate bat with a broad distribution extending from Belize to eastern Canada (van Zyll de Jong 1985). During the summer, maternity colonies of up to a dozen individuals roost in a variety of sites, including dead hardwood foliage (Veilleux et al. 2003), dead pine foliage (Perry and Thill 2007b), Spanish moss (Davis and Mumford 1962), caves (Briggler and Prather 2003) and buildings (Jones and Pagels 1968, Whitaker 1998). Although the species has a mostly contiguous distribution across its range, the population in Nova Scotia is likely disjunct (Broders et al. 2003).

The goal of our research was to understand the roost site requirements of tricolored bats in Nova Scotia. Specifically, our objectives were to: 1) identify roost sites used by maternity colonies of tricolored bats and to characterize those roosts at both the tree and landscape scale and 2) to develop a model for predicting presence of maternity colonies on the landscape by comparing known roost sites to potentially available sites in the same landscape.

Methods

Research site

From late May to mid-August 2003, 2004, 2007 and 2008 we trapped bats flying over a bridge on the Mersey River in Kejimikujik National Park and Historic site (UTM 324218E 4911265N), in south western Nova Scotia, Canada using up to five 12 m mist nets that were opened at sunset for an average of 120 minutes per trapping night. To

reduce potential handling stress, trapping did not occur during evenings with strong winds, precipitation or on nights where the temperature was less than 8 ° C (Parsons et al. 2003, Ciechanowski et al. 2007). The nets were checked every 10 minutes and all animals were removed immediately for processing. Bats were identified to species and we recorded mass (g), forearm length (mm), sex, age (determined by examining the degree of ossification of the phalanges (Anthony and Kunz 1977) and reproductive status. Bats from 2007 and 2008 were visually checked for ectoparasites on the wings, the ears and in the fur. All parasites seen were collected and placed in a 1.5 ml eppendorf tube (Eppendorf Industries) filled with 70% ethanol. Some tricolored bats received a 0.42 gram radio transmitter (Model LB-2, Holohil Systems, Carp, Canada), representing between 3.5 and 6% of the total mass of the animal (Aldridge and Brigham 1988), affixed dorsally using a nontoxic surgical adhesive (Skin-Bond, Smith & Nephew Inc., Largo, Florida). Bats were tracked daily to roost trees using a receiver (R2000 VHF Receiver: Advanced Telemetry Systems, Isanti, Minnesota, USA or HR-2000 Osprey VHF receiver: H.A.B.I.T. Research Limited, Victoria, British Columbia, Canada) and a three element yagi antenna (AF Antronics, Urbana, Illinois, USA) until the transmitter dropped off or the battery failed. All protocols were approved by the Saint Mary's Animal Care Committee and followed the ASM guidelines (Gannon et al. 2007). Work was conducted under permit from Parks Canada and the Nova Scotia Department of Natural Resources.

Roost site characterization

Roost locations in trees were often identified by searching the tree for bats using binoculars or by observing bats emerge at dusk. When located, height of the roost site (m) and distance and direction (degrees) from the bole were recorded. Additionally, for each roost site, a 0.1 hectare (17.9 m radius) circular plot centered on the roost tree was sampled to characterize the forest including tree species composition, diameter at breast height (DBH), dominant canopy height (using a clinometer; model PM-5/1520, Suunto, Finland) and canopy closure (the average closure as measured using a spherical densiometer one meter from the bole of the roost tree in each cardinal direction). Because bats roosted in *Usnea*, we developed a tiered system to assess and quantify the lichen coverage on trees (*Usnea* index of the roost or *uir*). We determined *a posteriori* that an index value of 2 was the minimum used by a maternity colony and spanned 1-25% total coverage. A classification of 1 meant no *Usnea* coverage while 5 represented 76 - 100% coverage. In addition to the known roost tree, all other trees within the plot deemed available ($UIR \geq 2$) were identified and characterized in the same way as the known roost tree. For reliability our *Usnea* classification was always made by only two observers. As well, we examined an additional 300 random plots. These plots were randomly placed within a circular area centered at the approximate geographic center of all tricolored bat maternity colonies identified in the study with a radius 10% larger than the distance from capture site to the furthest roost. The tree selected as “random” was the one closest to the random coordinates that was potentially available which meant it had *Usnea*, was greater than 6 m high and had a DBH of at least 10 cm.

Modeling

Data from 2003/2004 and 2007/2008 were pooled and trees were coded as either used (1, known roost site) or unused (0, random tree). While the tricolored bat appears to select different roost types in Nova Scotia than elsewhere in its range, a subset of variables for modeling were selected based on our observations and a consideration of the relevant literature. These included *psw* (percent softwood in the plot), *dtw* (distance to water in meters) and *nut* (number of trees with available usnea, i.e., $uir \geq 2$) which were selected based on sympatric species elsewhere that have been found to roost close to water and in areas with an abundance of trees which may emulate known roost sites. The center tree in the plot (either known roost or random) was coded as either being a spruce (including white (*Picea glauca*), black (*Picea mariana*) or red (*Picea rubens*)) or not (*spr*, 1 = spruce, 0 = other). Twelve *a priori* chosen logistic regression models were derived comparing known versus random roost sites and ranked with AIC_c, using Systat 12 (SPSS, Inc). These candidate models were derived based on research from elsewhere on this and other sympatric species (Broders 2004, Veilleux 2003; 2004, Vonhof et al 1996) as well as our own observations.

