

**THE EFFECTS OF FOREST FRAGMENTATION ON THE
FOREST-DEPENDENT NORTHERN LONG-EARED BAT
(*MYOTIS SEPTENTRIONALIS*)**

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**THE EFFECTS OF FOREST FRAGMENTATION ON THE
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(MYOTIS SEPTENTRIONALIS)**

By Lynne E. Henderson

ABSTRACT

The modification of formerly contiguous natural areas is a central concern to conservation biology because of the potential to negatively affect biological communities. Characterizing the effects of forest fragmentation is essential to understanding the response of populations of forest species to fragmentation. The goal of this thesis was to explore the effects of forest fragmentation on a forest-dependent bat species in an agriculturally-dominated landscape by; 1) relating the distribution of northern long-eared bats (*Myotis septentrionalis*) to forest loss and changes in forest composition; and 2) examining the movements and resource selection of female bats. The best predictor of bat distribution was the area of hardwoods, with the effect at the fragment level for females and at the landscape level for males. Female bat movements were found to be strongly associated with forest features. The availability of roosts, amount of structural clutter (tree density) and proximity to forested creeks best explained the spatial separation of roosting and foraging areas. This study demonstrates the impacts of forest management practices on bats and highlights the importance of incorporating the requirements of forest-dwelling bats into forest management plans to maintain bat populations.

June, 2007

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Chapter 1

The effects of forest fragmentation on the forest-dependent northern long-eared bat (*Myotis septentrionalis*): introduction

The modification of landscapes has a long history that tracks the development and expansion of settlements, agriculture and natural resource extraction (Forman & Godron 1986; Saunders *et al.* 1991). The anthropogenic fragmentation of formerly contiguous habitat of species is a central concern to conservation because of the large potential to influence local biodiversity (Andr n 1994; Franklin *et al.* 2002). In this thesis, habitat is defined as a concept to describe the resources and conditions (both physical and biological) of an area that permit occupancy and it is considered to be a species-specific term (Hall *et al.* 1997; Morrison 2001). Therefore, the process of fragmentation isolates remnant habitats independent from habitat loss (Fahrig 2003), and both the loss and isolation influence the quality of the remaining habitat for populations. The effects of fragmentation on populations can include disrupted dispersal (Cooper & Walters 2002), overcrowding (Zanette *et al.* 2000), edge effects (Andr n & Angelstam 1988; Huhta *et al.* 1999) and increased competition (Huxel & Hastings 1998). Characterizing and quantifying the effects of fragmentation on a species distribution and behaviour in landscapes is essential to understanding population responses to landscape fragmentation.

Studies investigating fragmentation have predominantly taken a community-level approach stemming from island biogeography theory (MacArthur & Wilson 1963; MacArthur & Wilson 1967) where the focus is on area and isolation effects (Ewers & Didham 2006; Haila 2002). Communities assessed for fragmentation effects have included small mammals (Bayne & Hobson 1998; Bowman *et al.* 2001; Nupp & Swihart 2000), amphibians (Silva *et al.* 2003; Weyrauch & Grubb 2004), and birds (Opdam *et al.* 1984; Uezu *et al.* 2005; Villard *et al.* 1999; Watson *et al.* 2004). These and other empirical studies demonstrate that the response to fragmentation is at the species level as

habitat and individual life history traits in behaviour are specific to species and landscape structure (Bright 1998; Harris & Reed 2002; Saunders *et al.* 1991; Tischendorf & Fahrig 2000). Furthermore, intra-specific variation in behaviour due to sex or reproductive status may also influence responses to habitat fragmentation (Bayne & Hobson 2001; Desrochers & Hannon 1997; Fraser & Stutchbury 2004). Species traits that may yield sensitivity to fragmentation include low reproductive capacity, resource specialisation, poor dispersal ability, sociality, and high trophic level position (Henle *et al.* 2004; Noss *et al.* 2006).

Bats as a group exhibit many of the fragmentation sensitivity traits such as low fecundity (Barclay & Harder 2003) and high longevity, (Arlettez *et al.* 2002; Keen & Hitchcock 1980) which can put them at risk for population declines (Fenton 2003; Findley 1993; Purvis *et al.* 2000). Recent work has demonstrated the negative effect of fragmentation on the species richness of forest bat communities (Bernard & Fenton 2003; Cosson *et al.* 1999; Crome & Richards 1988; de Jong 1995; Estrada & Coates-Estrada 2002; Gorresen & Willig 2004). Consistent with other animal groups studied, bat species exhibit a differential response to forest fragmentation depending on their specific life history traits or behaviours. These species-specific responses are further underscored in studies of response to logging, (Grindal 1996; Patriquin & Barclay 2003) and urban and agricultural expansion (Duchamp *et al.* 2004; Evelyn *et al.* 2003; Sparks *et al.* 2005). Species exhibiting a forest dependence, where the forest is required for multiple life history needs (foraging and roosting; Miller *et al.* 2003) are predicted to be vulnerable to fragmentation.

The volant nature of bats means that they are highly mobile and can cross different vegetation types efficiently and therefore may have access to multiple landscape

habitats (Fenton 1997). Studies show that some bat species will cross large distances to use remnant habitat fragments for foraging and roosting in fragmented landscapes (Bernard & Fenton 2003; Evelyn & Stiles 2003; Lumsden & Bennett 2005; Zielinski & Gellman 1999). In forest-agricultural landscapes in Europe, some bat species were found to use wooded linear landscape elements, such as hedgerows and riparian corridors, in commuting through or foraging in agriculturally dominated landscapes (Downs & Racey 2006; Limpens & Kapteyn 1991; Verboom & Huitema 1997). The specific vagility of a bat in a fragmented landscape will depend on the behavioural, morphological and ecological characteristics which dictate individual resource selection and use (Evelyn & Stiles 2003; Fenton 1997). Forest specialists are strongly associated with intact forested areas, and may exhibit lower vagility in a fragmented landscape depending on the specific compositions and configuration of remnant forest patches. Restricted vagility in fragmented systems is well documented for forest specialist birds (Bayne & Hobson 2001; Bélisle *et al.* 2001; Fraser & Stutchbury 2004; Huhta *et al.* 1999; Villard *et al.* 1999).

Animals select resources at a variety of scales (Johnson 1980; Orians & Wittenberger 1991) and bats in particular may select resources at multiple scales owing to their high vagility (Fenton 1997). The presence of bats in a landscape depends on a suite of interrelated conditions (e.g. prey abundance, suitable roosts, climate; Ford *et al.* 2006a). Although fragmentation is considered as a landscape process (Fahrig 2003) its effects occur over multiple scales by influencing specific habitat resources. In order to understand the effects of fragmentation on bats it is important to undertake focused studies on single species over multiple scales.

The northern long-eared bat is a widely distributed North American species ranging from the forests of British Columbia to Newfoundland and as far south as Florida (Caceres & Barclay 2000; van Zyll de Jong 1985). The life history of the northern long-eared bat is typical for temperate bat species with a period of activity in the summer and a hibernation period in the winter. In the late summer and early fall, male and female bats gather at hibernacula for swarming and mating activity prior to entering hibernation (Caire *et al.* 1979). In the summer, males and females disperse to forests from winter hibernacula. Female bats are more restricted in roosting choices in order to minimize energy expenditures associated with higher reproductive costs incurred from pregnancy and providing sole parental care to juveniles (Barclay 1991; Broders *et al.* 2006; Garroway 2006; Hamilton & Barclay 1994; Mclean & Speakman 1999; Willis *et al.* 2006). Females predominantly roost in deciduous tree species in maternity colonies (Broders & Forbes 2004; Foster & Kurta 1999; Menzel *et al.* 2002; Sasse & Pekins 1996) and males typically roost solitarily in either deciduous or coniferous trees (Broders & Forbes 2004; Ford *et al.* 2006b; Jung *et al.* 2004; Lacki & Schwierjohann 2001).

The northern long-eared bat is forest dependent since in addition to roosting in the forest, the species also forages in the forest interior (Broders *et al.* 2006; Jung *et al.* 1999; Lacki & Hutchinson 1999; LaVal *et al.* 1977; Owen *et al.* 2003). Wing morphology and echolocation call design reflect a species that is adept at gleaning and hawking prey aerially in structurally cluttered forest interiors (Broders *et al.* 2004; Faure *et al.* 1993; Fenton & Bogdanowicz 2002; Ratcliffe & Dawson 2003). The primary insect prey consumed by northern long-eared bats are Lepidopterans and Coleopterans (Brack & Whitaker 2001; Broders 2003; Carter *et al.* 2003).

The goal of this thesis was to assess the effects of forest fragmentation on bats by examining the response of a forest-dependent bat species, the northern long-eared bat (*Myotis septentrionalis*) to forest fragmentation in an agriculturally-dominated landscape. This thesis examined the effects of fragmentation on the northern long-eared bat at two different levels; first at the geographic and distributional level and second at a colony-range level. The specific objectives addressed in this thesis were:

Chapter 2: Quantifying the relationship between fragment characteristics (local and landscape level) and the presence of *Myotis septentrionalis* within the fragment to determine the best predictors of the distribution of the species.

Chapter 3: Determining the extent to which *Myotis septentrionalis* uses the forest-agricultural landscape by 1) following individual bats to identify roosting and foraging sites; 2) determining if movements in foraging and commuting are restricted to areas with forest cover; 3) characterizing and comparing the forest structure in roosting and foraging areas; 4) assessing the abundance of potential insect prey in foraging and roosting areas.

Chapters two and three are written as independent manuscripts for publication. In chapter two I have included data sampled in 2004 by an honours student in my modelling in addition to data sampled by myself in 2005. Statistical analysis and interpretation of the data in the chapter are my own.

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Chapter 2

Intra-specific effects of forest loss by fragmentation on the distribution of the northern long-eared bat (*Myotis septentrionalis*)

Abstract

The fragmentation of forests by the expansion of human activities is acknowledged as an important factor driving declines in forest species worldwide. Quantifying the effects of forest fragmentation is essential to understanding the response of populations of forest-dependent species. To examine the impacts of forest cover loss and changes in composition on forest-dependent bats, the effects of these factors on the distribution of the northern long-eared bat (*Myotis septentrionalis*) were studied as a case study. Forest fragments were surveyed in the fragmented forest-agricultural landscape of Prince Edward Island to assess occupancy of bats in fragments. Logistic regression and multimodel inference using Akaike's Information Criteria were used to identify potentially important predictor variables in influencing the distribution at the fragment and landscape level and quantify their effects. A compositional variable, area of hardwoods, was found to be the best predictor of presence of *M. septentrionalis*. The effects of fragmentation were found at the fragment level for females and at the landscape level for males. This case study emphasizes the importance of examining intra-specific resource selection in how it affects the response of a forest-dependent species.

Key words: forest fragmentation, AIC, Chiroptera, *Myotis septentrionalis*, distribution, landscape, PEI

Introduction

Landscape mosaics of natural and anthropogenic features (agricultural, urban and rural areas) have become a dominant landscape pattern across many regions of North America (Forman & Godron 1986). The fragmentation of formerly contiguous landscapes is a central concern to conservation because of the large potential to influence the persistence of biodiversity in these landscapes (Andr n 1994; Franklin *et al.* 2002; Lumsden & Bennett 2005). The process of habitat fragmentation isolates remnant areas independently from the original habitat loss (Fahrig 2003) and both loss and isolation influence the quality and quantity of resources available to maintain populations. Fragmentation therefore impacts populations by reducing immigration and population size, and by creating openings for invasion by exotic species (Law *et al.* 1999). Quantifying the effects of fragmentation on a species distribution is thus an important undertaking for determining the factors that regulate populations (Andr n 1999).

Studies investigating the effects of fragmentation on populations have primarily probed community-level responses in a manner derived from classical island biogeography theory (MacArthur & Wilson 1963; 1967). The dramatic ecological differences between forest fragments and agricultural areas have made the study of forest-agricultural landscapes an ideal setting to explore the effects of fragmentation on forest remnant and matrix processes (Kupfer *et al.* 2006). Community level studies in these landscapes have included amphibians, (Silva *et al.* 2003; Smith *et al.* 1996) small mammals (Bayne & Hobson 1998; Nupp & Swihart 2000) and woodland birds (Desrochers & Hannon 1997; Opdam *et al.* 1984; Villard *et al.* 1999). Recent research has demonstrated a differential response to fragmentation at the species level as species-specific life history characteristics such as vagility (D'Eon *et al.* 2002), niche breadth

(Swihart *et al.* 2003) and behaviour (Bélisle & Desrochers 2002; Bowman & Fahrig 2002) determine individual species response. Traits that confer a sensitivity to fragmentation include low reproductive capacity, resource specialisation, high trophic position, and poor dispersal ability (Henle *et al.* 2004; Noss *et al.* 2006).

Bats are the second most species rich order of mammals with approximately 1100 species world wide (Simmons 2005), and thus can be important contributors to a wide variety of ecological communities. Two critical components for persistence of bat populations are the availability of roosting and foraging resources, although the relative importance of each as limiting factors has yet to be resolved (Fenton 1997, 2003). Bats have a low reproductive potential (typical litter size of temperate species is 1 or 2 per year; Barclay & Harder 2003) and are long-lived with records in excess of 30 years (Arlettez *et al.* 2002; Keen & Hitchcock 1980) and even 40 years (Podlutzky *et al.* 2005). These traits make bats sensitive to large-scale environmental perturbations which may put them at risk for population declines (Findley 1993; Purvis *et al.* 2000). Fragmentation has the potential to directly impact bat populations by limiting essential roosting and foraging resources.

