MOVEMENTS AND RESOURCE SELECTION OF THE NORTHERN LONG-EARED MYOTIS (MYOTIS SEPTENTRIONALIS) IN A FOREST–AGRICULTURE LANDSCAPE

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The fragmentation of forests by the expansion of agriculture is recognized as an important factor influencing worldwide declines of forest-dependent species. Species that are forest dependent may be especially vulnerable to fragmentation because they have specialized resource requirements and may exhibit lower mobility in an agricultural matrix. We investigated movement patterns and resource selection of forest-dependent northern long-eared myotis (Myotis septentrionalis) in a forest–agricultural landscape on Prince Edward Island, Canada. Radiotelemetry was used to locate day-roosts and to estimate locations of female bats during nightly foraging bouts. Day-roost locations and foraging areas were mapped using a geographic information system to generally characterize the forest cover of foraging and roosting areas. Vegetative structure and insect prey availability were measured in the field and compared between foraging and roosting areas to describe resource selection at these sites. Movements of female northern long-eared myotis 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, although bats at 1 site seemed to exclusively use a barn during late pregnancy and lactation. Differences in prey availability did not explain the spatial segregation of roosting and foraging areas. Relative to roost areas foraging sites were more likely to be close to forested creeks and densely forested areas, whereas roost sites were characterized by the availability of potentially suitable roosts. This study demonstrates the importance of investigating movements and resource selection of individuals in fragmented landscapes because a specialization on forest resources can highly restrict the vagility of forest-dependent species to a local environment.

Key words: Chiroptera, forest fragmentation, forest structure, Prince Edward Island, radiotelemetry, roost trees

Agricultural intensification is a dominant force driving large-scale modifications to landscapes that result in the fragmentation of natural and seminatural areas. Fragmentation is considered a primary threat to global biodiversity (Franklin et al. 2002) and there is extensive literature documenting the negative effects of forest fragmentation on diverse species communities (Andrén 1994; Fahrig 2003). The theoretical basis for exploring fragmentation has been expanded from fundamental principles of island biogeography (MacArthur and Wilson 1967) to include matrix structure, and the arrangement of remnant habitat in describing the larger landscape context (Fahrig 2003; Haila 2002; Kupfer et al. 2006). Although our theoretical framework and knowledge of communities and species negatively affected by fragmentation have expanded, it is difficult to transfer this information to the management and conservation of individual species because data are often inadequate to describe how individuals of a species respond to a fragmented landscape. Recent work has demonstrated the importance of developing species-specific models that explore the arrangement of remnant habitat in the larger landscape independently from area effects in occupancy fragmentation studies (Betts et al. 2006; Villard et al. 1999). Prediction-of-occupancy models are useful for examining the effects of fragmentation on distributional patterns relative to localized landscape structure; however, they do not provide insights into how individuals use patchy landscapes. Behavioral responses at the level of the individual must be examined in order to mechanistically understand the effects of 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 studies of fragmentation. For example, studies have shown that linear landscape elements (i.e., riparian corridors and wooded hedgerows) are used by commuting and foraging bats (Downs and Racey 2006; Law...
of forest-dependent northern long-eared myotis (Hecker 1996).

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We investigated movement patterns and resource selection of forest-dependent northern long-eared myotis (Myotis septen-trionalis) in a fragmented forest–agricultural landscape. The northern long-eared myotis is a common, widely distributed, forest-dwelling species in North America that ranges from the fringes of British Columbia to Newfoundland in Canada as far south as Florida (Caceres and Barclay 2000). The morphology and echolocation call design reflect a species with highly maneuverable flight, and a flexible gleaning and hawking foraging strategy (Broders et al. 2004; Faure et al. 1993; Ratcliffe and Dawson 2003), thus facilitating foraging in cluttered forest interiors. Northern long-eared myotis are forest dependent, generally relying on forest features for both roosting and foraging (Broders et al. 2006; Carter and Feldhamer 2005; Hutchinson and Lacki 2000; Sasse and Pekins 1996). Little is known of the ecology of this species in a forest–agricultural landscape with only 1 study examining the roosting preferences of females in such a landscape (Foster and Kurta 1999). Males tend to roost singly, whereas females tend to form maternity colonies in cavities in deciduous trees (Broders and Forbes 2004; Foster and Kurta 1999; Menzel et al. 2002). However, there are instances of maternity roosts in coniferous species (Broders and Forbes 2004; Perry and Thill 2007). Because of the additional energetic costs related to reproduction imposed upon females relative to males, population persistence is likely most limited by the presence of females and thus we focused this study on assessing how female northern long-eared myotis move within a fragmented forest–agricultural landscape. Specifically, our objective was to determine the pattern of use of patches in a forest–agricultural landscape by female northern long-eared myotis by characterizing roosting and foraging sites in terms of forest structure, potential prey abundance, and spatial extent and context in the landscape; and by determining if movements within and between foraging and roosting areas are restricted to areas with forest cover.