Results

Although we trapped at more than twenty sites in and around Kejimikujik National Park, we were only successful at the Eel Weir bridge over the Mersey River (UTM: 20N 324218E 4911256N). Of 208 bat captures, 44 were tricolored bats: 7, 14, 15 and 8 in 2003, 2004, 2007 and 2008, in over 2293 net hours (1 net hour equaled 1 twelve m net open for one hr) respectively. We also captured 127 *M. lucifugus* (37 males and 90 females) and 37 *M. septentrionalis* (7 males and 30 females). We found no ectoparasites

on any tricolored bat, but fleas, *Myodopsylla insignis* and bat bugs, *Cimex adjunctus* were found on *M. lucifugus*. The wing mite, *Spinturnix americanus* was found on both *M. lucifugus* and *M. septentrionalis*. With the exception of seven individuals captured in 2007 at a roost tree, all tricolored bats tracked to all colonies were trapped at the Eel Weir location. Thirty-two adult females and 1 adult male were radio tracked over four summers. Although the male was tracked for 19 days to eight different roost trees, it always roosted alone and outside of areas used by female colonies, so the data for the male were not included in the analysis. The transmitters lasted from 1 – 19 days (mean = 8.4) and we located 99 different roost trees used on 261 bat days (2.6 bat days per roost). While bats roosted in a variety of trees, including red maple (*Acer rubrum*, $n = 6$), balsam fir (*Abies balsamea*, $n = 3$), eastern larch (*Larix laricina*, $n = 3$), white birch (*Betula papyrifera*, $n = 1$), white pine (*Pinus strobes*, $n = 2$), and yellow birch (*Betula alleghaniensis*, $n = 2$), they primarily roosted in conifers, mostly spruce ($n = 82$, 83%). No matter the tree species, all roosts were in *Usnea* lichen ($n = 99$, 100%) and the mean distance to water was 212 m. The center trees of the 300 random plots were both coniferous ($n = 174$, 58%) and deciduous ($n = 126$, 42%), dominated by white pine ($n = 67$, 22.3%) and red maple ($n = 65$, 21.6%). The prevalence of *Usnea* lichen on trees in the study area was low with only 11 of the center trees in random plots had any visible *Usnea*. Random trees averaged 550 m from water (Table 1).

Of the 12 candidate models, the model which included the variables *uir*, *dtw nut* and *psw* had nearly a 95% chance of being the best model, given the data, and therefore we use only this model for inference (Table 2). The *uir* ($\beta = 2.363$, SE = 0.387) variable was strongly positively correlated with bat presence, while *nut* ($\beta = 0.223$, SE = 0.058)

and *psw* ($\beta = 0.04$, $SE = 0.014$) weakly positively predicted presence (Figure 1). Variable *dtw* ($\beta = -0.005$, $SE = 0.002$) had a weakly negative correlation with bat presence. The best predictor of presence, *uir*, demonstrated that for each 25% increase in *Usnea* coverage in the tree there was a 10.6 times higher probability of use by tricolored bats.

Discussion

The singular use of *Usnea trichodea* lichen as a roosting medium by tricolored bats in Nova Scotia appears to be a novel adaptation relative to elsewhere in their range. In Indiana, tricolored bats roost in the dead foliage of hardwood trees, specifically oak, which while not as common as in Indiana, are still plentiful in Nova Scotia (Nova Scotia Department of Natural Resources 1999). Veilleux (2003) hypothesized that the use of foliage versus tree cavities as a roosting medium was potentially due to interspecific competition for roosts; however in Nova Scotia, with only two other forest bats there should be less competition. . The use of foliage by bats for maternity colonies in Canada is limited to tricolored bats. Silver-haired bats (*Lasionycteris noctivagans*) roost in small maternity colonies in tree cavities (Betts 1998) while two of the other tree bats found in northern latitudes, the hoary (*Lasiurus cinereus*) and eastern red (*Lasiurus borealis*) which also use foliage as roosts but roost singly (van Zyll de Jong 1985, Perry and Thill 2007a). The affinity for a specific roost substrate by tricolored bats coupled with larger numbers of individuals found together suggests that there may be energetic as well as protective benefits to the use of *Usnea* by this species.

Several bird species, including the olive-headed weaver (*Ploceus olivaceiceps*) in eastern Africa and the northern parula (*Parula americana*) in eastern North America use *Usnea* lichen as a nesting substrate. The lichen reduces energy costs by providing

insulation leading to a stable microclimate and also camouflage against predators (Nuttall 1998, Bay 1999). This is relevant to tricolored bats, given that they enter torpor during the day. A reduction in the amount of energy needed to arouse from torpor due to the insulating properties of *Usnea* is an added benefit. Both the northern parula and tricolored bat use Spanish moss (*Tillandsia usneoides*) (Torres and Leberg 1996, Menzel et al. 1999), but bats in Nova Scotia use *Usnea*, suggesting that there is a similar benefit from both epiphytic species in these geographically isolated locations.

While *Usnea* lichen in boreal forests is common on conifers in bottomland locations due to lower temperatures and higher relative humidity (Gauslaa et al. 1998), there were hardwood trees (typically *Acer* or *Betula* spp.) within the roosting areas of tricolored bats which we deemed potential roost sites ($uir \geq 2$) but these were usually not known to be used. This could be due to higher amounts of foliage and canopy closure in the tree crowns. The preferential use of dead or dying spruce, which usually has both fewer and smaller branches closer to the crown and an open canopy, would provide benefits via microclimatic variation and increased control over exposure to solar radiation at roosting locations.

Ectoparasite loads have been suggested as a mechanism causing regular roost switching in cavity-roosting bat species (Lewis 1995, ter Hofstede and Fenton 2005). Females in maternity colonies usually have a higher prevalence of parasites than conspecific males which roost singly (Hurka 1964). Bats in Nova Scotia, including the northern long-eared (*Myotis septentrionalis*) and the little brown bat, both of which are cavity-roosting species, harbor at least 4 species of ectoparasites (Poissant and Broders 2008) which is similar to those found on other populations in North America (Whitaker

and Wilson 1974, Sasse and Pekins 2000). While elsewhere tricolored bats are found with ectoparasites, none have been collected from bats in Nova Scotia despite sampling both at summer roost sites and hibernacula (Poissant and Broders, 2008). Usnic acid, found uniquely in *Usnea* lichens, does have anti-insect and anti-microbial properties (Ingolfssdottir 2002) suggesting a possible link between the use of *Usnea* lichen roosts as a way of reducing the parasite prevalence. Tricolored bats commonly give birth to twins which are uncommon compared to other bats in Nova Scotia. Tricolored bats are also both smaller and shorter lived than other bats in the province (Fujita and Kunz 1984) so a reduction in parasite loading may mean the difference between the survival or death of juveniles and long term fitness of individuals (Giorgi et al. 2001).