Several studies have explored the effects of fragmented landscapes on bats using community level surveys (Bernard & Fenton 2003, 2007; Cosson *et al.* 1999; Crome & Richards 1988; de Jong 1995; Estrada & Coates-Estrada 2002; Gorresen & Willig 2004). Previous work has also shown that bats respond to alterations in forest structure from harvesting via changes in roost selection and foraging activity (Crampton & Barclay 1998; Grindal 1996; Patriquin & Barclay 2003; Sedgely & O'Donnell 2004). These studies have concentrated on forested environments and illustrate that the differential response by individual species to fragmentation is affected by unique roosting and

foraging site preferences and behaviours. Forest generalists that are able to use a wide variety of landscape elements, (Russ & Montgomery 2002) may be neutrally or positively affected by fragmentation through the creation of forest-edges (Grindal & Brigham 1999). Species exhibiting a forest-dependence, where forests are required for multiple aspects of life histories (e.g., foraging and roosting), are likely more vulnerable to forest loss and fragmentation (Lane *et al.* 2006). Few studies have quantitatively addressed the effects of forest fragmentation on individual bat species despite the large number of forest dwelling bats (although see Evelyn & Stiles 2003; Lumsden *et al.* 2002; Sedgeley & O'Donnell 2004 for notable exceptions on roosting ecology).

In this study the distribution of the northern long-eared bat (*Myotis septentrionalis*) was examined in a forest-agricultural mosaic on Prince Edward Island (PEI), Canada. The forests of PEI are part of the Acadian forest region, and are characterized by both broadleaf deciduous and boreal coniferous species (Sobey & Glen 2002, 2004) including sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), red spruce (*Picea rubens*) and balsam fir (*Abies balsamea*) (Farrar 1995). PEI has been subjected to nearly three centuries of intense anthropogenic activities such as shipbuilding, timber harvesting and agricultural intensification. The clearing of land peaked in the early twentieth century with approximately 70% of the island's forests being cleared (Loo & Ives 2003). As a result, the current landscape is highly fragmented in which disturbed and regenerated forest patches are embedded in a matrix of agriculture and the current forest cover is approximately 45%. The extensive fragmentation on PEI is expected to impact the distribution of local animal populations, and studies have assessed the impacts on small mammals (Hartling & Silva 2004; Silva 2001) and amphibians (Silva *et al.* 2003). The goal of this research was to quantitatively assess the

effects of forest fragmentation on bats through a case study on the distribution of the northern long-eared bat (*Myotis septentrionalis*).

The northern long-eared bat (*Myotis septentrionalis*) is a common, widely distributed species in North America that ranges from the fringes of British Columbia to Newfoundland and as far south as Florida (Caceres & Barclay 2000; van Zyll de Jong 1985). Morphology and echolocation call design reflect a high degree of manoeuvrability in flight, and a flexible gleaning and hawking foraging strategy, (Faure *et al.* 1993; Fenton & Bogdanowicz 2002; Norberg & Raynor 1987; Ratcliffe & Dawson 2003) thus facilitating foraging in cluttered forest interiors. The species is forest dependent as it uses the forest interior for both foraging and roosting (Broders *et al.* 2006; Broders *et al.* 2003; Foster & Kurta 1999; Hutchinson & Lacki 2000; Jung *et al.* 1999; Sasse & Pekins 1996). Females predominantly roost in deciduous tree species in maternity colonies (Broders & Forbes 2004; Foster & Kurta 1999; Menzel *et al.* 2002) and males typically roost solitarily in either deciduous or coniferous trees (Ford *et al.* 2006; Jung *et al.* 2004; Lacki & Schwierjohann 2001). It follows that in response to these gender differences in roost site selection, the distribution of *M. septentrionalis* among forest patches may vary between the sexes (Barclay 1991; Mills *et al.* 1996).

The effects of forest cover loss and compositional changes in forest stands were emphasized rather than isolation or landscape figuration measures as determinants of the species distribution. The objective of this research was to assess if the loss of forests via fragmentation is influencing the distribution of *M. septentrionalis*. Specifically I wanted to: 1) determine if area- or compositional-type variables were better at predicting bat presence in a fragment; 2) determine if there were intra-specific differences in the distribution and 3) determine the level (fragment or landscape) of the effects.

Methods

Study sites

Field surveys were conducted in July and August of 2004 and from June to August of 2005 in 88 forest fragments across Prince Edward Island (Figure 1). For this study a fragment was defined as an area of continuous forest that was entirely separated from other such forested areas by roads, fields, residential areas, etc. Survey fragments were selected based on a number of criteria. At a broad scale fragments were selected to sample across the island and to collectively encompass a range in size (2 to >2100 ha). At a local scale fragments were selected for access to land (permission from private landowners and access by vehicle) and the availability of suitable trap sites. Sites were selected with no *a priori* knowledge of bat distribution or fragment composition.

Trapping surveys

Each forest fragment was trapped on two different nights using harp traps (Austbat Research Equipment, Lower Plenty, Victoria, Australia). In 2004 sampling occurred from 27 July to 25 August and in 2005 from 09 June to 17 August. Where it was possible in 2005, sampling nights were in different seasons. Fragments sampled on the same night were clustered spatially due to travel-time constraints. In the instances where visits were not separated seasonally due to logistical constraints, fragments were never sampled on consecutive evenings. Traps were placed along forested trails or old roads and where possible trapped at two different sites within each fragment since some sites may be more successful at capturing bats than others (Mills *et al.* 1996). In three fragments where no established trails or roads existed, mist nets (Avinet, Dryden, New York) were set up in open areas under the canopy as an alternative. Trapping over two nights was done to balance controlling for temporal variation in bat activity and to survey

many fragments over a large spatial area, following Mills' (1996) suggestion that two or three trap nights is sufficient to estimate presence of bat species in an area.

Traps were deployed at sunset, left for approximately eight hours, and checked before sunrise. In the fragments where mist nets were used, nets were set up for a minimum of three hours following sunset and were checked every ten minutes, to capture the peak in bat activity, which occurs following sunset (Hayes 1997). All captured bats were identified to species with sex and weights recorded, and were released at the site of capture before sunrise. On several occasions when traps were checked I found only bat feces and was unable to identify the species or sex of bats that were captured and escaped. Therefore, presence of bats in a fragment for distributional modelling was determined as the in-hand identification of the species and sex in two nights of sampling. Methods for capture and handling of bats were approved by the Saint Mary's Animal Care Committee and under permit from the Prince Edward Island Department of Energy, Environment and Forestry, and Parks Canada.

Fragment and landscape characteristics

Spatial characteristics thought to be important in determining the presence of northern long-eared bats were quantified for each survey fragment using ArcGIS Geographic Information System (GIS; version 9.1, ESRI, California, USA) and GIS land use data from the PEI Corporate Land Use Inventory (2000). GIS data were derived from interpretation of aerial photographs taken in 2000 (1:17,500; B&W). Since each sex exhibits sex-specific preferences in stand selection (Broders & Forbes 2004), variables quantifying the stand composition of forests were included. Characteristics at the forest fragment level assessed included total fragment area, and the area of both deciduous and coniferous stands (hereafter hardwoods and softwoods). Hardwood and softwood stands

were classified as containing $\geq 75\%$ hardwood and softwoods species respectively.

Fragment size, in particular, has been consistently reported as influencing the distribution of mammals and birds in fragmented systems (Nupp & Swihart 2000; Uezu *et al.* 2005; Villard *et al.* 1999). The composition of the remnant forest fragments in a fragmented landscape has also been shown to be important in determining the distribution of birds and mammals as it directly impacts the resources that are available to populations (Betts *et al.* 2006; Bowman *et al.* 2001).

To assess the effects of landscape characteristics on the presence of northern long-eared bats, a two kilometre radius buffer zone was generated around the mid-point of a line joining the two trapping sites (or from the individual trap site if only one were available) to create a circular 12.6 km² buffer. I chose a two kilometre radius as the approximate scale of movements for female northern long-eared bats (Broders *et al.* 2006). Spatial characteristics determined for each buffer used the same classifications as the fragment characteristics and included total forest area, and the total area of hardwood and softwoods stand in the buffer.

Statistical analyses

Analyses were performed on three bat 'groups', male *M. septentrionalis*, female *M. septentrionalis* and both sexes, *M. septentrionalis* combined. A logistic regression framework (Hosmer & Lemeshow 2000) was used to identify which level (i.e., fragment and landscape) and which specific variables were important for predicting bat 'group' distribution and to quantify their effects. Individuals of a group present at a fragment were coded as 1, and fragments in which individuals of a group were not trapped were coded as 0. The fit of models was assessed on the global model for each bat group prior

to the model selection analysis (Burnham & Anderson 2002) to formally test the assumption that the data fit a logistic model. Hosmer and Lemeshow's goodness of fit test was used where p-values ≥ 0.05 indicate that the data sufficiently fit the model (Hosmer & Lemeshow 2000).

Following a review of relevant literature on the roosting and foraging ecology of *M. septentrionalis*, and on the effects of fragmentation on habitat loss for other bat species with a similar life-history, a set of nine *a priori* candidate models was constructed (Table 1). A small sample size (88 surveyed fragments) and low proportion of response events per covariate restricted the analysis to univariate or bivariate models (Burnham & Anderson 2002; Hosmer & Lemeshow 2000). To avoid problems of multicollinearity, area and compositional variables were not included in the same models.

The second order Akaike's Information Criterion (AIC_c) was used to rank the candidate models for each group using S-PLUS 2000 (MathSoft Engineering and Education 1999). AIC differences (Δ_i) were calculated over all models in the candidate set to compare the empirical support for each model with respect to the best model. Akaike weights (w_i) were calculated for each model and are interpreted as weight of evidence that a particular model is the best model, of the candidate set, fitting the data. I constructed a 95% confidence set of models for each bat group by summing ranked model Akaike weights to ≥ 0.95 (Burnham & Anderson 2002).

A model-averaging technique was used to calculate the relative importance weights (Nw_i) of each variable found in the 95% confidence set in order to assess which variables best predicted the presence of *M. septentrionalis* in a fragment for each bat group. Model averaging is a useful technique for obtaining parameter estimates with reduced bias when no single model is clearly found to be the best model of the candidate

model set (Burnham & Anderson 2002). Model-averaged parameter estimates (i.e., the effect size; β) with estimated unconditional standard errors (SE; Burnham & Anderson 2002) were calculated for the three top predictor variables for each bat group. Odds ratios were calculated for the top predictor variable of each bat group. These ratios are an association measure to express the likelihood of a presence outcome relative to a change in the predictor variable (Hosmer & Lemeshow 2000). To assess the relative importance of fragment level variables in contrast to landscape level variables, relative importance weights were summed over all fragment variables and over all landscape level (buffer) variables for each group.

Results

A total of 56 northern long-eared bats (*M. septentrionalis*) were captured in 28 of the 88 surveyed forest fragments. Female bats were found in 16 fragments, males in 17 with both sexes found in 5 fragments. The smallest forest fragment that females were found in was 17.1 ha composed largely of hardwoods (11.8 ha). Males were found in a comparable minimum sized forest fragment with an area of 15.9 ha that was composed primarily of softwoods (14.2 ha). A positive relationship between forest area and presence was consistently found among all groups (Table 2).

For the group, male and female *M. septentrionalis* combined, the 95% confidence set consisted of eight of the nine models. The top ranked model for *M. septentrionalis* included the landscape level variable, buffer hardwoods, with an Akaike weight of 0.369 and the second best ranked model included the variables buffer hardwoods and buffer softwoods, and had an Akaike weight of 0.138 (Table 2). The best predictor variable in determining the presence of *M. septentrionalis* in a forest fragment was buffer hardwoods

with a relative importance weight of $Nw_i = 0.519$ and a model averaged parameter estimate of $\beta_{bhw} = 0.0047$ (SE = 0.0021; Table 3). The odds of *M. septentrionalis* presence in a fragment, for an increase of 100 hectares of hardwoods in the buffer, increase by 1.60 ($\exp(0.0047 \times 100)$; 95% CI: 1.06 – 2.40). The sum of the relative importance weights for fragment and buffer variables was 0.350 and 0.699 respectively. Hosmer and Lemeshow's goodness of fit test indicated that the global model adequately fit the data ($p = 0.561$).

For the group, male *M. septentrionalis*, the 95% confidence set consisted of eight of the nine candidate models. The top-ranked model for male *M. septentrionalis* presence in a fragment included the landscape variable, buffer hardwoods, with an Akaike weight of 0.305 (Table 2). The second best ranked model contained the variable buffer forest area with an Akaike weight of 0.153. The best predictor variable was buffer hardwoods with a relative importance weight of 0.426 and the model averaged parameter estimate was $\beta_{bhw} = 0.0035$ (SE = 0.0020; Table 3). The odds of male *M. septentrionalis* presence in a fragment, for an increase of 100 hectares of forest in the buffer, increase by 1.41 ($\exp(0.0035 \times 100)$; 95% CI: 0.95 – 2.11). The sum of the relative importance weights for fragment and buffer variables was 0.361 and 0.690 respectively. Hosmer and Lemeshow's goodness of fit test indicated that the global model adequately fit the data ($p = 0.714$).

For the group, female *M. septentrionalis*, the 95% confidence set again consisted of eight of the nine models. The top ranked model for female *M. septentrionalis* included the variables fragment hardwoods and fragment softwoods, and had an Akaike weight of 0.180. The second ranked model included the variable fragment hardwoods, and had an Akaike weight of 0.171 (Table 2). There were in fact five models with Akaike weights \geq

0.100 indicating high model uncertainty in selecting one best model. The best predictor variable for females was fragment hardwoods with a relative importance weight of 0.369 and a model averaged parameter estimate of $\beta_{\text{fhw}} = 0.0051$ (SE = 0.0039; Table 3). The odds of female *M. septentrionalis* presence in a fragment, for an increase of 50 hectares of hardwoods in the forest fragment, increase by 1.08 ($\exp(0.0051 \times 50)$); 95% CI: 0.77 – 1.29). The sum of the relative importance weights for fragment and buffer variables contrasts that found for males, with values of 0.585 and 0.465 respectively. Hosmer and Lemeshow's goodness of fit test indicated that the model adequately fit the data ($p=0.296$).