**MATERIALS AND 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 5,660 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 entirely covered at 98% with the current 45% forest coverage a result of 3 centuries of land clearing for farming and timber extraction (Loo and Ives 2003). The forests of PEI are part of the Acadian forest region, which is characterized by broadleaf deciduous and boreal coniferous species (Sobey and Glen 2004) including sugar maple (Acer saccharum), yellow birch (Betula alleghaniensis), red spruce (Picea rubens), and balsam fir (Abies balsamea).

We selected 2 study areas (Wheatley River and Greenvale; Fig. 1) that differed in both the total area of forest at the site and spatial configuration of patches (i.e., different distances to nearest neighboring forest patch and different-sized forest patches). Study sites were delineated as a 1,100-m-radius circle (the approximate movement distance of female M. septentrionalis) centered on the weighted (by number of roost trees) center of the roosting area. 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 centers. Individuals were tracked in only 1 area at a time. There were a total of three 1- to 2-week-long tracking sessions for bats at each site from June to August 2006. Using an alternating approach, bats were tracked in 1 site for the life of radiotransmitters and then we alternated to the next site for a tracking session. This design allowed for summer-long tracking sessions at each site and therefore a comparison of the 2 bat colonies over the entire reproductive season.

**Capture and radiotracking.**—Adult female northern long-eared myotis 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 hedgerows). Body mass, 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 or the expression of milk or both (Appendix I; Racey 1988). Radiotransmitters (0.35 g, model LB-2N; Holohil Systems Ltd.,

and Chidel 2002; Limpens and Kapteyn 1991; Verboom and Huitema 1997) and others highlight the importance of scattered trees in agricultural areas as important foraging areas (Law et al. 2000; Lumsden and Bennett 2005). The responses of bats to forest fragmentation have primarily been assessed by community-level surveys investigating how species composition or diversity, or both, change in remnant patches or differ from those in contiguous areas in the tropics (Bernard and Fenton 2007; Cosson et al. 1999; Crome and Richards 1988; de Jong 1995; Estrada and Coates-Estrada 2002; Gorresen and Willig 2004).

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Carp, Ontario, Canada) were attached to bats between the scapulae using surgical adhesive (Skin-Bond; Smith and Nephew United, Largo, Florida). Bats were followed using telemetry receivers (R-1000; Communications Specialists Inc., Orange, California; and R2000; Advanced Telemetry Systems, Inc., Isanti, Minnesota) and 3-element yagi antennas (AF Antronics, Urbana, Illinois). Methods for capture and handling of bats were approved by the Saint Mary’s Animal Care Committee in accordance with guidelines approved by the American Society of Mammalogists (Gannon et al. 2007), 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). We considered a variable signal as indicating the bat was flying (foraging or commuting) and a constant signal intensity taken to indicate the bat was stationary. To locate foraging bats, 2 or 3 observers at georeferenced telemetry stations simultaneously took bearings to triangulate a location for individuals at 30- to 60-min intervals. Bats rarely, if ever, moved beyond the range of reception of our receiving system in both study sites. 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. Foraging locations for each animal were estimated in the field using the maximum-likelihood estimation technique (Nams 2006). If a location was determined to be unreliable (large error ellipse) new bearings were immediately taken. Analyses were restricted to locations where bats were deemed to be flying. Locations with error ellipses of >10 ha were immediately discarded and of the remaining locations, 70% of error ellipses were <3 ha and 40% were <1 ha. We included locations with error ellipses of >3 ha if the error ellipse encompassed ≥1 of the telemetry locations and we could confidently rule out a large portion of the ellipse as containing the location of the bat for a total of 231 locations.

Estimated foraging locations were imported into ArcGIS geographic information system (GIS), version 9.1 (ESRI, Redlands, California) with land-use data from the PEI Corporate Land Use Inventory (Prince Edward Island 2000) to obtain the forest cover for each location. Geographic information system data were derived from interpretation of aerial photographs taken in 2000 (1:17,500; black and white). Forest cover types were classified into 3 categories, deciduous-dominated (≥75% deciduous species), mixed woods (≥26% coniferous species), and open (agricultural fields, roads, residential areas, or water). Because we tracked only a small number of bats (21) for short periods (2–7 days each), 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 group of individuals that occupy, share, and interact in a roosting area (Burland and Worthington Wilmer 2001) and radiotagged bats at each study site were never located in the other study site.