The intraspecific variation in roost site selection documented here, relative to conspecific populations (Veilleux et al. 2003, Perry and Thill 2007b, O’Keefe et al. 2009) suggest that caution should be used when making local management decisions based on data collected elsewhere. We documented the exclusive use of *Usnea* lichen as a roosting substrate for this species. The use of this resource has not been documented previously and suggests a generalist behavior for this species which may help explain its broad distribution across many ecotypes. The larger colony size, lack of visible ectoparasites and lower movement between roost sites relative to colonies roosting in dead leaves suggest that *Usnea* lichen may be a higher quality substrate for roosting and its use should be explored elsewhere where the range of *Usnea trichodea* and the tricolored bat overlap. The importance of peripheral populations (Lesica and Allendorf 1995) coupled with the development of this novel roosting behavior underscores the importance of conserving this population of tricolored bats in Nova Scotia.

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Table 1: Mean (SD) values for tree and plot characteristics for known and random roost trees of female tricolored bats in Kejimikujik National Park, Nova Scotia, Canada, 2003 - 04, and 2007-08

Characteristic	Known	Random
DBH of roost tree (cm)	24.3 (7.3)	23.8 (10.5)
Height of roost tree (m)	16.5 (3.7)	15.7 (4.2)
Distance to water (dtw; m)	211.9 (124.7)	549.7 (422.7)
Canopy closure (cc; %)	31 (10)	23 (14)
Softwood in plot (psw; %)	61.8 (17.5)	36.9 (20.8)

Table 2: Difference in the Akaike Information Criteria score between the i^{th} and top ranked logistic model, Akaike and sum of Akaike weights (w_i , $\sum w_i$) for predicting presence of tricolored bats in Kejimikujik National Park, Nova Scotia, Canada in 2003/2004 and 2007/2008 for known roosts and random trees

Rank	Model variables	Δ_i	w_i	$\sum w_i$
1	uir, dtw, nut, psw	0	0.946	0.946
2	uir, dtw, nut	6.4	0.038	0.984
3	uir, dtw, nut, spr	8.3	0.015	0.998
4	uir, dtw, psw	14.1	<0.01	>0.999
5	uir, nut	15.8	<0.01	>0.999
6	uir, dtw	21.0	<0.01	>0.999
7	uir	35.2	<0.01	>0.999
8	dtw, nut, spr	90.7	<0.01	>0.999
9	nut, spr	110.8	<0.01	>0.999
10	nut	149.8	<0.01	>0.999
11	spr	210.1	<0.01	>0.999
12	dtw	284.0	<0.01	>0.999

Table 3: Multi-model inference model parameter estimates (β) with standard error (SE) and the odds ratio with 95% confidence intervals (CI). The model ranked 1 was the only model included in this analysis as its weight was approximately 95%, with model 2 having a weight of 3.7% (see Table 2).

Rank	Variable	β (SE)	Odds ratio (CI)
1	uir	2.363 (0.387)	10.626 (4,975, 22.696)
1	dtw	-0.005 (0.002)	0.995 (0.99, 0.999)
1	nut	0.223 (0.058)	1.25 (1.116, 1.399)
1	psw	0.04 (0.014)	1.041 (1.012, 1.07)