Discussion

This study suggests that the fragmentation of forests on PEI likely affects the distribution of *M. septentrionalis* through the loss of forest cover and specifically the loss of hardwood stands. Consistent among all groups was a positive relationship between forest area and presence which supports previous contentions that this species is indeed a forest dependent species. Positive associations with woodland habitat and higher bat activity have been documented in community surveys conducted in rural landscape mosaics (Gehrt & Chelsvig 2003; Walsh & Harris 1996b) underscoring the importance of woodlands to a variety of bat species in providing essential roosting and foraging resources (Estrada & Coates-Estrada 2002; Grindal & Brigham 1999; Lumsden *et al.* 2002; Vonhof & Barclay 1996). Both buffer forest area and fragment area are measures of the amount of forest available at different scales, and therefore support the expected negative effect of forest cover loss on the probability of presence of *M. septentrionalis*. Negative effects of forest cover loss on bats is well documented from processes such as

forest harvesting (Grindal 1996; Patriquin & Barclay 2003), urban expansion (Duchamp *et al.* 2004; Evelyn *et al.* 2003; Sparks *et al.* 2005) and agricultural intensification (Russ & Montgomery 2002; Wickramasinghe *et al.* 2003). All three processes have long occurred on PEI, and the resultant extensive clearing of forested areas is expected to negatively affect forest species.

The compositional variables quantifying the area of hardwoods were consistently the top predictors in determining presence for all groups. The relationship of hardwood area was positively related to presence of northern long-eared bats at either the fragment or landscape level. Numerous studies have documented use of hardwood species by females (Broders & Forbes 2004; Foster & Kurta 1999; Menzel *et al.* 2002; Owen *et al.* 2003; Sasse & Pekins 1996) and also by males (Ford *et al.* 2006; Jung *et al.* 2004; Lacki & Schwierjohann 2001) although males have also been shown to roost in softwood species (Broders & Forbes 2004; Jung *et al.* 2004). The large number of tree species and types (hardwood or softwood) used by northern long-eared bats across its range, suggest that there is considerable flexibility in roost tree species selection by the species in choosing trees of appropriate characteristics in a specific landscape (Carter & Feldhamer 2005; Ford *et al.* 2006). This may be particularly applicable to males as they do not face the same energetic constraints as females in roost selection (Broders & Forbes 2004). On PEI, male northern long-eared bats may be selecting hardwood species with appropriate thermal and structural characteristics in the context of the available forest. Further work would be required to determine roost trees used by male northern long-eared bats on PEI.

As expected, given the strong selection female *M. septentrionalis* exhibit for hardwood species, the area of softwoods at the fragment level was negatively related to presence for females. The effect size of fragment softwoods on female presence (i.e., the

magnitude of the parameter estimate) is larger than for fragment hardwoods although negative as opposed to positive. For males, area of softwoods was also negatively related to presence although at the landscape level. Softwood variables ranked as third for males and as second best for females in predicting presence and in both cases the parameter estimates overlapped zero indicating minimal effect. Univariate models composed of softwood variables never ranked higher than sixth position for any of the groups and softwood variables that did appear in high ranking models were always paired with hardwood variables. This further supports the importance of hardwoods to females and suggests that males may also roost in hardwood trees on PEI.

For male *M. septentrionalis*, the effects of forest fragmentation on PEI appear to be at the landscape level. The top three predictor variables were at the landscape level and the top variable was buffer hardwoods. Furthermore, the sum of the relative importance weights shows that variables at the landscape level are more important than those at the fragment level. Males do not face the same energetic constraints as females do with carrying the costs of pregnancy and nursing and thus may be less selective of their roosting trees (Broders & Forbes 2004; Broders *et al.* 2006) as they do not have to select trees to achieve the same thermal benefits as females. Males typically roost as solitary individuals (Broders & Forbes 2004; Jung *et al.* 2004; Lacki & Schwierjohann 2001) and do not have to select roost trees suitable for colonies as females do. Therefore, males may have a larger number of trees available to them in a landscape because they exhibit a greater flexibility in tree selection compared to females. It follows then that males may be able to use a smaller forest fragment or a fragment containing a low hardwood composition compared to females as there are more trees that are available to males. This may explain why the threshold of response to forest fragmentation is at the

landscape level. Males may have a broader base of available trees in terms of type (hardwood or softwood) and also in selection of suitable roost features such as roost size or type (and therefore microclimate characteristics). This may translate to an area effect where with more trees available to males, roosting areas are expected to be smaller.

Smaller minimum roosting areas for *M. septentrionalis* males (relative to females) were found in New Brunswick (Broders *et al.* 2006) and the minimum amount of hardwoods in a forest fragment for males on PEI was smaller compared to females (1.7 ha to 11.8 ha respectively). This supports that the response for males may be at the landscape level where males use smaller roosting areas as there are more trees available to them. Therefore males may be present in fragments with a lower hardwood composition and thus males do not respond to hardwood loss at the fragment level. It is expected that a threshold exists where the loss of hardwoods from a landscape will negatively affect the presence of males if they are selecting hardwood species for roosting. As hardwoods were found to be important for male *M. septentrionalis* on PEI, then an overall loss of hardwood trees would be expected to influence the distribution of males at the larger landscape level.

In contrast to males, the effects of fragmentation for female *M. septentrionalis* on PEI were found at the fragment level. Two of the three top predictor variables were fragment variables and the sum of the relative importance weights shows that variables at the fragment level are more important than those at the buffer level. Female bats expend greater energy than males in reproduction and rearing of their young, (Barclay 1991; Hamilton & Barclay 1994; Mclean & Speakman 1999) thus there is greater selection pressure on females for selecting suitable foraging and roosting areas that can minimize energetic costs. In particular, the roosting requirements of female bats are considered as

more critical (Mills *et al.* 1996) as their energetic demands can be double during periods of lactation (Kurta *et al.* 1990). Communal roosting by female bats can reduce thermoregulatory costs (Kerth *et al.* 2001b; Willis & Brigham 2004), and through cooperative breeding, the cost of rearing young (Kerth *et al.* 2001a; Wilkinson 1992). Selection of roost trees would then also occur at a colony level where a larger roosting area is required for suitable roost trees for individuals of the colony during different reproductive periods (Garroway 2006; Willis & Brigham 2004). The cost of reproduction for females may translate to an area effect where with less trees available to females (due to more stringent roosting requirements), roosting areas are larger. It is expected that fragments that do not contain a large enough hardwood resource base, to support a colony, will not have female bats present and therefore the response to forest fragmentation is expected to be initiated at the fragment level.

It is only recently that intra-specific differences in behaviour have been examined in the context of a species response to fragmentation. Reproductive status has been shown to restrict the movements of birds in fragmented systems with the sex that is responsible for parental care exhibiting lower mobility (Bayne & Hobson 2001; Fraser & Stutchbury 2004; Harris & Reed 2002). Lumsden *et al.* (2002) demonstrated that roost tree locations for female lesser long-eared bats (*Nyctophilus geoffroyi*) were predominantly in contiguous forest and roosts of lactating females were located entirely in the un-fragmented forest. Roosts of males, in the same study area, were situated in a wide array of landscape elements (woodland remnants, scattered trees, vineyards). These studies illustrate how the differential cost of reproduction dictates intra-specific differences in resource selection and behaviour and therefore response to fragmentation.

In this study, I show that the fragmentation of forests has effects on northern long-eared bats at different spatial scales for each sex. The area of hardwoods was the variable of importance consistently across all groups; for females its importance is at the fragment level and for males at the landscape level. The analytical framework of this analysis demonstrates the importance of understanding the role of intra-specific variation in species responses to landscape changes. Had the species distribution only been quantified at the species level, then the fragment level effect for females would have gone undetected. Effective conservation and management plans for forest-dependent species in landscape mosaics, must incorporate the specific resource requirements for each sex in order to maintain viable populations.

The results of this study show the importance of maintaining adequate stands of hardwood trees for the persistence of *Myotis septentrionalis* populations on PEI. The overall effects of hardwood areas are not clearly pronounced and distinct thresholds for minimum conservation areas would be difficult to estimate. This may be due to the imperfect detection of the species in a fragment from the sampling protocol. The problematic issue of imperfect detection has recently been investigated in how it influences wildlife-habitat models. Methods have been developed and implemented to incorporate site histories of occupancy in order to obtain a detection probability which can be further incorporated into a wildlife models (MacKenzie 2005; MacKenzie *et al.* 2002; Yates & Muzika 2006). The study design of two sampling visits did not allow for site detection probabilities to be derived and included, and thus in certain instances false absences were recorded and therefore did not contribute accurate information on how the forest measures influence presence. As a result, it is likely that effect sizes are underestimated as the parameter estimates were found to be positive (Gu & Swihart

2004). However, as the effects of hardwoods were found over all analyzed groups, this suggests that these effects are not spurious.

This study supports the contention that the fragmentation of forests is affecting the distribution of the northern long-eared bat on Prince Edward Island. The effects are most pronounced at the landscape level for males and at the fragment level for females. Previous work on other temperate bat species has also shown a clear forest/woodland association of bats that inhabit forest-agricultural mosaic landscapes (Downs & Racey 2006; Russ & Montgomery 2002; Walsh & Harris 1996a, 1996b). The results of this study highlight that although bats are a highly mobile group, a specialization on forest resources can produce sensitivity to the effects of forest fragmentation. The development of conservation plans for the species from the models should be approached with caution. Although there is quantitative evidence supporting effects of forest loss, direct threshold determinations (e.g., minimum fragment size) from the effect sizes would likely underestimate the true magnitude of effects. As this analysis focused on aspects of the roosting ecology of the species, further work exploring how fragmentation has affected foraging habitat for the species may yield additional insights on how the species uses the greater landscape.

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Table 1. Set of nine *a priori* candidate logistic regression models for predicting the probability of presence of northern long-eared bats (*Myotis septentrionalis*) in a forest fragment on Prince Edward Island.

Model	Description
1	fragment area
2	buffer forest area
3	fragment area, buffer forest area
4	fragment hardwoods
5	fragment softwoods
6	fragment hardwoods, fragment softwoods
7	buffer hardwoods
8	buffer softwoods
9	buffer hardwoods, buffer softwoods

Table 2. Difference in Akaike's Information Criterion (AIC_c) between the i th and the top ranked model (Δ_i), Akaike weights (w_i) and the sum of the Akaike weights ($\sum w_i$) for all models explaining the probability of presence of northern long-eared bats (*Myotis septentrionalis*) in a forest fragment on Prince Edward Island.

Model	Δ_i	w_i	$\sum w_i$
<i>M. septentrionalis</i> (male and female)			
buffer hardwoods	0	0.369	0.369
buffer hardwoods, buffer softwoods	1.97	0.138	0.507
fragment hardwoods	2.16	0.125	0.632
buffer forested area	2.25	0.120	0.752
fragment hardwoods, fragment softwoods	3.15	0.076	0.828
fragment area	3.34	0.069	0.897
fragment area, buffer forest area	4.02	0.049	0.946
fragment softwoods	5.02	0.030	<u>0.976</u>
buffer softwoods	5.49	0.024	1.000
male <i>M. septentrionalis</i>			
buffer hardwoods	0	0.305	0.305
buffer forest area	1.38	0.153	0.458
buffer hardwoods, buffer softwoods	2.10	0.106	0.564
fragment hardwoods	2.22	0.100	0.664
fragment area	2.41	0.091	0.755
fragment softwoods	2.63	0.082	0.837
buffer softwoods	2.80	0.075	0.912
fragment area, buffer forest area	3.52	0.052	<u>0.964</u>
fragment hardwoods, fragment softwoods	4.26	0.036	1.000
Female <i>M. septentrionalis</i>			
fragment hardwoods, fragment softwoods	0	0.180	0.180
fragment hardwoods	0.10	0.171	0.351
buffer hardwoods	0.59	0.134	0.485
buffer forest area	0.72	0.125	0.610
fragment area	0.85	0.118	0.728
buffer softwoods	1.32	0.093	0.821
fragment softwoods	1.97	0.067	0.888
buffer hardwoods, buffer softwoods	2.10	0.063	<u>0.951</u>
fragment area, buffer forest area	2.57	0.050	1.000

Underlined value denotes the delineation of the 95% confidence set (sum of the Akaike weights comprising $\geq 95\%$ of Akaike weights).

Table 3. Relative importance weights (Nw_i) for the three top predictor variables, and the model averaged parameter estimates (β_i) and unconditional standard errors (SE) in determining probability of presence in a forest fragment on Prince Edward Island.

Variables	Nw_i	β_i (SE)
<i>M. septentrionalis</i> (male and female)		
buffer hardwoods	0.519	0.0047 (0.0021)
fragment hardwoods	0.206	0.0052 (0.0035)
buffer forest area	0.173	0.0016 (0.0010)
Male <i>M. septentrionalis</i>		
buffer hardwoods	0.426	0.0035 (0.0020)
buffer forest area	0.212	0.0012 (0.0010)
buffer softwoods	0.188	-0.0005 (0.0033)
Female <i>M. septentrionalis</i>		
fragment hardwoods	0.369	0.0051 (0.0039)
fragment softwoods	0.260	-0.0080 (0.0096)
buffer hardwoods	0.207	0.0026 (0.0021)

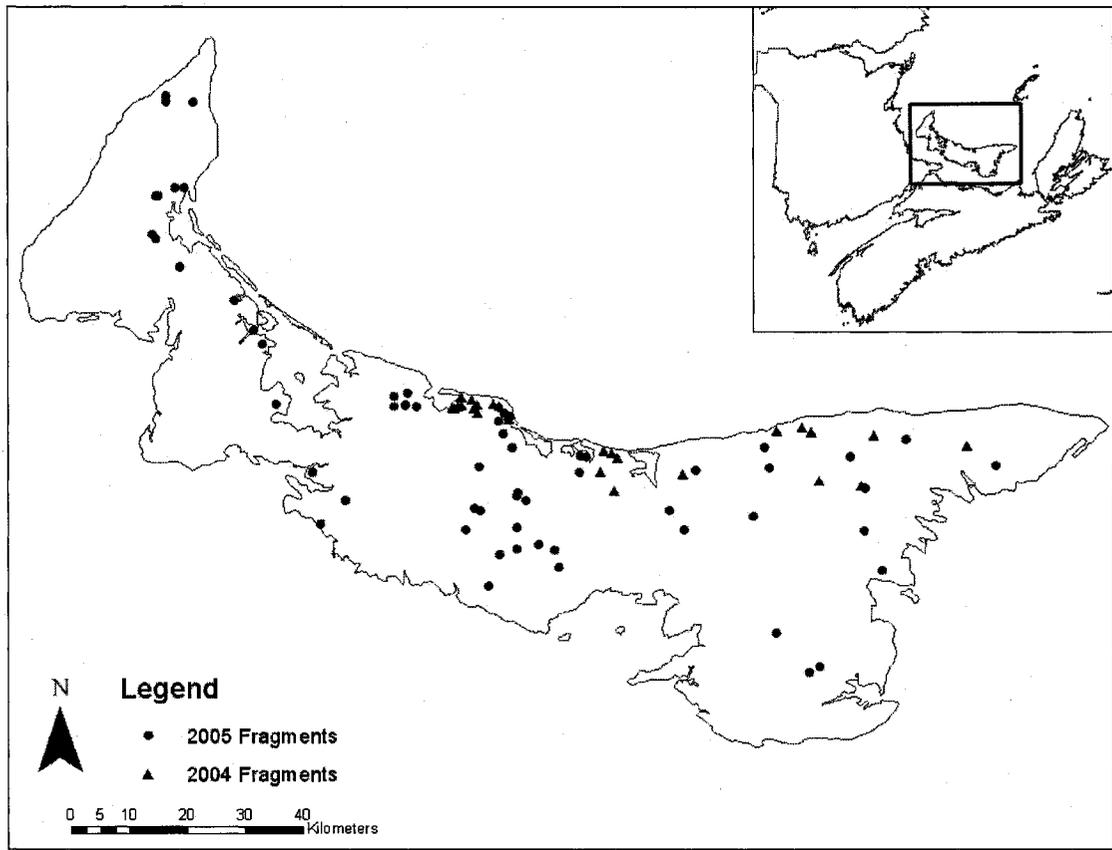


Figure 1. Locations of 88 surveyed forest fragments on Prince Edward Island (46°30'N, 63°00'W), by year, that were trapped to assess the effects of forest fragmentation on the distribution of the northern long-eared bat (*Myotis septentrionalis*).