Day-roosts were georeferenced using a global positioning system (Garmin International, Inc., Olathe, Kansas) with an
accuracy of ≤10 m. Minimum roosting areas were calculated as the minimum convex polygon encompassing all appropriate roosts using ArcView GIS (version 3.2) and the Animal Movement extension (Hooge and Eichenlaub 1997). Minimum areas were calculated because individual bats were tracked for only a short period of time and not throughout the entire season. We calculated minimum roosting areas at the level of each colony to facilitate comparison to other roosting and movement studies of *M. septentrionalis*. We also calculated minimum roosting areas for individual bats where 3 or more different roosts were located.

To characterize area available to bats at each study site, we 1st estimated the weighted center of colony roosting areas (weighted by number of roost trees) and used the maximum distance a bat was recorded from a roost (1,100 m) to generate a 7.07-km² circular “landscape.” Because previous research on northern long-eared myotis suggested a strong association with forest (Broders et al. 2006; Jung et al. 1999; Sasse and Pekins 1996), it seemed implausible that all areas within the circular landscape would be truly available to bats. Thus, forest features were buffered within the circular landscape to a distance of 78 m (the maximum distance of an estimated bat location found from the nearest forest edge or hedgerow) and the resulting buffered area around forest features was considered to be an “available” area. A G-test (Sokal and 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. Similar to minimum roosting areas, minimum foraging areas were calculated as the minimum convex polygon encompassing 100% of the telemetry locations for individual bats that had a minimum of 5 estimated foraging locations in order to compare foraging dynamics by the species to other similar studies.

**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 2 areas. In each plot the density of trees (total number of trees > 10 cm diameter at breast height), total number of deciduous trees, total number of coniferous trees, dominant canopy height (using a clinometer—model PM-5/1520; Suunto, Vantaa, Finland), number of potential roost trees (trees defined as decay class 2 or greater, with obvious defects), and the distance to the nearest forest covered creek (using ArcGIS) were measured. Dominant canopy height was calculated as the average of 5 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, we randomly generated coordinates within the foraging areas of each colony and established similar 0.1-ha plots at 15 (Greenvale site) and 14 (Wheatley River site) locations. Foraging and roosting plots were pooled across study sites because statistical significance testing suggested that the data were not different.

To identify variables that best described the differences between foraging and roosting areas, a comparison of areas was carried out using a logistic regression framework. Foraging plots were coded as 1 and roosting plots coded as 0. To account for correlation between variables, multivariate components were constructed using a correlation matrix–based principal component analysis with a varimax rotation. The generated principal component scores were used as the independent variables in the logistic regression (Aguilera et al. 2006) in S-Plus (version 7.0; Insightful Inc., Seattle, Washington). Components with eigenvalues >1 were used in the regression because components with values <1 explain less of the variation than the original variables (Kaiser 1960). The dependent variable was permuted (keeping the number of each vegetation plot type constant) and parameter estimates (PEs) were calculated 9,999 times. We considered components to have a significant effect if the parameter estimate was >97.5% or <2.5% of the permuted values (2-tailed test) and the confidence interval of the parameter estimate did not overlap 0. Variables with loadings of <−0.6 and >0.6 (arbitrarily chosen) were considered as having important effects. Goodness of fit of the model was assessed with Hosmer and Lemeshow’s goodness-of-fit test where P-values ≥ 0.05 indicate that the data sufficiently fit the model (Hosmer and Lemeshow 2000).

**Insect abundance.**—To assess and compare the abundance of potential insect prey in foraging and roosting areas (Kunz 1988), positively phototactic volant insects were sampled in ultraviolet-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 run for approximately 180 min at 2 m above ground level. 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, 1 trap was placed in the approximate center of the roosting area and remained fixed throughout all sampling nights. Another trap was placed in 3 or 4 different locations within each foraging area, coinciding with telemetry effort in the area, and was moved nightly to sample specific areas used by individual 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 (45× maximum magnification). Analysis of available insect biomass was restricted to maximum body lengths found for insect prey of northern long-eared and little brown myotis (*Myotis lucifugus*—Coleoptera, 9 mm; Diptera, 16 mm; Lepidoptera, 15 mm; Trichoptera, 12 mm; Hymenoptera, 11 mm; and all other orders, 12 mm—Broders 2003). Insects fitting size classifications were weighed on an electronic balance to the nearest 1.0 mg (wet weight) to approximate the weights of fresh samples (Mackay and Kalff 1969). Roosting and foraging sample types were pooled across study sites because 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 analyzed by Wilcoxon’s matched-pairs test (Sokal and Rohlf 1995) in SYSTAT (Systat Software, Inc., Chicago, Illinois).
RESULTS