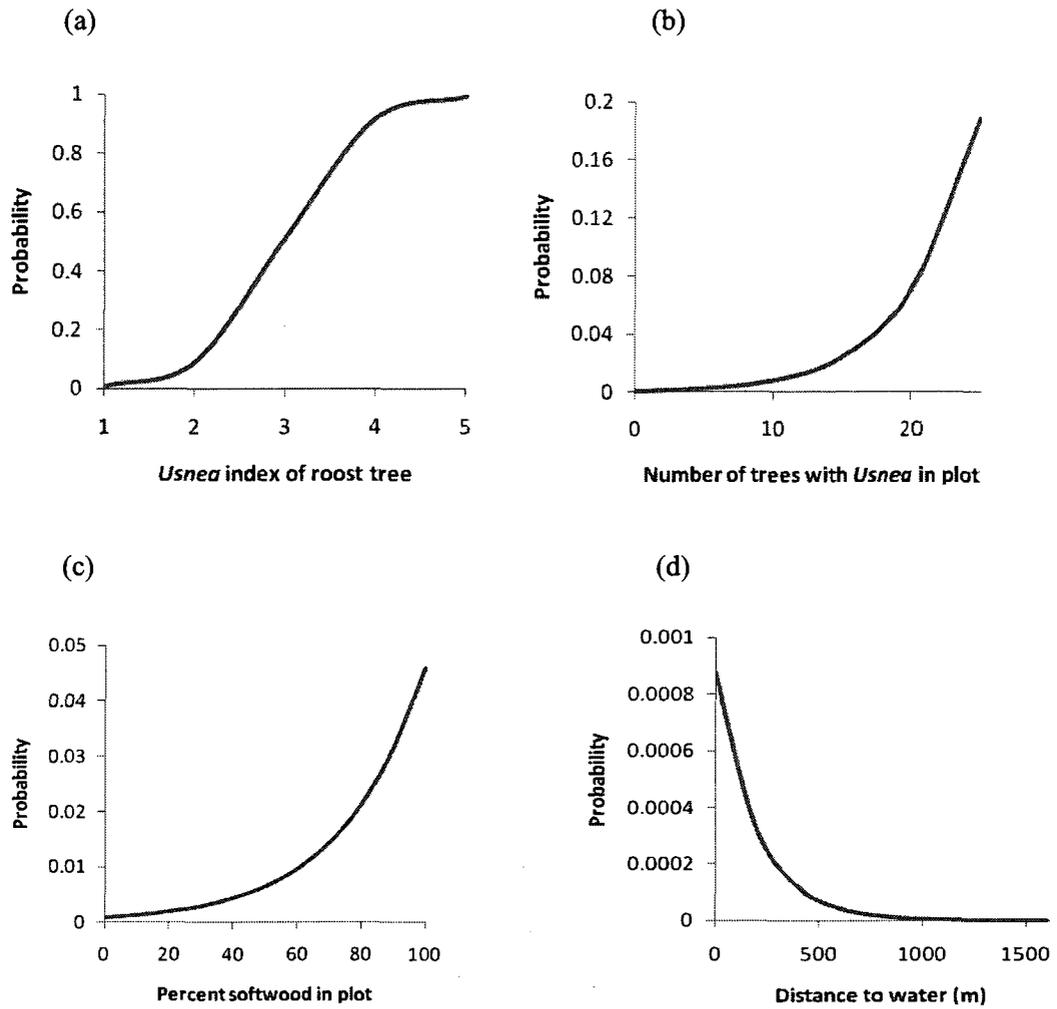


Figure 1: Logistic curves showing the probability of use by tricolored bats in Kejimikujik National Park (2003 – 04 and 2007 – 08) as (a) *Usnea* index of the roost tree (1-5), (b) number of other trees with *Usnea* in the plot (0 – 26), (c) percent softwood (0 – 100) and (d) distance to water (3 – 1860 m)

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CHAPTER 3

Social and spatial dynamics of the tricolored bat, *Perimyotis subflavus*

Abstract

During the summers of 2003/2004 and 2007/2008 one male and thirty-two female tricolored bats (*Perimyotis subflavus*) that were trapped at a bridge over the Mersey River in Kejimikujik National Park, Nova Scotia, Canada were tracked to roosts using radio telemetry. Spatially, the 111 roost trees that were identified formed a clumped dispersion on the landscape, representing nine distinct roosting areas. There was no evidence that individual bats roosted in more than one area in the same or different years thus we suggest that tricolored bats exhibit fidelity to a particular roost area, live in closed roosting groups but share foraging space. Roost switching between trees within areas occurred regularly with bats using a particular tree, on average, for 1.7 ± 1 (SD) consecutive days. Bats rarely returned to previously used trees after roost switching, potentially due to an excess of available trees within roosting areas and variable microclimates within roosts.

Introduction

It is now well known that the incidence of sociality (Hinde 1976) among animals is ubiquitous (Whitehead 2008) and the benefits of this sociality are potentially numerous (Beauchamp 1999, Ebensperger et al 2004, Lehmann et al 2007). Likewise, over the last couple of decades sociality has been documented in many species of bats. Given the high variability in their environment, their longevity (Brunet-Rossini and Austad 2004), and the potential for interactions to occur in roosts (Hurst and Lacki 1999, Kerth 2003, O'Farrell and Studier 1975) there are a number of potential causes and consequences of sociality (Kerth 2008). It seems likely that social animals would benefit because of the information transfer about, for example, foraging sites (Wilkinson 1985), and roosts (Kerth and Reckardt 2003). Characterizing the nature of these social interactions (Hinde 1976, Whitehead 2008) aid in our understanding of the ecological and evolutionary processes at work. However, in cryptic species such as bats characterizing such abstract phenomenon are difficult, and this likely explains the paucity of such investigations until recently.

Many bat species exhibit fidelity to feeding and roosting areas within and among years (Kerth and Konig 1999, O'Donnell 2000, Vonhof and Gwilliam 2007) and most temperate species live in colonies which are highly female biased or where males are completely absent (Garroway 2007, Safi 2008). This could be due, at least in part, to variable energy demands. Male bats do not appear to participate in rearing of young (Lacki and Schwierjohann 2001) and therefore may have lower energy demands than females and might select areas to reduce competition for prey with females (Encarnacao et al 2005).

The purpose of our study was to investigate the dynamics of sociality in a temperate forest dwelling bat (tricolored bat, *Perimyotis subflavus*) during the summer. During summer, female tricolored bats form maternity colonies, typically in tree foliage (Veilleux et al. 2003, Perry and Thill 2007). They also have been found to use *Usnea* lichen (Poissant, 2009) Spanish moss, (Barbour and Davis 1969), buildings (Jones and Pagels 1968, Whitaker 1998) and caves (Briggler and Prather 2003). Females are known to roost together and males are solitary (Veilleux and Veilleux 2004, Perry and Thill 2007). Specifically, our objectives were to determine: 1) if maternity colonies were 'closed' or 'open' social groups and 2) whether roosting groups exhibited an affinity to a particular area that is allopatric with other roosting groups.

Methods

From late May to mid-August 2003, 2004, 2007 and 2008 bats were trapped over the Mersey River at the Eel Weir in Kejimikujik National Park and Historic site (UTM 324219E 4911255N), in south west Nova Scotia, Canada, using mist nets that were checked at least every 10 minutes and all captured animals removed immediately. Bats were identified to species and we recorded body mass (g), forearm length (mm), sex, age (based on the degree of ossification of the phalanges (Anthony and Kunz 1977) and reproductive status (determined by gentle palpation of the abdomen or the presence of bare nipples). Bats were either banded with a plastic split ring band (2003/2004) or were injected intrascapularly with a 12 mm PIT tag (EID-ID 100 implantable transponders, EIDAP Inc., Sherwood Park, AB; 2007/2008). PIT tagged bats were subsequently identified using either hand held readers following capture or remotely using antennas deployed at roost sites. Some bats had a 0.42 g radio transmitter (LB-2N, Holohil

Systems Limited, Carp, ON) affixed dorsally using surgical adhesive (Skin Bond; Smith and Nephew United Inc., Largo, FL, USA). Transmitters represented 3.5 – 6% of body mass (5%, Aldridge and Brigham 1988). All protocols were approved by the Saint Mary's Animal Care Committee and conducted under permit from Parks Canada and the Nova Scotia Department of Natural Resources.