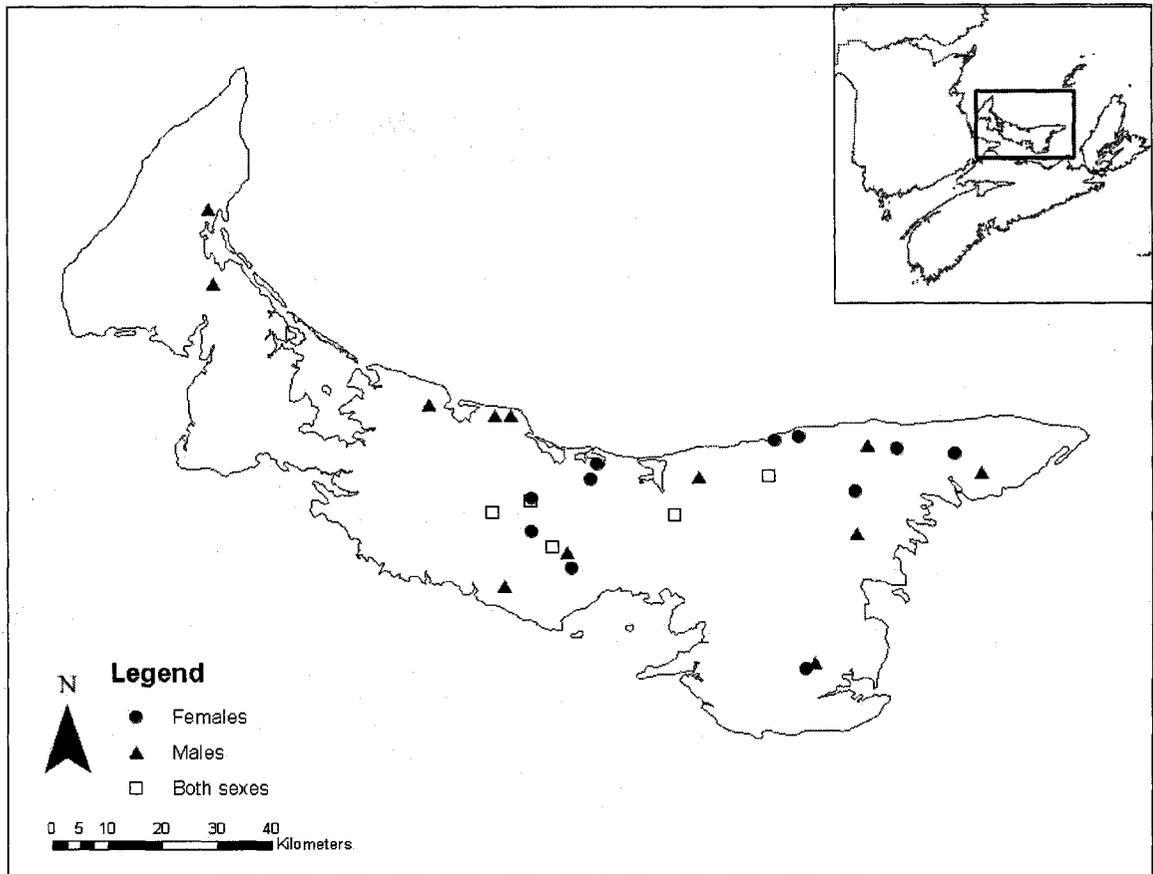


Figure 2. Surveyed forest fragments on Prince Edward Island where presence of *M. septentrionalis*, by sex, was confirmed through trapping in 2004 and 2005.

Chapter 3

Movements and characterization of roosting and foraging areas of the northern long-eared bat (*Myotis septentrionalis*) in a forest-agriculture landscape

Abstract

The fragmentation of forests by the expansion of agriculture is recognized as an important factor influencing forest species declines worldwide. Species that are forest dependent may be especially vulnerable to fragmentation because they have specialized resource requirements and may exhibit lower mobility in the agricultural matrix. To investigate this problem, the movements and resource selection of a forest-dependent bat, the northern long-eared bat (*Myotis septentrionalis*) were examined in a forest-agricultural landscape on Prince Edward Island, Canada. Radiotelemetry was used to follow female bats in nightly foraging and to locate day roosts. Locations were analyzed using a Geographic Information System to generally characterize site selection and spatial aspects of foraging and roosting. Vegetative structure and insect prey availability were compared between foraging and roosting areas to further characterize resource selection within the greater landscape. Female northern long-eared bat movements were constrained to forest features and foraging areas were concentrated along forest covered creeks with bats roosting predominantly in deciduous trees within the same forest fragment. Prey availability did not differ between foraging and roosting areas. The availability of roosts, proximity to forested creeks best explained the spatial segregation of roosting and foraging areas. This study demonstrates the importance of investigating movements and resource selection in fragmentation studies as a specialization on forest resources can restrict the vagility of forest-dependent species at a localized level.

Key words: forest fragmentation, PEI, radiotelemetry, Chiroptera, forest structure, landscape context, bats

Introduction

Agricultural intensification is a dominant force driving large-scale modifications to landscapes which result in the fragmentation of natural and semi-natural areas. Fragmentation is considered a primary threat to global biodiversity, (Franklin *et al.* 2002) and it is generally believed that its consequences are negative on most species (Saunders *et al.* 1991). It is not surprising then, that there is extensive literature documenting the negative effects of forest fragmentation on diverse species communities such as amphibians, birds and mammals (see Andr en 1994; and Fahrig 2003 for reviews). The theoretical basis in exploring fragmentation has been expanded from fundamental island biogeography principles (MacArthur & Wilson 1967), to include ideas of landscape ecology such as matrix structure and remnant habitat configuration (Fahrig 2003; Forman & Godron 1986; Haila 2002; Kupfer *et al.* 2006). Although our theoretical framework and knowledge of communities and species negatively affected from fragmentation have expanded, quantitative data for conservation planning that are transferable to similar species are still lacking.

Recent work has demonstrated the importance of developing species-specific models that explore landscape context independently from area effects in occupancy fragmentation studies (Betts *et al.* 2006; Villard *et al.* 1999). Occupancy prediction models are useful in examining the effects of fragmentation on distributional patterns relative to localized landscape structure; however, they do not provide insights into how individuals may perceive and use patchy landscapes. In order to mechanistically understand the effects of fragmentation behavioural responses at the level of the individual must be examined. Two important aspects of behaviour are resource selection and movement as the use of particular landscape elements may provide essential

knowledge into the effects of forest fragmentation on population dynamics (Wiens 1994). Indeed, studies of movements made by forest birds in fragmented systems have yielded unique insights into the mobility of birds in homing trials (Bélisle *et al.* 2001), gap-crossing decisions (Desrochers & Hannon 1997) and in describing mobility differences between reproductive and non-reproductive individuals (Bayne & Hobson 2001; Fraser & Stutchbury 2004).

Bats have recently become the subject of many studies investigating the effects of forest fragmentation. The volant nature of bats potentially confers a high degree of mobility within landscapes (Fenton 1997), and therefore bats are an interesting study group for fragmentation studies. For example, studies have shown that linear landscape elements (i.e. riparian corridors, wooded hedge-rows) are used by commuting and foraging bats (Downs & Racey 2006; Law & Chidel 2002; Limpens & Kapteyn 1991; Verboom & Huitema 1997) and others highlight the importance of scattered trees in agricultural areas as important foraging areas (Law *et al.* 2000; Lumsden & Bennett 2005). The responses of bats to forest fragmentation have primarily been assessed by community level surveys investigating how species composition and/or diversity changes in remnant patches or differs from contiguous areas (Bernard & Fenton 2007; Cosson *et al.* 1999; Crome & Richards 1988; de Jong 1995; Estrada & Coates-Estrada 2002; Gorresen & Willig 2004).

As with other groups studied, the response of bats to fragmentation is specific to individual species as it reflects species-specific life history traits such as differences in roosting and foraging site preferences and behaviours. Species that are forest generalists in that they are able to use a wide variety of landscape elements, (Russ & Montgomery 2002) may be neutrally or positively affected by fragmentation through the creation of

forest-edges (Grindal & Brigham 1999) and opportunistic use of anthropogenic features (e.g. lights in foraging; Geggie & Fenton 1985; Haupt *et al.* 2006). Species that specialize on forest resources, where forests are required for multiple aspects of life histories (e.g., foraging and roosting), are more likely to be vulnerable to forest loss and fragmentation (Lane *et al.* 2006). Few studies have investigated resource selection within a fragmented landscape (although for exceptions see Bontadina *et al.* 2002; Evelyn & Stiles 2003; Lumsden *et al.* 2002; Sedgeley & O'Donnell 2004), and movements of bats have primarily been inferred from capture-recapture studies (Bernard & Fenton 2003; Bianconi *et al.* 2006).

In this study the effects of forest fragmentation on bats were investigated through a case study of the movements and resource selection of the northern long-eared bat (*Myotis septentrionalis*). The northern long-eared bat is a common, widely distributed forest-dwelling species in North America that ranges in the west from the fringes of British Columbia to Newfoundland in the east and as far south as Florida (Caceres & Barclay 2000; van Zyll de Jong 1985). The morphology and echolocation call design reflect a species with highly manoeuvrable flight, and a flexible gleaning and hawking foraging strategy, (Faure *et al.* 1993; Fenton & Bogdanowicz 2002; Norberg & Raynor 1987; Ratcliffe & Dawson 2003) thus facilitating foraging in cluttered forest interiors. The species is considered as forest dependent as it is commonly recorded and captured in the forest interior and studies in forested landscapes have found that it uses the forest for both foraging and roosting (Broders *et al.* 2006; Broders *et al.* 2003; Carter & Feldhamer 2005; Hutchinson & Lacki 2000; Jung *et al.* 1999; Sasse & Pekins 1996). Little is known of the species ecology in a forest-agricultural landscape, with only one study examining the roosting preferences of females in such a landscape (Foster & Kurta 1999). Females

form maternity colonies and predominantly roost in deciduous tree species (Broders & Forbes 2004; Foster & Kurta 1999; Menzel *et al.* 2002), and since females bear higher costs associated with reproduction, this study focused on assessing how female northern long-eared bats move in and use a forest-agricultural landscape. Specifically, the objective was to determine the pattern of use of the forest-agricultural landscape by female *Myotis septentrionalis* by:

- 1) Characterizing roosting and foraging sites in terms of forest structure, potential prey abundance and spatial extent and context in the landscape
- 2) Determining if movements within and between foraging and roosting areas are restricted to areas with forest cover

Methods

Study area

Fieldwork was conducted on Prince Edward Island (PEI), Canada, near the community of Hunter River (46°35'N, 63°35'W). PEI encompasses an area of approximately 5660 km² and the province is a complex mosaic of regenerated and disturbed forest patches interspersed among agriculture. The historical forest cover of the island was nearly 98% with the current 45% forest distribution being a result of three centuries of clearing for farming and timber extraction (Loo & Ives 2003). The forests of PEI are part of the Acadian forest region which are characterized by broadleaf deciduous and boreal coniferous species (Sobey & Glen 2002, 2004) including sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), red spruce (*Picea rubens*) and balsam fir (*Abies balsamea*) (Farrar 1995).

Two study areas, Wheatley River and Greenvale (Figure 1), were selected that differed in both the total area of forest at the site and spatial configuration (i.e., different distances to nearest neighbouring forest patch and different sized forest patches). The Wheatley River site had an approximate forest cover of 18% and the Greenvale site 31% and the sites were 4 km apart from their centres. Logistical constraints limited the ability to simultaneously track individuals in both study areas. There were a total of three 1-2 week long tracking sessions for bats at each site from June-August, 2006. This design allowed for a comparison of the two bat colonies over the entire reproductive season.

Capture and radiotracking

Adult female northern long-eared bats were captured using harp traps (Austbat Research Equipment, Lower Plenty, Victoria, Australia) placed on forested trails or along linear forest features (forest patch edges or tree-lined hedge-rows). Weight, age and reproductive status were recorded for all captures. Bats were identified as pregnant by gently palpating the abdomen and as lactating by the presence of bare patches around nipples and/or the expression of milk (Racey 1988). Radiotransmitters (model LB-2N Holohil Systems Ltd., Carp, Ont., Canada) were attached to bats between the scapulae using surgical cement (Skin-Bond, Smith and Nephew United, Largo, Florida, USA). Bats were followed using telemetry receivers (R-1000, Communications Specialists Inc., California USA and R2000, Advanced Telemetry Systems, Inc., Minnesota USA) and three-element yagi antennas (AF Antronics, Illinois, USA) to locate day-roosts and characterize nightly foraging movements. Methods for capture and handling of bats were approved by the Saint Mary's Animal Care Committee and under permit from the Prince Edward Island Department of Energy, Environment and Forestry.