Bats were tracked daily to roost trees using an R2000 VHF Receiver (Advanced Telemetry Systems, Isanti, MN, USA) or HR-2000 Osprey VHF receiver (H.A.B.I.T. Research Limited, Victoria, BC) and a three-element yagi antenna (AF Avitronics, Urbana, IL, USA) until the transmitter dropped off or the battery died (up to three weeks). Bats were visually located within roost trees using binoculars. Known roost sites were plotted in ArcGIS 9.3 using UTM's (NAD83, Zone 20N, ≥ 5 m accuracy) collected for each tree using hand held GPS units. For all colonies that used ≥ 5 roost trees we delineated 100% convex polygons using Hawth's Analysis Tools (Beyer, 2004) in ArcGIS 9.3 to determine the minimum size of roosting areas for each colony.

Results

Forty-four tricolored bats (43 females, 1 male) were captured between 12 May and 20 August in 2003-2004 and 2007-2008; 37 at the Eel Weir location and 7 at a roost tree. Captures were highest during the period of 27 May - 10 June each year (23%), with limited success after late June. Despite intensive trapping, no other two week period during the summer resulted in more than 5% of the total tricolored bat captures. We deployed 38 transmitters on 33 bats (32 female, 1 male; 5 females were tracked 2 different times). Bats were tracked for an average of 8.4 ± 5.2 days (range 1 – 19), for a

total of 216 “bat-days” (one bat-day represents tracking one bat to a roost tree on any day).

Each individual (female and male) was assigned to 1 of 9 spatially distinct roosting areas except for one which was never located despite extensive searching. Except for three cases early in the season and only on the day following capture, we found no evidence that bats roosted with individuals from other than their own roosting area. All 5 individuals tracked in multiple years used the same roosting areas.

Roost group sizes, based on counts at roost sites, ranged from 1 to 18 individuals (mean = 10; $n = 38$). The upper range and average is likely conservative as estimates were difficult due to height of roost relative to ground and bats roosting in a clump. Since the identification of new roost areas decreased over the span of the study, it would appear that most of the roosting areas in the system have been identified (Figure 1). Six initial roosting areas were located in 2003 with one new area in each of 2004, 2007 and 2008 (Figure 2). One individual captured in 2003 and 2008 and another captured in 2007 and 2008 used the same roost area in both years, and were both captured and recaptured at the same location. Four bats with PIT tags also roosted in the same roost area in successive years.

The average number of individuals tracked from each roosting area was 3 (range 1 – 7) and the average number of roost trees located in each area was 12 (range 3 – 29). Females tracked for > 1 day used 4.1 ± 1.9 SD roosts trees, using any one tree for 1.7 ± 1 SD (range 1 – 6) consecutive days. Once the colony switched to a new roost tree the incidence of them returning to previous trees was low (3 in 4 years). The male we tracked used 8 roost trees over 19 days. Individuals from all colonies foraged at the

bridge site with the distance between capture and roosting sites ranging from 303 - 6288 m. Roost area size for colonies with greater than five trees was 0.2 – 77.4 ha (mean = 17.8 ha, Table 1).

Discussion

We found multiple disjunct roosting areas used by the tricolored bats within Kejimikujik. Bats exhibited fidelity to roosting areas and generally returned to this central place within one day of release post capture. The maximum colony size appears larger in Nova Scotia than in foliage roosts in Indiana (<10; Veilleux et al 2003) and Arkansas (13; Perry and Thill 2007) but less than reported in buildings (29; Whitaker 1998). Buildings may provide more stable microclimates than foliage with a reduced risk of predation, thereby supporting larger colonies. Veilleux et al (2003) also reported that pregnant tricolored bats appeared to move as a group during multiple roost switches but this did not occur in Nova Scotia. Variation in cluster size within colonies in Nova Scotia between days could reflect a fission-fusion social organization but more data are needed to confirm this.

We found no evidence of movement among roosting areas by any bats within or between years. This supports the prediction that these bats form closed social roosting groups, which is similar to the conclusion of Kerth and Konig (2002). We tracked bats for 8.4 days on average, and although females switched roosts regularly they never roosted with individuals within the roost area of another colony. One possible explanation for frequency of roost switching is an excess of available trees and variable microclimates between roost sites (i.e., position of roost relative to canopy, sun or distance to water) which may better suit individuals or groups depending on their needs at

a given time (i.e., group size, reproductive condition, weather) (Kunz 1982, Wilde et al. 1995).

The lone male we tracked had an affinity to a roosting area, switched roosts regularly, and also used the same lichen (*Usnea trichodea*) as females for a roosting substrate. Males of the other sympatric species in Nova Scotia typically roost separately from females and usually under bark rather than within cavities (Broders and Forbes 2004). This suggests single tricolor bats may benefit from using *Usnea* lichen compared to roosting under bark. During the period he was tracked the male did not return to previously used trees once roost switching occurred, but if a tree was used over multiple days, the same roost within a tree was used. The male roosted alone for the life of the transmitter (19 days), in an area distinct from other roost sites but in an area that would appear to be available for a maternity colony (i.e., many available trees, close to water, above average *Usnea* coverage).

Trapping success over all four years was much higher in late May to early June, presumably coinciding with colony formation. This success was followed by a quick decline through the middle of June and no captures after the third week of June to the second week of July. Limited captures occurred in late July and early August. Of the six bats captured after 10 July, at least two roosted alone and showed no signs of pregnancy or post-lactation when captured. One other was a juvenile, captured on 29 July, which gives an estimate of birth of the last week of June or first week of July (Barbour and Davis 1969). While it could be suggested that bats were becoming habituated to the mist net setup and were therefore caught less (Esberard 2006), the timing of reduced captures also coincides with giving birth. It would be expected that female bats would both reduce

the distance traveled and time foraging as their mass increased with young (Shiel et al. 1999, Daniel et al. 2008), to maximize potential energy gain, and captures would decrease accordingly. The lack of captures from late June to mid-July further supports the assumption of decreased captures due to limited distance foraging by pregnant females during this time period.

Females were found in groups of 2 – 18, although several individuals roosted singly in late July. This may be due in part to colony fragmentation, particularly of females who may have been non-reproductive during the summer. The majority of roosting areas identified over the four years of this study (6) were found in 2003 with one each per year in 2004, 2007 and 2008. It is estimated that the population in this system is limited to 80 to 100 individuals based on emergence counts at roost sites and number of roost areas.

In conclusion, female forest dwelling tricolored bats roost have an intra- and inter-year fidelity to a particular roosting area that they share with other individuals. There was no evidence that individuals roosted in or with individuals assigned to other roosting areas and therefore these roosting groups appear to be “closed”. Despite this, individuals of all colonies shared foraging space.

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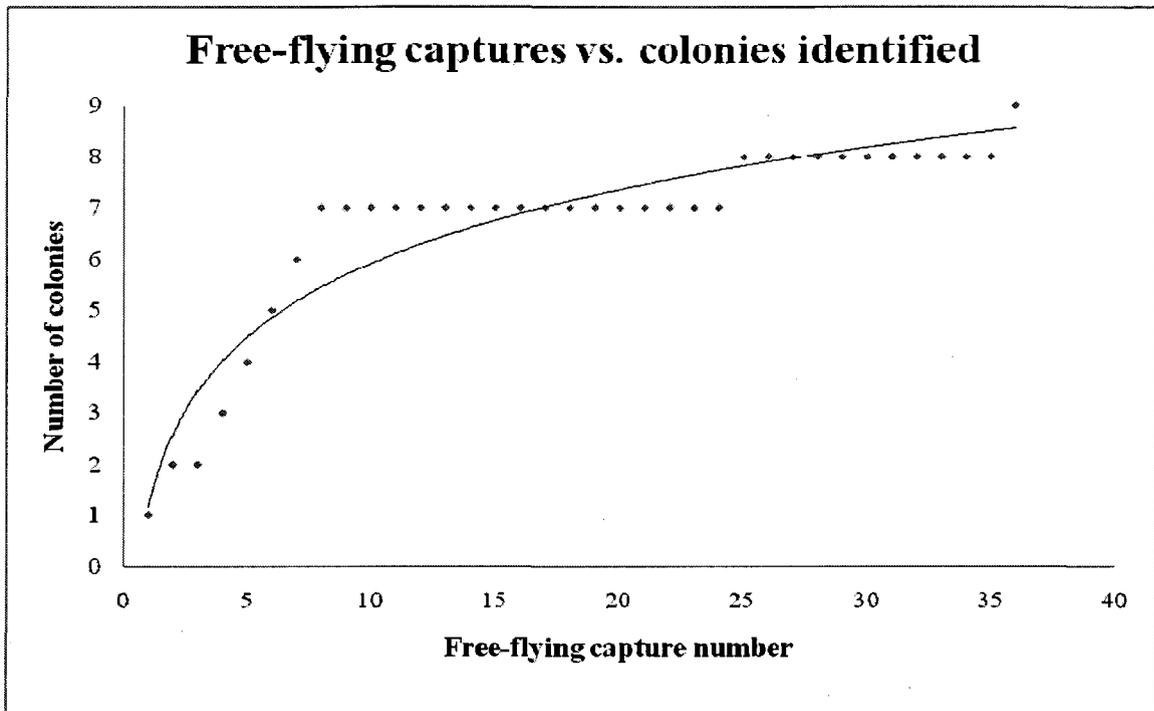


Figure 2: Number of new colonies found as a function of number of free-flying captures over the Mersey River in Kejimikujik National Park, 2003, 2004, 2007, and 2008.