Foraging bats were tracked beginning the night after a transmitter was attached until the transmitter fell off or failed for an average of 4.6 days per bat (range 2-7 days). To locate foraging bats, 2-3 observers at geo-referenced telemetry stations simultaneously took bearings to triangulate a location for individuals at 30-60 minute intervals. The program Locate III (Nams 2006) was used to plot bearings in the field and to assess if a location was reliable by examining the size and shape of the error ellipse. If a location was determined to be unreliable (large error ellipse) new bearings were immediately taken. A variable signal was considered as indicating the bat was flying (foraging or commuting) with a constant signal intensity indicating the bat was stationary.

Day-roosts were geo-referenced using a global positioning system (Garmin International, Kansas, USA) with an accuracy of ≤ 10 m. Minimum roosting areas (MRAs) were calculated at two levels to facilitate comparison to other roosting and movement studies of the species using ArcView Geographic Information System (GIS; version 3.2 ESRI, California USA). The first was for individual bats where three or more roosts were located and second at the level of each bat colony. MRAs were calculated as the minimum convex polygon encompassing all appropriate roost trees.

Foraging locations for each animal were estimated using the maximum likelihood estimation technique in Locate III as > 5 bearings per bat were never recorded (Nams 2006). Analysis was restricted to locations where bats were deemed as flying. Locations with error ellipses of >10 ha were immediately discarded and of the remaining locations, 70% were < 3 ha and 40% were < 1 ha. I included locations with error ellipses of > 3 ha if the error ellipse encompassed ≥ 1 of the telemetry locations and I could confidently rule out a large portion of the ellipse as containing the location of the bat.

Estimated locations were overlaid into ArcGIS (version 9.1) with land use data from the PEI Corporate Land Use Inventory (2000) to obtain the forest cover for each location. GIS data were derived from interpretation of aerial photographs taken in 2000 (1:17,500; B&W). Forest cover types were classified into three categories, deciduous-dominated ($\geq 75\%$ deciduous species), coniferous-dominated mixedwoods (75-26% coniferous species), and open (agricultural fields, roads, residential areas, water). Because I tracked only a small number of individuals and each individual for only 2-7 days, the locations for individuals at each study site were pooled and inferences are therefore at the colony level for each study site. A colony was considered to be a community of individuals that occupy, share and interact in a roosting area (Burland & Worthington Wilmer 2001).

To characterize area available to bats at each study site, I first estimated the center of colony roosting areas and used the approximate maximum movement distance of female bats recorded from roosts (1100 m) to generate a 7.07 km² circular 'landscape'. As previous research on *M. septentrionalis* suggested a strong forest association (Broders *et al.* 2006; Foster & Kurta 1999; Jung *et al.* 1999; Sasse & Pekins 1996) it seemed implausible that all areas within the circular landscape would be truly available to bats. Therefore, forest features were buffered within the circular landscape to a distance of 78 m (the maximum distance a bat location was found from the nearest forest edge or hedgerow) and the resulting buffered area around forest features was considered as 'available' area (Figure 2.). A G-test (Sokal & Rohlf 1995) was used to compare the proportion of each cover type of the telemetry locations with the proportion of area of each cover type available to determine if bats used forested areas and open areas in proportion to their availability. Minimum foraging areas (MFAs) were also calculated in

the GIS as the minimum convex polygon encompassing 100% of the telemetry locations for individual bats that had a minimum of 5 foraging locations estimated.

Characterization of forest structure

The vegetative structure of roosting and foraging areas was characterized in the field in 0.1 ha (17.8 m radius) plots to compare the forest structure between the two areas. In each plot the density of trees (total number of trees > 10 cm dbh), total number of deciduous trees, total number of coniferous trees, dominant canopy height (using a clinometer; model PM-5/1520, Suunto, Finland), number of potential roost trees (trees defined as \geq decay class 2 with obvious defects) and the distance to the nearest forest covered creek using a GIS was measured. Dominant canopy height was calculated as the average of five trees judged as representative of the dominant canopy of the plot.

Roosting area plots were centered on identified bat roost trees and measurements were taken when no bats were known to be roosting within trees. To vegetatively characterize foraging areas, I randomly generated coordinates within the foraging areas of each colony then established similar 0.1 ha plots at the first 15 (Greenvale site) and 14 locations (Wheatley River site). Plot types were pooled across study sites as statistical significance testing suggested the data were not different. Comparison of roosting versus foraging areas was carried out using stepwise logistic regression (forward with backward elimination) to identify variables that best described the differences between foraging and roosting areas using Systat software (version 10, SPSS, Inc. 2000). Foraging plots were coded as 1 and roosting plots coded as 0 (Hosmer & Lemeshow 2000). Fit of the model was assessed with Hosmer and Lemeshow's goodness of fit test where p-values \geq 0.05 indicate that the data sufficiently fit the model (Hosmer & Lemeshow 2000).

Insect Prey abundance

In addition to differences in vegetative characteristics it was likely that prey abundance was also important in determining bat foraging areas (Grindal 1996; Kusch *et al.* 2004). To assess the abundance of potential insect prey in foraging areas and roosting areas, positively phototactic volant insects were sampled in UV light traps placed in both areas over 28 nights in July and August of 2006. Light traps with automatic timers were turned on at dusk and ran for approximately 3 hours at 2 m AGL. Insects were trapped concurrently with telemetry work in a given study area such that insect availability was assessed only when transmitters were on individuals in an area. In each study area, one trap was placed in the approximate center of the roosting area and remained fixed throughout all sampling nights. Another trap was placed in 3-4 different locations within each foraging area, coinciding with telemetry effort in the area, and was moved nightly to follow the foraging movements of multiple bats. Individual insect traps were randomized throughout the study to minimize any bias of a particular trap.

All captured insects were preserved in 70% ethanol and identified to order following Borror and White (1970) using a dissecting microscope (45X maximum magnification). Analysis of available insect biomass was restricted to maximum body lengths found for insect prey of *Myotis septentrionalis* and *M. lucifugus* (Broders 2003; Coleoptera 9mm; Diptera 16mm; Lepidoptera 15mm; Trichoptera 12mm; Hymenoptera 11mm, all other orders 12mm). Insects fitting size classifications were weighed on an electronic balance to the nearest 1.0 mg (wet weight) as wet weights of alcohol preserved samples have been shown to approximate weights of fresh samples (Mackay & Kalff 1969). Plot types were pooled across study sites as statistical significance testing suggested no difference. Differences in available total biomass (all insect orders), moth

(Lepidoptera) biomass and beetle (Coleoptera) biomass between foraging and roosting areas were analysed by paired *t* tests or where normality assumptions were violated, Wilcoxon's matched-pairs test in Systat (Sokal & Rohlf 1995).

Results

Foraging and roosting locations and movements

I followed 21 female bats over 45 tracking nights (21 in Greenvale, 24 in Wheatley River) and tracked them to 37 day roost trees and a barn on the edge of the forest. Females were found to roost in maple trees (*Acer rubrum* and *A. saccharum*) except for one white birch (*Betula papyrifera*) used in late August. In the Wheatley River site, females were found to day-roost in the walls of a storage barn that was constructed of a wood frame overlaid with aluminium siding. Females used the barn from late June through to mid-August and used trees in early July and in late August. Individuals emerging from the barn were captured on one occasion to confirm the presence of *M. septentrionalis*. Access to the barn was limited to this initial visit and thus the determination of the exact roosting site in the barn was not possible. The colony level MRA of the roost trees in Wheatley River was 0.30 ha ($n = 9$ roost trees) with a straight line distance of 435 m between the barn and the centre of the forest roosting area. In Greenvale the main colony MRA was approximately 4.13 ha ($n = 21$ roost trees) with two bats using other roost trees ($n = 7$) outside of this area in early June. The total roost area for all identified roost trees in Greenvale was 31.1 ha. Roosting areas were wholly in one stand of deciduous-dominated trees in both sites.

Foraging areas in both study sites were concentrated along forest covered creeks (Figure 3) and included deciduous-dominated and deciduous- and coniferous-dominated

mixedwood stands. MFAs were approximately 6 times larger than MRAs. In Greenvale, one female bat conducted a long-distance commuting flight outside its regular foraging range at an estimated distance of 1136 m from its day roost. In Wheatley River, another female bat conducted a similar long distance flight at an estimated distance of 1163 m and thus I estimated the movement distance for female bats as 1100 m on PEI. Females emerging from roosting in the barn were visually observed to fly along narrow tree-lined hedgerows rather than crossing the open field in navigating to foraging areas (Figure 3).

In Greenvale, females did not use cover types for foraging in proportion to their availability ($G = 76.89, p < 0.001$). Open areas were used less than expected given their availability and areas under forest cover (both deciduous and coniferous dominated) were used more than expected given their availability (Figure 4). In Wheatley River, females again did not use cover types in proportion to their availability ($G = 95.34, p < 0.001$). Open areas were used less and forested areas were used more than expected given the availability of each in the study area (Figure 4). The proportions of the three cover types used was different for each study site (Figure 5) as shown by the heterogeneity G-test ($G = 15.37, p < 0.001$).

Characterization of roosting and foraging areas

Three important variables were identified in differentiating between foraging and roosting vegetation plots (Table 2). These variables were tree density (as total trees in the plot), distance to the nearest forest covered creek, and number of potential roost trees in the plot. A negative relationship was found for the number of potential roost trees where the odds of a plot being in a foraging area, for an increase of five trees, decrease by a factor of 35 (odds ratio = 0.028; $\exp(-0.715 \times 5)$). Tree density had a positive relationship where the odds of a plot being in a foraging area, for an increase of 20 trees, increase by

3.25 ($\exp(0.059 \times 20)$). A negative relationship was found for distance to nearest forest covered creek where the odds of a plot being in a foraging area, for an increase in 50 m distance from the creek, decrease by a factor of 3 (odds ratio = 0.333; $\exp(-0.022 \times 50)$). The final model thus characterizes foraging areas as situated closer to forest covered creeks ($\beta_{\text{creek}} = -0.022$ (SE = 0.011)), with more structural clutter (high tree density; $\beta_{\text{clutter}} = 0.059$ (SE = 0.027)), and fewer potential roost trees ($\beta_{\text{roosts}} = -0.715$ (SE = 0.255)) compared to roosting areas.

Differences in insect abundance between foraging and roosting areas

Foraging areas had approximately equal or less available insect biomass, as represented by the wet weight of light trapped insects, compared to roosting areas. There was no significant difference in the available total insect biomass between foraging and roosting areas ($t = -1.005$, $d.f. = 27$, $P > 0.05$; Figure 6). No significant difference was found for the available moth biomass between foraging and roosting areas ($t = -0.966$, $d.f. = 27$, $P > 0.05$; Figure 6). Available beetle biomass was significantly different between foraging and roosting areas (Wilcoxon's matched pairs, $Z = -2.057$, $P < 0.05$; Figure 6) with 18 out of 28 pairwise comparisons having greater beetle biomass in roosting areas over foraging areas.

Discussion

Roosting and foraging site selection

Preference for deciduous roost trees by female northern long-eared bats on PEI was consistent with previous studies of roost tree selection for the species. Most studies have been undertaken in relatively intact forested landscapes where females were found to roost predominantly in deciduous tree species in deciduous-dominated stands (Broders

et al. 2006; Carter & Feldhamer 2005; Lacki & Schwierjohann 2001; Menzel *et al.* 2002; Owen *et al.* 2003; Perry *et al.* 2007; Sasse & Pekins 1996). In a forest-agricultural landscape in Michigan, females were also found to exclusively use deciduous species (Foster & Kurta 1999). The large variety of tree species used by the species across all study locales likely reflects the availability of localized roosting resources of the area (Carter & Feldhamer 2005; Ford *et al.* 2006) where selection is likely for preferred micro-site characteristics of roosts (i.e., roost type, size, shape and thermal microclimate; Garroway 2006; Kunz & Lumsden 2003; Lausen & Barclay 2006; Sedgeley 2001; Sedgeley & O'Donnell 2004). In addition to the larger temporal and spatial landscape fragmentation of the forests across the island, forest management practices by independent owners influence the availability of suitable roost trees at a small scale (≤ 20 ha). These localized harvesting practices may be further removing trees that contain suitable roosts within a stand, and therefore roost trees with appropriate microclimates and structure for bats on PEI may tend to be maple species that have been left standing by land owners.

Recent studies of northern long-eared bats indicate a predominantly forest-dwelling species; in particular, females have been shown to roost colonially in trees during the maternity period (Broders & Forbes 2004; Foster & Kurta 1999; Garroway 2006; Menzel *et al.* 2002; Sasse & Pekins 1996). There are only limited records of roosting by northern long-eared bats in man-made structures (Brandon 1961; Caceres & Barclay 2000; Cope & Humphrey 1972; van Zyll de Jong 1985). The discovery and timing of use of a barn by a maternity colony in the Wheatley River site may provide insights into roost selection by reproductive females. Pregnant and lactating bats were found to roost in the barn while non-reproductive bats were found to use trees. This

suggests that reproductive females are selecting different roosts for different needs associated with reproduction. Intra-annual variation in roost tree selection between reproductive and non-reproductive females has recently been demonstrated for this (Garroway 2006) and other species (Veilleux *et al.* 2004).

Female bats experience energetic costs in maintaining high body temperatures for foetal growth, during lactation, and to maintain high temperature for juvenile development (Hamilton & Barclay 1994; Kurta *et al.* 1990; Sedgely 2001; Vonhof & Barclay 1996). Energetic benefits can be achieved by selecting warm communal roosts (Barclay 1991; Wilde *et al.* 1995) and also by selecting cooler roosts which may allow individuals to enter torpor and delay parturition during times of environmental stress (Willis *et al.* 2006). Lausen and Barclay (2006) demonstrated that big brown bat juveniles (*Eptesicus fuscus*) roosting in man-made structures became volant 1 to 2 weeks earlier than juveniles from natural roosts. In this study a comparison of thermal microclimates or judgement of the timing of volancy in juveniles between tree and barn roosts was not undertaken; however, the use of the barn in Wheatley River may represent an alternative for reproductive bats in the site with suitable maternity roost trees lacking in the area. As one female in the site initially roosted in a tree and then moved to the barn for a subsequent two nights, it is likely that the entire colony has knowledge of both tree roosts and the barn; where bats with previous experience with the barn transferred this knowledge to new members as they communally shared roosts (Kerth *et al.* 2001; Ratcliffe & ter Hofstede 2005).

In forested landscapes in eastern North America, *M. septentrionalis* were most commonly recorded and captured in structurally complex forest stands, (Broders *et al.* 2003; Lacki & Schwierjohann 2001; Owen *et al.* 2004) and to a lesser extent in

association with vernal pools and forest streams (Brooks & Ford 2005). Northern long-eared bats have been shown to forage primarily in forest interiors below the canopy (Broders *et al.* 2006; Lacki & Hutchinson 1999; LaVal *et al.* 1977; Owen *et al.* 2003; Patriquin & Barclay 2003) which is consistent with the flexible gleaning and hawking strategy of the species (Broders *et al.* 2004; Faure *et al.* 1993; Fenton & Bogdanowicz 2002; Ratcliffe & Dawson 2003). Foraging areas on PEI were centered along forest covered creeks, and compared to roosting areas, were found to be more structurally cluttered. Riparian areas are considered as critical resource areas for many bat species because they support higher concentrations of prey, provide drinking areas and act as unobstructed commuting corridors (Downs & Racey 2006; Grindal *et al.* 1999; Racey & Swift 1985; Racey *et al.* 1998; Rydell *et al.* 1994). No evidence was found to suggest that prey availability was greater in foraging areas than roosting areas on PEI for northern long-eared bats. The sampling design with UV light attractant traps is inherently biased towards positively photo-tactic prey (Black 1974; Kunz 1988) and therefore may have been unable to detect other important non-phototactic prey consumed by northern long-eared bats.

Aerial insect abundance (i.e., moth and beetles) is more temporally stable in forests than over water (Barclay 1991) and the flexible foraging strategy of northern long-eared bats enables them to glean insects from vegetation as well as capture aerial prey in the interiors of forests (Ratcliffe & Dawson 2003). Thus, bats may also be selecting foraging areas for reasons other than insect densities if abundances are not limiting between foraging and roosting areas. Although water stress is often thought of as of secondary importance next to food intake in reproductive energetic costs, it has been shown that pregnant and lactating bats must drink sufficient water to maintain water

balance and thus proximity to water may be an important aspect of foraging area selection (Adams & Thibault 2006; Mclean & Speakman 1999; Speakman *et al.* 1991). In addition there may also be an effect inherent in the landscape where, as a result of centuries of agricultural intensification, fragmented forest stands containing creeks or streams may be the last option for northern long-eared bats, thus restricting colonies to these areas. In mapping the forest types of PEI, Sobey and Glen (2004) noted that current deciduous forests were often situated as large, connected multi-parcel stands at the back of farms with good drainage and steeper slopes (i.e., presence of creek or stream).

The availability of suitable roosts is important in determining the distribution of female northern long-eared bats on PEI. Female bats in particular face a trade-off in balancing foraging and roosting needs and should therefore select these areas both to capitalize on appropriate resources (i.e., suitable trees or high abundances of insect prey) and also to minimize costs in travel between the two (Henry *et al.* 2002). Roost trees for cavity-roosting bats are typically found in stands with less structural clutter (i.e., open canopies; Kalcounis-Rüppell *et al.* 2005; Perry *et al.* 2007). Similarly in this study, foraging and roosting areas were found to be best structurally differentiated in terms of the availability of roost trees and also in overall tree density. The higher availability of roost trees in the roosting area reflects that these areas were situated in mature deciduous stands. These stand types have a greater chance of having trees with cavities (or other similar damage creating roosts) compared to the mixedwood stands that contained the foraging areas. As prey availability was not found to differ between roosting and foraging areas, this suggests, in conjunction with use of the barn, that the availability of roosts appears to be an important resource for bats in the fragmented forest landscape of PEI.

Movement and spatial dynamics

In both study sites females used areas under forest cover more than expected and open areas less than expected indicating a restriction of movements to forested areas. Furthermore, the locations of bats classified as in open areas clustered around forest features with a maximum distance from a forest feature of only 78 m. The capture of bats in traps positioned along forest-field edges and hedge-rows also demonstrates the use of forest linear landscape elements by bats in moving through the landscape. In particular, the observations of flight paths travelled by bats emerging from the building roost indicated that female *M. septentrionalis* would not cross open fields directly but followed a hedge-row consisting of a narrow line of trees when crossing the landscape. These observations are similar to those of other temperate bat species that have been shown to follow linear forest features in navigating within agriculturally dominated landscapes (Downs & Racey 2006; Entwistle *et al.* 1996; Limpens & Kapteyn 1991; Murray & Kurta 2004; Verboom & Huitema 1997; Winhold *et al.* 2005). Tree-lined linear features may also be important in offering protection from predators and wind, and may act to concentrate insect prey (Grindal 1996; Verboom & Spoelstra 1999). The observations of rapid and direct flights from the barn roost to forest foraging areas may demonstrate commuting behaviour along the hedgerows in the landscape (Limpens & Kapteyn 1991; Murray & Kurta 2004). The concentrations of telemetry locations in open areas that were clustered along forest patch edges or wooded creeks, likely indicates bat were foraging opportunistically along edges in many instances (Downs & Racey 2006).

The number of locations classified under open areas was noticeably different between the two study sites and likely reflects the different composition and configuration of forest patches at each site. The Wheatley River site had less forest cover (18%

Wheatley River, 31% Greenvale) and also contained more linear forest features (tree-lined hedgerows, forest-field edges and smaller, linear forest patches). Therefore, forested foraging areas are more constrained and possibly limiting in the Wheatley River site and a higher proportion of commuting and foraging movements classified as open may reflect the more highly fragmented nature of the study area. There is also likely misclassification error in locating bats on linear features from a combination of error in telemetry triangulations and from the resolution of the GIS forest cover data. However, the clustering of open locations near forest features suggests that movements by northern long-eared bats are in close association with forest elements. In the Greenvale site, the number of locations under deciduous cover was elevated compared to the Wheatley River site. This likely reflects tracking a large number of lactating females in the site that regularly returned to roost trees during the night presumably to nurse juveniles (Entwistle *et al.* 1996; Henry *et al.* 2002; Murray & Kurta 2004).

Spatial use of the landscape by females reflects the fragmented nature of the forest landscape on the mobility and resource selection of bats. Movement distances between capture and first roost ($285 \text{ m} \pm 121$) were smaller than those found for northern long-eared bats in forested landscapes (New Brunswick 1001 m; Broders *et al.* 2006; New Hampshire 602 m; Sasse & Pekins 1996). Females tracked by Broders *et al.* (2006) and Owen *et al.* (2003) also used larger foraging areas (46 ha and 65 ha respectively) than females on PEI (6.0 ha). Overall the magnitude of movements demonstrated by females on PEI were most similar to those found for a maternity colony of northern long-eared bats in a similar agriculturally-dominated landscape in Michigan (Foster & Kurta 1999). This suggests that the activities of northern long-eared bats are constrained in landscapes where areas of suitable forest cover are limiting. In both of the study areas on PEI, the

selection of roosting and foraging resources and the range of movements by female bats suggests that forest fragmentation operates at a small 'patch level' scale where bats are restricted to forest patches and do not use the greater landscape.

The findings of this study show that a forest specialization can restrict the vagility of bats in a forest-agricultural landscape. Northern long-eared bat movements were strongly associated with forest features with foraging areas centred along forest covered creeks. Bats were found to roost in the forest interior although females in the more fragmented study area (Wheatley River) used a building during pregnancy and nursing, which may demonstrate an alternative strategy by the colony to persist in a landscape with fewer roost tree resources. The importance of woodlands in agricultural landscapes for bats is stressed by studies which document higher bat activity and captures in woodlands or along wooded linear features (Bernard & Fenton 2003; Bianconi *et al.* 2006; Bontadina *et al.* 2002; Russ & Montgomery 2002; Walsh & Harris 1996; Wickramasinghe *et al.* 2003). By following individuals throughout the night over multiple nights this analysis was able to detect fine movements made by bats in foraging and commuting and demonstrates the importance of forest features in multiple aspects of the species' ecology.

At a broader scale, this study highlights the importance of assessing how mobility and resource selection of animals change in response to human-dominated landscapes. Although the study did not specifically investigate spatial configuration and context, the slight differences in behaviour and roost selection by individuals between the two study areas demonstrates that the configuration and connectivity of resources also plays a key role in how animals use human modified landscapes. Fragmentation is a landscape level process; however, it also operates at smaller scales and has the potential to impact

resources at a localized level for populations as demonstrated in this study. In order to develop effective conservation plans, a detailed understanding of resource selection and behaviour of a species is required as both the composition and configuration at a local and landscape scale can affect persistence.

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Table 1. Spatial measures of landscape use by individual *Myotis septentrionalis* females on Prince Edward Island, Canada, 2006.

	Mean	SD
Distance to first roost (m; $n = 21$)	285	121
Distance between successive roosts (m) ^a	227	161
Min. roosting area (MRA; ha; $n = 12$)	1.13	1.04
Min. foraging area (MFA; ha; $n = 17$)	6.09	5.83

^aDistances between successive roosts do not include instances where the individual roosted in the same location on successive days.

Table 2. Mean (SD) plot-level forest characteristics assessed to compare the forest structure of roosting and foraging areas of female *M. septentrionalis* on Prince Edward Island.

	Foraging plots	Roosting plots
Density of trees (total trees)*	61 (35)	42 (11)
Count of potential roost trees*	2 (2)	10 (5)
Distance to creek (m)*	43(33)	153 (81)
Dominant canopy height (m)	19 (4)	21 (3)
Count of deciduous trees	24 (15)	33 (12)
Count of coniferous trees	37 (28)	9 (12)

* Denotes variables identified as important in differentiating between foraging and roosting vegetation plots

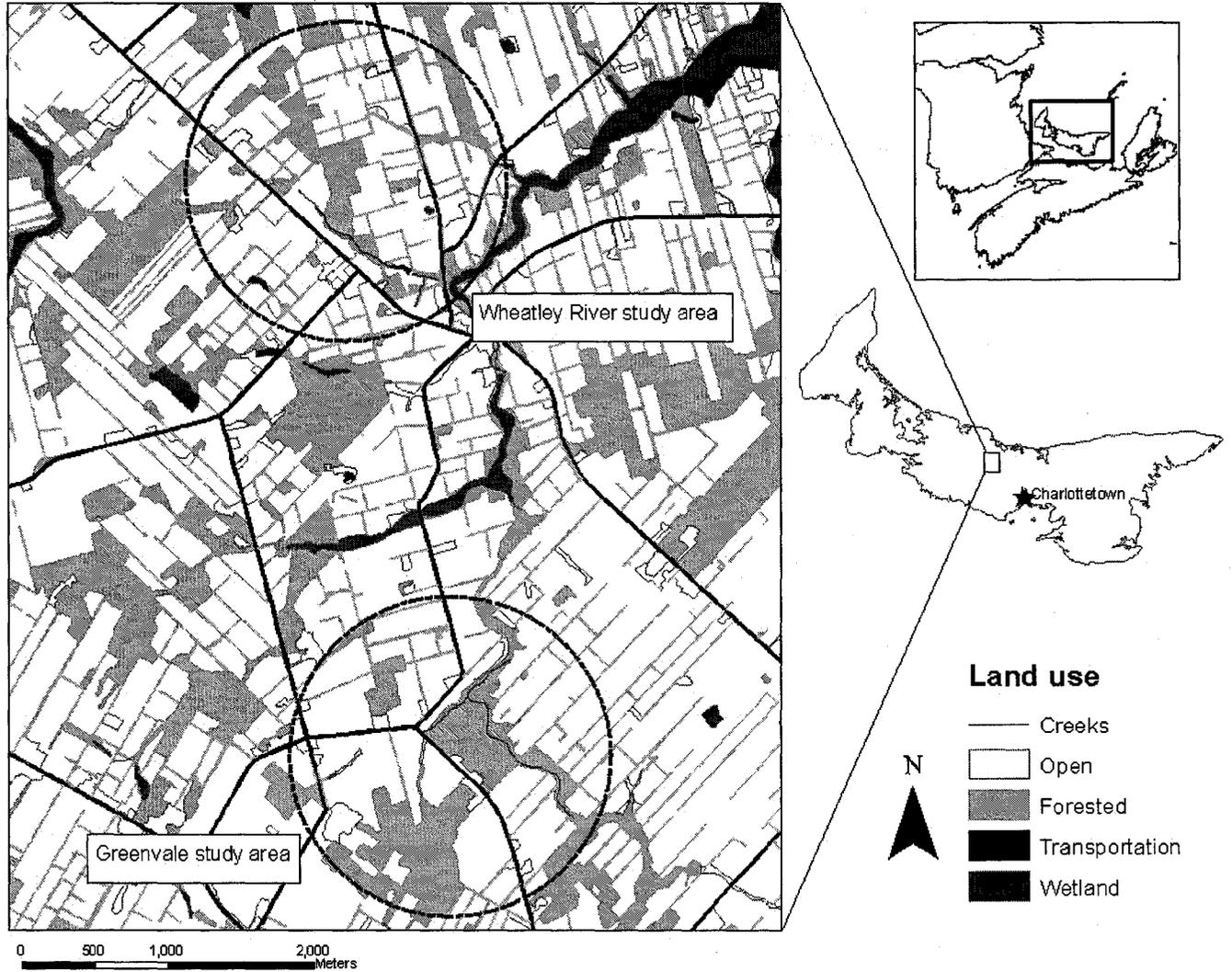


Figure 1. Location of Wheatley River and Greenvale study areas, on Prince Edward Island. Study areas are delineated as an 1100 m radius (the approximate movement distance of female *M. septentrionalis*) circle centred on the weighted (by number of trees) centre of the roosting area.