Tricolored bat roosting areas in
Kejimikujik National Park, Nova Scotia, Canada

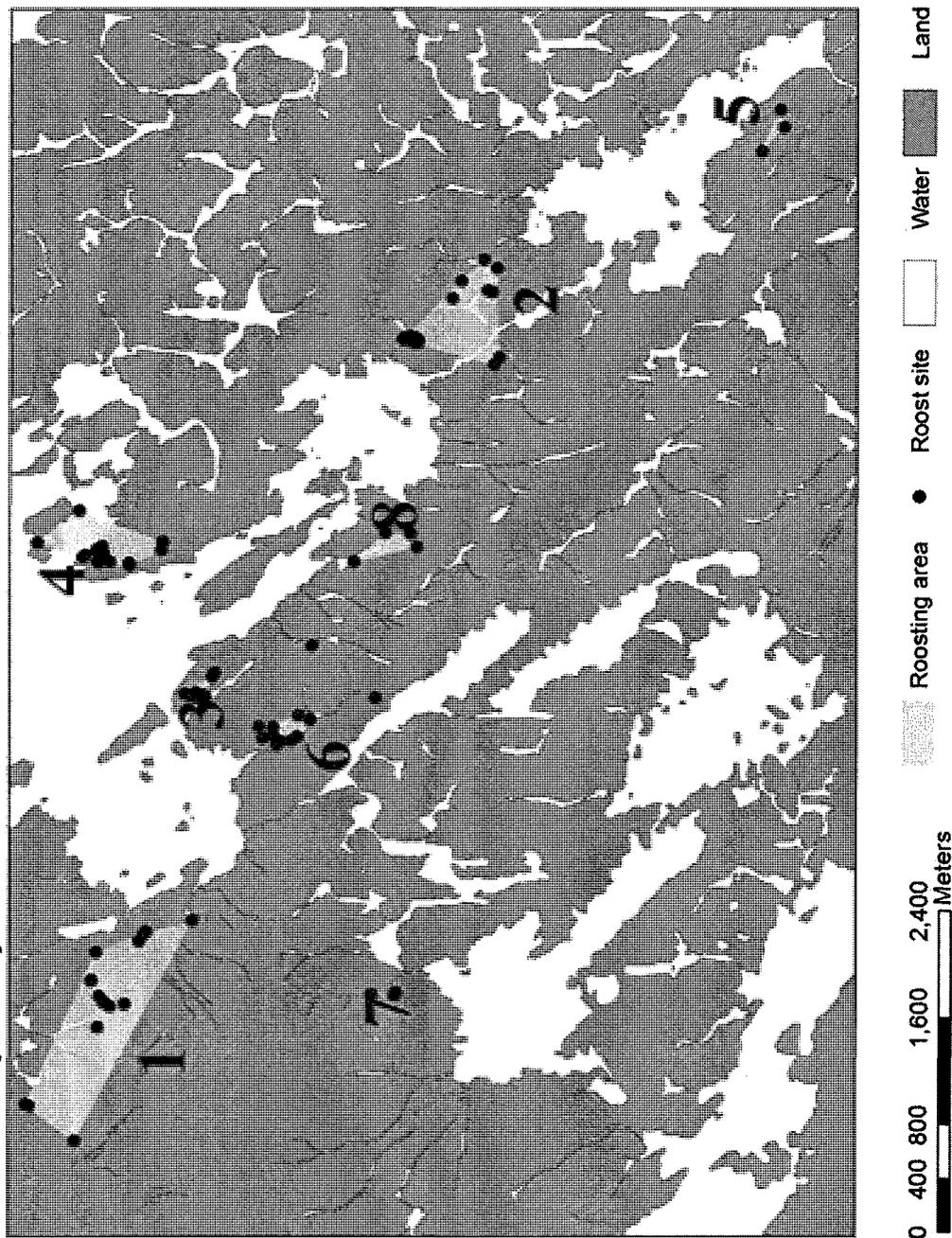


Figure 3: Distribution of tricolored bat roost trees in Kejimikujik National Park. Two trees between colonies 6 and 8 are outliers from colonies 3 and 6; bats roosted here on the day following release. These trees were not included in the MCP analysis.

Table 4: Roost area size based on minimum convex polygon calculations (Hawths Tools) for maternity colonies identified in Kejimikujik National Park in 2003/2004 and 2007/2008. Colonies with less than 5 identified roost trees were not included.

Colony number	Bats tracked	Number of trees located	Area (hectares)
1	4	16	77.4
2	7	31	31.2
3	6	19	1.6
4	5	15	21.4
6	3	12	5.0

CHAPTER 4

Roosting and social ecology of the tricolored bat: synthesis

Over four summers, trapping occurred in and around Kejimikujik National Park at various locations but was focused at the Eel Weir site in the south of the park. Of 44 tricolored bats captured; 33 bats were fitted with transmitters and tracked to 110 unique trees over 216 bat days. Spatially, the trees used by females were clumped into 8 distinct roosting areas and one solitary-roosting male roosting territory. Although all free-flying bats were captured at the same location, the distance to these territories varied from 0.3 km to 6.4 km. Captures consistently peaked from May 27 – June 10 each year, suggesting that this site may be socially important at this time to all individuals in the system. This could be due in part to early summer colony formation; conceivably after colonies form and females near parturition they remain closer to their roosting territory while foraging to conserve energy (Daniel et al. 2008). Captures dropped precipitously after June 10; it appeared that overall activity was reduced at this location and it would therefore be advantageous to locate areas of high activity for future work.

Roost site characteristics of female tricolored bats are different than that found elsewhere. In the north-eastern United States the species has been found roosting in the dead foliage of hardwood trees, usually oak (Veilleux et al. 2003;2004, Perry and Thill 2007), but in Nova Scotia this species only used *Usnea trichodea* as a roosting substrate. This epiphytic lichen grows well in areas of higher humidity (Huiskes et al. 1997). As such, trees that bats roosted in were usually spruce, as they grow in lowland areas of poor drainage (Farrar 1995), which during the summer experience higher humidity. As well, trees were most common in areas where the water table was within 0.5 m of the surface and close to large bodies of water. Based on these data and observations it appears that the species is limited in its distribution to a very specific range of locations which are

environmentally determined. Within these areas, roosting sites do not appear to be limited but they do limit the size of a roosting territory of a given colony. Kejimikujik National Park has limited locations which could be considered suitable for the roosting purposes of the species based on the findings on this project. As such, it seems that the bulk of colonies within commuting distance of the bridge capture site have been identified, as the majority were found in the first summer, with a single territory identified in each successive year. The apparent lack of reuse of trees suggests that it may be necessary to protect areas and not just trees within areas. The mechanism behind which tree is used in a particular area is not completely understood, so the arbitrary selection of which trees to preserve may not be as beneficial as might be expected.

The female maternity colonies were small; the maximum number of individuals seen at one roost site was 18, and there was no evidence of individuals moving between colony territories within or between years. Females were found to have an affinity to a particular area, even among years, suggesting the local population is territorial in terms of roosting. Research elsewhere on sociality in bats has not determined that the closed societies are composed of individuals that are directly related (Kerth et al. 2002), but there is evidence that when new colonies form, it is done by individuals which are more closely related or are found to have non-random associations over the course of the summer with one another (Kerth 2008). The social aspect of colony formation is one that needs further study. The Kejimikujik system represents an ideal location for this work. There are multiple colonies composed of a small number of individuals relative to sympatric bat species in Nova Scotia and they have small spatial distribution.