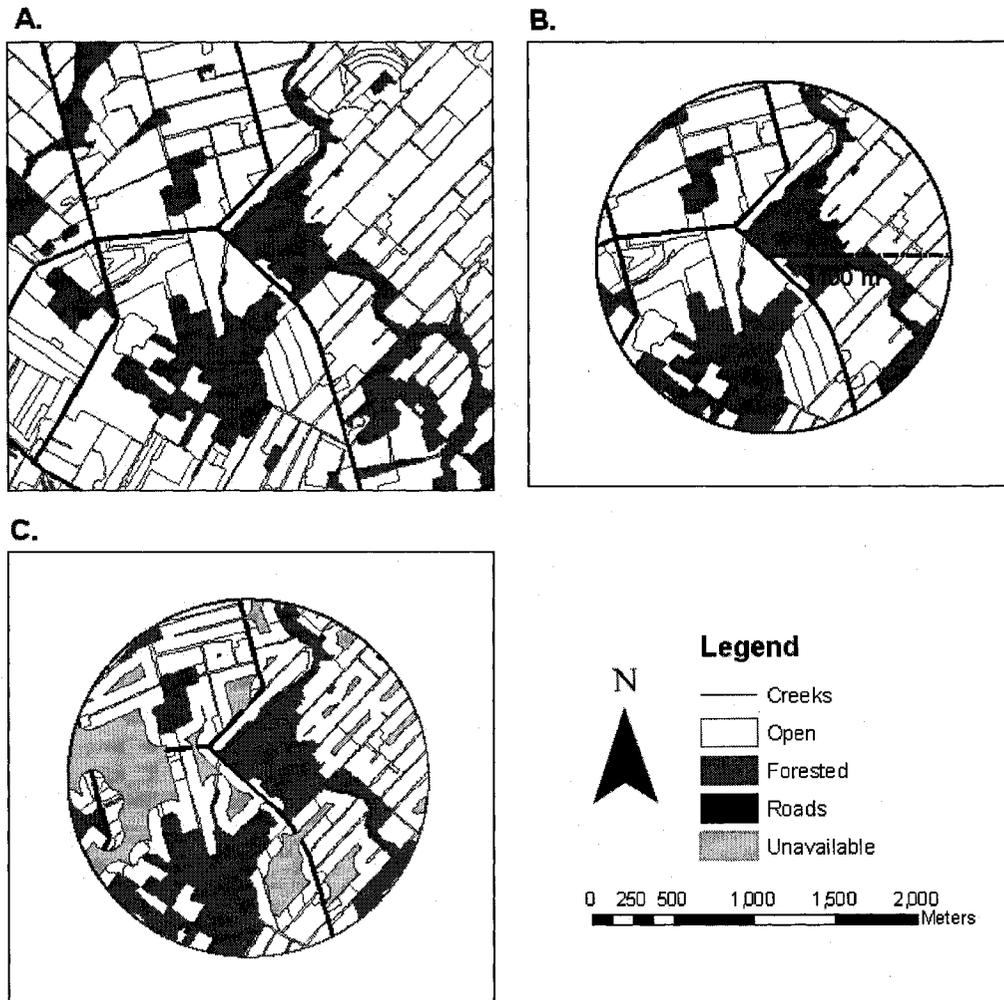


Figure 2. Multi-step buffering process conducted in a Geographic Information System to assess areas available to female northern long-eared bats (*M. septentrionalis*) on PEI. A) Land use layer in the Greenvale study site showing areas of forest cover B) Buffer of 1100 m radius used to generate a circular landscape around the weighted centre of the colony roosting area C) Forest features buffered to a distance of 78 m to isolate out areas considered as 'available'.

a. Greenvale

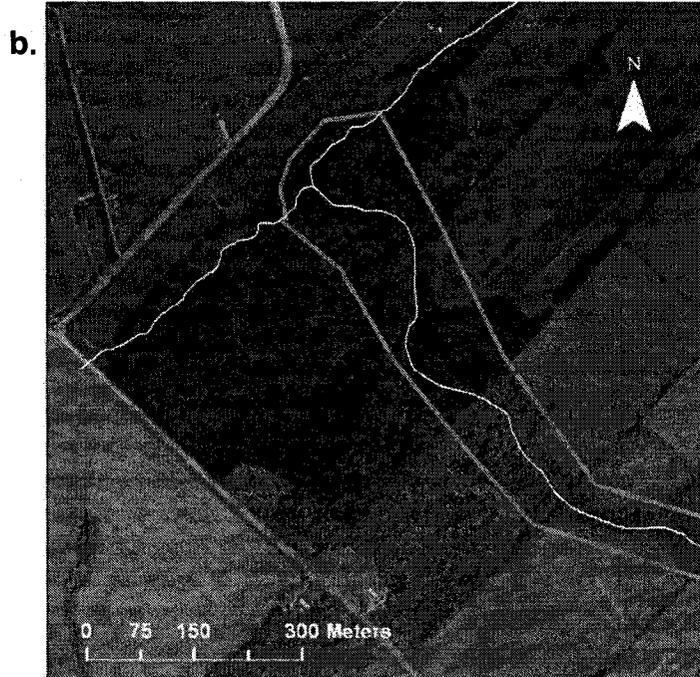


Figure 3. Roosting and foraging areas of female *Myotis septentrionalis* identified through radiotelemetry in a) Greenvale and b) Wheatley River, Prince Edward Island, June to August, 2006. Flight paths show the directions bats traveled from the barn to foraging areas.

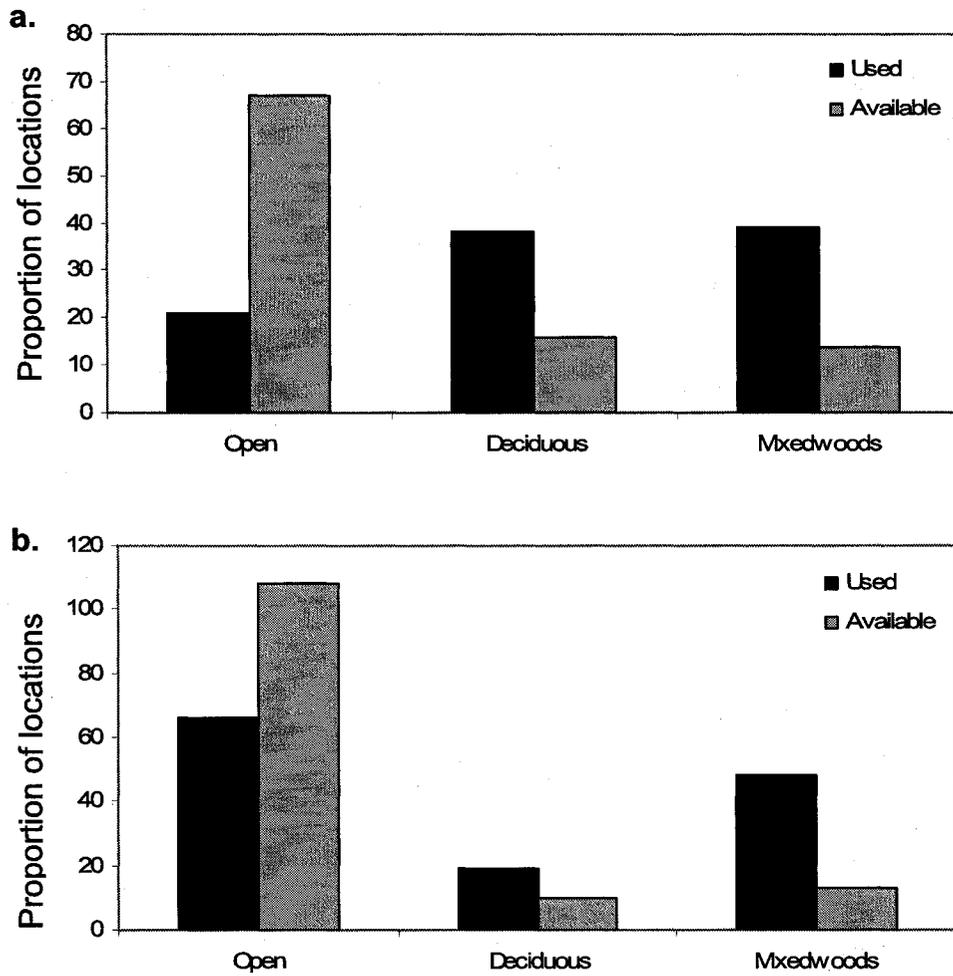


Figure 4. The proportion of telemetry locations of each cover type category used (where bats were recorded as flying) compared to the proportion of available cover in a) Greenvale and b) Wheatley River, Prince Edward Island, 2006.

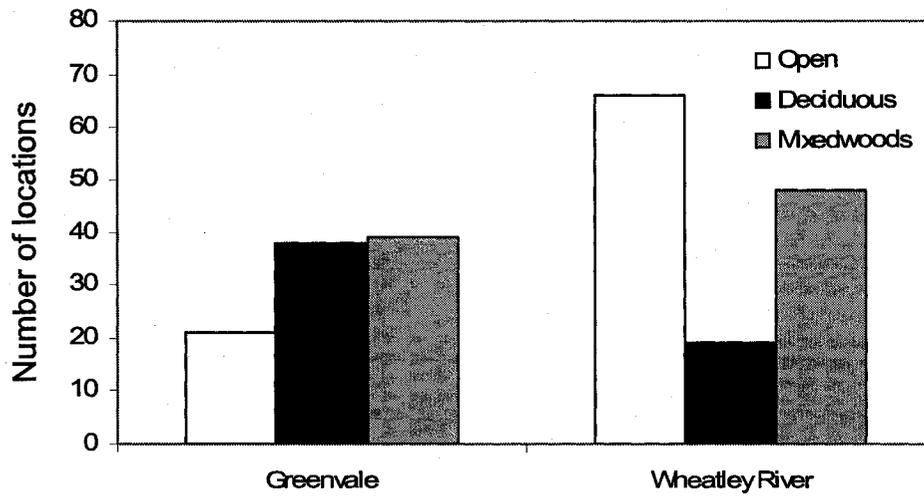
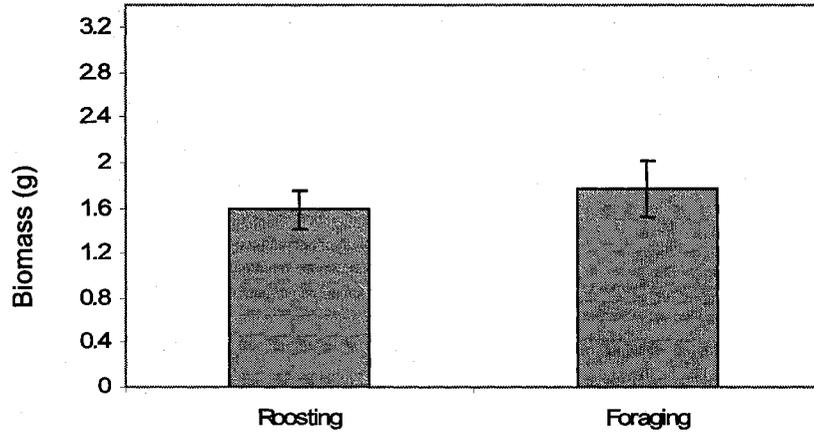
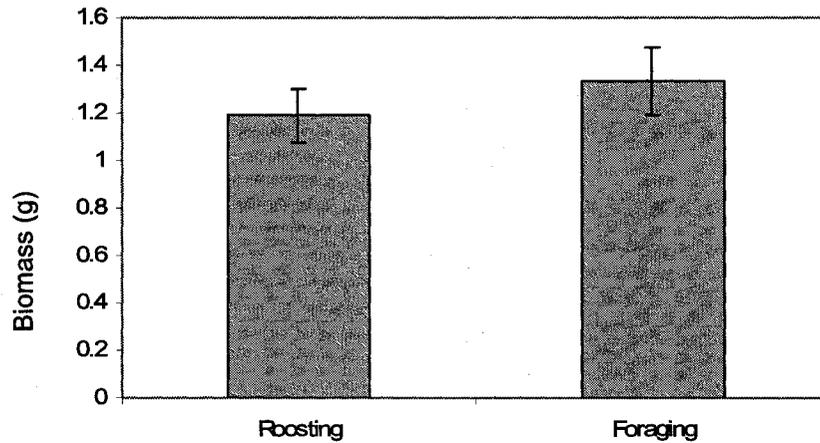


Figure 5. The number of telemetry locations (where bats were recorded as flying) in each cover type category used at each study site (Greenvale; Wheatley River) on Prince Edward Island, 2006. Cover type categories were classified as open (agricultural fields, roads, water), deciduous (composed of $\geq 75\%$ of deciduous tree species), and mixedwoods (composed of $\geq 26\%$ of coniferous tree species).

a. Total insects



b. Moths



c. Beetles

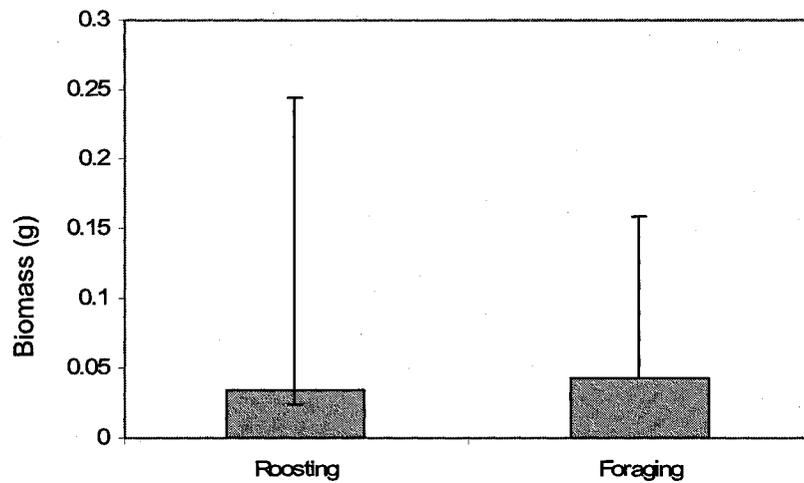


Figure 6. Insect catches at roosting and foraging sites on Prince Edward Island obtained on 28 evenings during July and August, 2006 expressed as a) mean (\pm SE) total biomass (g wet weight) of insects per sample, b) mean (\pm SE) moth (Lepidoptera) biomass (g wet weight) per sample and c) median (\pm IQ (inter-quartile) range) beetle (Coleoptera) biomass (g wet weight) in each sample.