The strength of the top AIC_c ranked logistic model relative to the other candidate models underscores the specific roosting requirements of this species in Nova Scotia. Tricolored bats prefer *Usnea* lichen as a roost medium and short commuting distance to water and therefore use areas that support this need, and are likely therefore severely constrained by their environment. For appropriate roosting areas to exist for tricolored bats in Nova Scotia, several attributes need to be satisfied. First, the geology and topography of the area must support areas of poor drainage. Having a water table close to the surface promotes areas that are marshy or swampy, and in the long term favors tree growth of species such as spruce and maple which have shallow roots (Farrar 1995). As these areas experience succession, the canopy becomes increasingly open, allowing for evaporation of ground water through the mosses on the surface, providing higher humidity which in turn results in higher growth rates for lichens such as *Usnea*. Over time, many trees in these small areas become covered with *Usnea* and suitable roosting areas are created for the species. The trees that were most heavily laden with *Usnea* were usually dead or dying and the probability of bat presence increased with the percent coverage of *Usnea* in a particular roost tree. Since *Usnea* appears to grow slowly and favor dead spruce in the system, this is an important factor that must be considered when deciding which areas need to be set aside as potentially suitable roost territories. Snags, which are usually not suitable for commercial purposes, are usually removed during thinning in private woodlots and commercial operations. The removal of these trees from areas which may support tricolored bat maternity colonies is most certainly detrimental.

The marked decrease in acoustic activity of tricolored bats as you move east from Kejimikujik National Park (Farrow 2007) suggests that there may be a lack of available

areas for maternity colonies to use during the reproductive season. Kejimikujik may be acting as an island for this species in Nova Scotia; it has been protected for 40 years, resulting in the establishment of areas that are ideally suited to this species. Over the long term, for the species to expand, more of these areas will need to be identified and maintained. The first step in this process would be to identify areas of a) shallow depth to ground water b) poor drainage (i.e., lower elevation relative to the landscape) and c) stands of trees which are dominantly softwood. A GIS could be used to determine these if they areas exist and where they are located. It is also important to understand the effect, if any, that the intensive logging in southwest Nova Scotia may be having on this species. The potentially small, disjunct population of this species in Nova Scotia could be an important pool of genetic material in the future as biological and anthropogenic pressures reduce the populations of tricolored bats in the northeastern United States.

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APPENDIX I



Figure 4 : Eel Weir site, across the Mersey River in Kejimikujik National Park. Location of intensive trapping effort over four summers, 2003/4 & 2007/8. Tops of masts are 10 m above river. 10 cm x 10 cm lumber with rope and pulley system used to hoist nets.



Figures 5 & 6: Maternity colony (left) and lone male (right) roosting in typical umbrella of *Usnea* lichen. Photos taken in Kejimikujik National Park, June 2007.



Figure 7: View north from Eel Weir trapping location toward George's Lake. Bats were typically seen foraging over the water around sunset.



Figure 8: Female tricolored bat (name: Alana) roosting on small branch, transmitter is visible pointing upward from between shoulder blades, June 9, 2007.



Figure 9: 2008 Kejimkujik bat team. From left: JAP, HMH and CGA, June 2008.

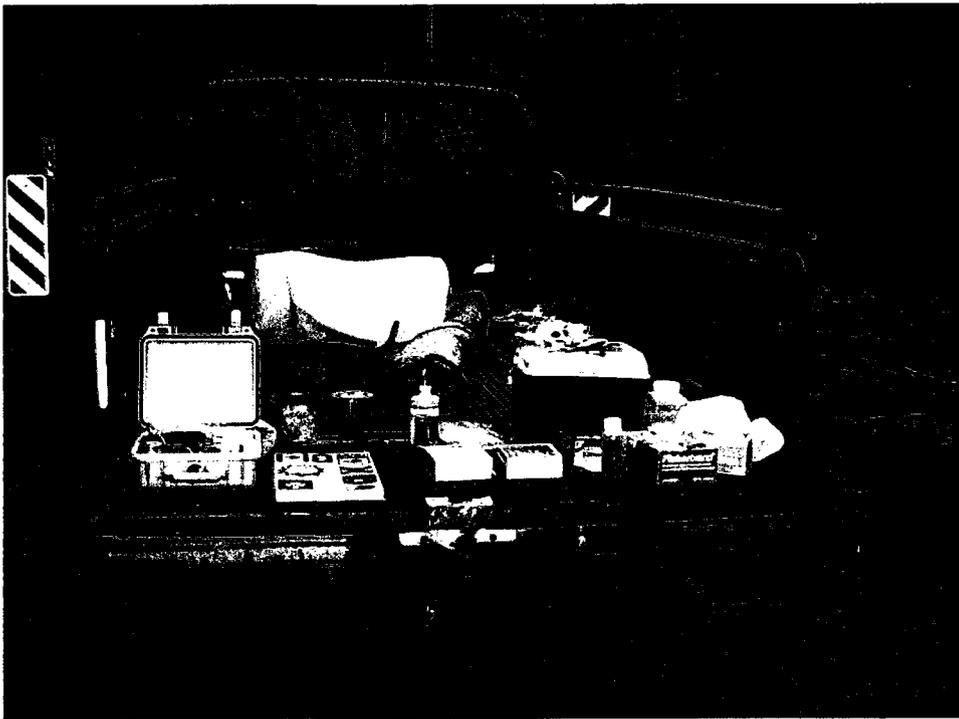


Figure 10: Mobile field station setup for processing bats. Capture kit on left, containing scale, sampling instruments, transmitters, PIT tags; genetic sampling equipment on right