Chapter 4

The effects of forest fragmentation on the forest-dependent northern long-eared bat (*Myotis septentrionalis*): synthesis

The goal of this thesis was to explore the effects of habitat fragmentation on bats by examining the response of a forest-dependent bat species, the northern long-eared bat, to forest fragmentation. By investigating the effects over multiple spatial scales using multiple analytical techniques, a more comprehensive understanding was achieved of how fragmentation influences resource selection and behaviour and therefore structures the distribution of a fragmentation-sensitive species.

On PEI, there is strong evidence to suggest that the availability of suitable roosts is driving site selection and therefore the distribution of *M. septentrionalis*. The top predictor variable in determining presence of bats was the area of deciduous dominated stands and the relationship of deciduous stand area was positively related to presence for both males and females. For males the variable is important at the landscape level and for females at the fragment level. In tracking female bats, individual *M. septentrionalis* preferentially roosted in deciduous trees species contained wholly within deciduous-dominated stands. Females in one study area were also found to roost in a barn during the energetically demanding periods of pregnancy and lactation. As previously discussed, the fragmentation of forests on PEI has likely reduced the total availability of suitable roosts such that bats, in selecting roosts with appropriate microclimates, (Garroway 2006; Kunz & Lumsden 2003; Lausen & Barclay 2006) selected roosts in the study landscapes provided by deciduous trees and a building.

The effects of forest fragmentation on PEI appear to be operating on female *M. septentrionalis* at a localized 'fragment level' which suggests a restriction to forested areas. Female presence was found to be best predicted by a compositional variable: deciduous stand area, at the fragment level. The magnitude of movements and minimum roosting and foraging areas for females were smaller than those found for the species in

forested landscapes (Broders *et al.* 2006; Owen *et al.* 2003; Sasse & Pekins 1996), which supports the contention that activities of female *M. septentrionalis* are constrained in landscapes with lower forest cover. Commuting and foraging movements were found to be primarily under areas of forest cover with the locations of bats in open areas strongly clustering around forest features. Further, the flight paths of females emerging from the building roost followed tree-lined hedge-rows where bats avoided crossing open fields directly in navigating from roost to foraging grounds. As female foraging and roosting areas were primarily associated with forests, habitat for female *M. septentrionalis* on PEI is forest stands. Together these findings demonstrate that a highly mobile species, from resource specialization, can be restricted in vagility from behavioural traits within a landscape.

In investigating the effects of fragmentation with the goal to elucidate the impacts on populations, it is important to bear in mind the temporal scale of studies. The anthropogenic fragmentation of landscapes is quite recent in the context of the evolutionary histories of species and therefore precludes the understanding of the long-term impacts (Ewers & Didham 2006). Further confounding inferences is the lack of a historical reference on the status and dynamics of many populations, such as *M. septentrionalis* on PEI, which can complicate our ability to detect and quantify the effects of fragmentation. The most likely scenario to be encountered by conservation managers is a population with little information on dynamics and history in a pre-existing fragmented landscape (Saunders *et al.* 1991). Thus undertaking multi-scale studies probing how fragmentation influences the resources required by a species is critical in constructing widely applicable solutions to ensure the persistence of populations in human modified landscapes.

This study provides information on how a forest-dependent species inhabits and uses a forest-agriculture land mosaic. The results of this study should aid land managers in incorporating the requirements of forest-dwelling bats into future management plans. Specifically this study illustrates the importance of identifying and maintaining roosting and foraging areas as well as a connectivity between the two for bats. Although this study explored many aspects of how forest fragmentation affects the northern long-eared bat there are still further research avenues that warrant investigation.

1. This study focused on how fragmentation affects the ecology of the species during the summer. There is little information known about the movements and selection of bats during autumn when they move to winter hibernacula. If bats use forests during their localized regional migration then the effects of forest fragmentation may also be impacting populations during the swarming and mating season. Also to my knowledge winter hibernacula for the bats of PEI are not well known and require further study.
2. Information is lacking on population demographics for many bat species owing to the challenge of studying volant, nocturnal mammals. Long-term monitoring studies are needed to account for temporal environmental variations between years such that habitat relationships and population dynamics can be properly interpreted. A combination of techniques such as radiotelemetry, marking (e.g. banding or passively integrated transponders) and new modelling techniques that incorporate site histories and detection probabilities will allow for a holistic understanding of the effects of fragmentation on bat populations.

3. The resource selection portion of this study focused on female *M. septentrionalis* and as the distribution of male and female bats was found to be related to deciduous stands at different spatial scales, the movements and resource selection of male *M. septentrionalis* should also be investigated. The results will allow for a comprehensive understanding of how forest fragmentation affects the species.

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Appendix A

Location, forest measures and presence data of surveyed forest fragments

Location, forest measures and presence (1) or no evidence of presence (0) data for each of the eighty-eight surveyed fragments. ID = fragment number, ArcGIS name = name used in GIS analysis, Year = year fragment was trapped, UTM E = easting coordinates NAD83 Zn 20 format, UTM N = northing coordinates NAD83 Zn 20 format, farea = fragment area (ha), fhw = hardwood composition of fragment (ha), fsw = softwood composition of fragment (ha), bfor = forest area in buffer (ha), bhw = hardwood area in buffer (ha), bsw = softwood area in buffer (ha), pfemale = presence of female *M. septentrionalis*, pmale = presence of male *M. septentrionalis*. Note: UTM coordinates are for the mid point of two trapping sites or for the single trap site if there was only one suitable site.

ID	ArcGIS name	Year	UTM E	UTM N	farea	fhw	fsw	bfor	bhw	bsw	pfemale	pmale
1	Wpei01 f1	2005	416924	5201490	212	61	60	445	101	115	0	0
2	Wpei01 f2	2005	416949	5200656	77	12	16	468	112	143	0	0
3	Wpei01 f3	2005	418642	5185903	232	43	53	534	116	87	0	1
4	Wpei01 f4	2005	420141	5185816	54	20	13	501	62	77	0	0
5	Wpei01 f6	2005	415634	5184439	21	5	3	174	69	31	0	0
6	Wpei01 f7	2005	415303	5184560	17	11	0	174	71	32	0	0
7	Wpei02 f1	2005	421655	5200574	78	3	39	564	69	159	0	0
8	Wpei11 f2	2005	414595	5177838	21	15	5	366	138	40	0	0
9	Wpei11 f7	2005	415303	5176991	135	62	21	323	166	48	0	0
10	Wpei11 f8	2005	419423	5172167	233	26	72	535	105	173	0	1
11	Wpei12 f1	2005	428836	5166190	154	48	17	579	167	185	0	0
12	Wpei22 f1	2005	433708	5158569	71	0	9	239	27	73	0	0
13	Wpei22 f9	2005	432024	5160960	26	0	3	218	56	48	0	0
14	Wpei22 f10	2005	436054	5148089	28	14	0	185	80	16	0	0
15	Cpei11 f5	2005	456536	5149301	134	72	8	255	125	25	0	0
16	Cpei11 f7	2005	458843	5149998	78	41	1	227	93	16	0	1
17	Cpei11 f8	2005	458477	5148083	24	14	0	211	100	16	0	0
18	Cpei11 f9	2005	458409	5147834	17	8	2	183	82	15	0	0
19	Cpei11 f10	2005	456400	5147531	13	0	1	191	90	13	0	0
20	Cpei12 f1	2005	460398	5147655	80	27	11	172	75	23	0	0
21	Cpei12 f3	2005	474555	5145040	161	28	35	293	55	85	0	0
22	Cpei12 f5	2005	475203	5142999	10	0	7	83	9	38	0	0
23	Cpei12 f6	2005	474558	5147397	58	13	10	425	123	115	0	0
24	Cpei12 f7	2005	475548	5146502	67	7	36	350	62	119	0	0
25	Cpei12 f8	2005	476161	5145558	15	0	11	229	41	96	0	0
26	Cpei12 f9	2005	476529	5145885	2	0	2	190	25	94	0	0

ID	ArcGIS name	Year	UTM E	UTM N	farea	fhw	fsw	bfor	bhw	bsw	pfemale	pmale
27	Cpei21 f5	2005	442386	5136245	66	37	4	123	68	16	0	0
28	Cpei21 f6	2005	448089	5131412	35	29	0	178	86	25	0	0
29	Cpei21 f9	2005	443776	5127184	130	54	23	235	120	33	0	0
30	Cpei22 f5	2005	476927	5140488	41	0	1	111	16	20	0	0
31	Cpei22 f10	2005	477691	5126605	17	12	0	217	129	39	1	0
32	Cpei22 f12	2005	477580	5132196	49	31	4	198	88	24	1	1
33	Cpei22 f13	2005	477812	5132680	78	31	5	201	85	31	1	0
34	Cpei22 f14	2005	479213	5131253	11	11	0	234	126	22	0	0
35	Cpei22 f15	2005	468869	5126245	64	13	6	829	342	179	0	0
36	Cpei22 f16	2005	471362	5129574	23	16	0	623	287	81	0	0
37	Cpei22 f17	2005	470436	5130002	386	193	27	756	355	105	1	1
38	Cpei22 f18	2005	471120	5137241	251	124	40	519	294	56	0	0
39	Cpei23 f1	2005	488446	5136224	59	29	2	502	188	89	1	0
40	Cpei23 f2	2005	489616	5139052	38	2	9	167	34	31	1	0
41	Cpei23 f7	2005	481465	5123658	69	62	0	212	138	23	1	1
42	Cpei23 f11	2005	488592	5139228	7	0	0	226	42	63	0	0
43	Cpei32 f1	2005	474745	5121952	40	32	6	432	269	59	0	0
44	Cpei32 f2	2005	477572	5122973	52	52	0	192	141	20	0	0
45	Cpei32 f3	2005	472778	5116397	29	10	13	695	415	105	0	1
46	Cpei33 f1	2005	484155	5122635	60	29	12	158	71	39	0	1
47	Cpei33 f3	2005	484977	5119723	58	42	1	172	120	20	1	0
48	Epei04 f1	2005	560233	5137462	362	243	38	832	551	89	0	1
49	Epei11 f1	2005	503964	5129653	83	4	29	413	37	173	1	1
50	Epei11 f7	2005	506580	5126279	623	87	186	575	83	212	0	0
51	Epei11 f8	2005	508415	5136699	39	8	0	398	169	51	0	1
52	Epei11 f9	2005	520393	5140539	91	21	34	604	120	138	0	0
53	Epei11 f10	2005	518513	5128532	464	149	119	830	243	234	0	0
54	Epei12 f7	2005	535108	5138906	133	13	66	675	194	209	0	0
55	Epei12 f8	2005	521192	5136959	132	18	33	643	104	223	1	1
56	Epei12 f9	2005	537425	5126023	227	38	78	582	68	235	0	1
57	Epei12 f10	2005	537779	5133432	295	79	90	850	178	191	0	0
58	Epei13 f5	2005	544711	5141996	105	48	28	945	334	125	1	0

ID	ArcGIS name	Year	UTME	UTM N	farea	fhw	fsw	bfor	bhw	bsw	pfemale	pmale
59	Epei22 f1	2005	522413	5108215	81	31	2	627	168	127	0	0
60	Epei23 f1	2005	540679	5119260	126	11	53	963	94	364	0	0
61	Epei30 f1	2005	529752	5102274	114	34	4	661	184	92	0	1
62	Epei30 f2	2005	528070	5101324	250	71	27	1306	156	528	1	0
63	FR1H1	2004	466595	5147669	17	2	3	164	24	50	0	0
64	FR2H2	2004	466811	5147451	6	0	0	187	31	55	0	0
65	FR3H1	2004	466962	5147503	2	2	0	208	35	64	0	0
66	FR4H1	2004	467641	5147898	6	0	0	272	35	101	0	0
67	FR5H1	2004	468225	5148019	10	0	5	291	41	111	0	0
68	FR6H1	2004	468150	5149334	44	0	28	150	19	77	0	0
69	FR7H1	2004	470000	5148937	6	6	0	215	30	110	0	0
70	FR8H1	2004	470362	5147380	33	7	12	390	91	107	0	0
71	FR9H1	2004	471014	5148097	16	2	12	267	62	98	0	1
72	FR10H1	2004	470940	5146671	103	12	23	395	103	81	0	0
73	FR11H1	2004	473746	5148182	151	74	26	279	104	64	0	1
74	FR12H1	2004	474713	5147770	65	14	10	366	111	108	0	0
75	FR13H1	2004	476174	5145557	8	0	3	228	40	96	0	0
76	FR14H1	2004	492692	5140122	134	3	112	349	37	215	0	0
77	FR15H1	2004	494189	5139725	140	16	69	503	88	235	0	0
78	FR16H1	2004	495048	5138941	41	8	12	580	136	207	0	0
79	FR17H1	2004	492222	5136357	960	358	178	814	301	138	0	0
80	FR18H1	2004	494614	5133114	525	95	215	614	165	172	0	0
81	FR19H1	2004	506330	5136082	479	241	61	689	334	48	0	0
82	FR20H1	2004	522488	5143504	86	8	57	106	11	64	1	0
83	FR21H1	2004	526879	5144040	75	9	27	428	69	220	1	0
84	FR22H1	2004	528462	5143275	61	0	54	444	69	271	0	0
85	FR23H1	2004	529786	5134863	961	301	243	758	292	145	0	0
86	FR24H1	2004	537027	5134104	290	79	90	609	178	179	1	0
87	FR25H1	2004	539297	5142688	1254	451	334	979	392	164	0	1
88	FR26H1	2004	555402	5140991	2171	947	333	1012	663	79	1	0