Foraging and roosting locations and movements.—We followed 21 female bats over 45 tracking nights (21 nights in Greenvale and 24 nights in Wheatley River) and tracked them to 37 day-roost trees and a barn on the edge of the forest. Females roosted almost exclusively in maple trees (A. rubrum and A. saccharum) except for 1 white birch (Betula papyrifera) used in late August. In both sites, roosting areas were wholly in 1 stand of deciduous-dominated trees. At the Wheatley River site, in addition to roosting in trees, females roosted in a storage barn that was constructed of a wood frame overlaid with metal siding. Females used the barn from late June through to mid-August and used trees in early June and in late August. Individuals emerging from the barn were captured on 1 occasion to confirm the presence of northern long-eared myotis. 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 minimum roosting area 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 forest roosting area. In Greenvale, the main colony minimum roosting area (defined as when females were reproductive) was approximately 4.13 ha (n = 21 roost trees) with 2 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. Foraging areas in both study sites were concentrated along forest-covered creeks (Fig. 2) and included deciduous-dominated and mixed-wood stands. Minimum foraging areas were approximately 6 times larger than minimum roosting areas (Table 1). In Greenvale, 1 female bat conducted a long-distance commuting flight outside its regular foraging range at an estimated distance of 1,136 m from its day-roost. Similarly, in Wheatley River, another female engaged in a similar long-distance flight at an estimated distance of 1,163 m and thus we estimated the movement distance for bats at approximately 1,100 m on PEI. Females emerging from roosting in the barn in Wheatley River were observed to fly along narrow, tree-lined hedgerows rather than crossing the open field while commuting to foraging areas (Fig. 2).

In Greenvale, females did not forage in cover types 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-dominated and mixed woods) were used more than expected given their availability (Fig. 3). 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 (Fig. 3). The proportions of the 3 cover types used were different for each study site, as shown by the heterogeneity G-test (G = 15.37, P < 0.001).

Characterization of roosting and foraging areas.—Two principal components explained 77% of the variation and were included as independent variables in the regression analysis. Both components had significant effects (component 1: PE = −2.443, 95% confidence interval [95% CI]: −1.13, −3.75, P = 0.0002; component 2: PE = 3.146, 95% CI: 1.42, 4.87, P = 0.002). Hosmer and Lemeshow’s (2000) goodness-of-fit test indicated that the model adequately fit the data (P = 0.324). Component 1 was most heavily loaded with the variables distance to creek, canopy height, number of potential roost trees, and number of deciduous trees in the plot (Table 2). The negative parameter estimate for this component indicates that foraging plots were situated closer to forest covered creeks, contained fewer deciduous and potential roost trees, and had a lower canopy height compared to roosting plots. Variables loaded most heavily on component 2 included the number of coniferous trees and total number of trees in the plot (Table 2). The positive parameter estimate for this component indicates that foraging plots had more structural clutter from higher tree densities and contained a larger proportion of coniferous trees relative to roosting plots.

Insect abundance in foraging and roosting areas.—Foraging areas had approximately equal or slightly less available prey biomass, as represented by the wet mass of light-trapped insects, compared to roosting areas (Z = 0.336, P > 0.05). For specific insect orders, no significant difference was found between foraging and roosting areas for moths (Z = 0.660, P > 0.05) but beetle biomass was significantly greater in roosting areas than in foraging areas (Z = −2.057, P < 0.05) for 18 out of 28 pairwise comparisons.

DISCUSSION

Selection of roosting and foraging sites.—Preference for deciduous roost trees in deciduous-dominated stands by female northern long-eared myotis on PEI was consistent with previous studies of roost-tree selection in relatively intact forested landscapes (Broders and Forbes 2004; Lacki and Schiewerjohann 2001; Owen et al. 2003; Perry et al. 2007; Sasse and Pekins 1996). In a forest–agricultural landscape, females also exclusively used deciduous species (Foster and Kurta 1999). The large variety of tree species used by this species across all study locales likely reflects the availability of localized roosting resources of the area (Ford et al. 2006), where roost selection is for preferred microsite characteristics (i.e., roost type, size, shape, and thermal microclimate—Garroway and Broders 2008; Lausen and Barclay 2006; Sedgeley 2001; Sedgeley and O’Donnell 2004; Willis et al. 2006b). In addition to the larger temporal and spatial landscape fragmentation of the forests across the island, there are smaller stand-level processes occurring on PEI that structure the island’s forests. Approximately 88% of island is privately owned with private woodlots (average of 18 ha in size) accounting for 97% of the island’s wood production (Government of Canada 1997). Therefore, forest management practiced by independent owners may further influence the availability of suitable roost trees at a small scale (≤20 ha). These localized harvesting practices may remove trees that contain suitable roosts within a stand, and therefore roost trees with appropriate microclimates and structure for bats on PEI tend to be maple species that have been left standing by land owners.
Fig. 2.—Roosting and foraging areas of female *Myotis septentrionalis* identified through radiotelemetry in a) Greenvale and b) Wheatley River, Prince Edward Island, Canada, June–August 2006. Flight paths characterize the pattern of movements of bats along hedgerows as they traveled from the barn to foraging areas.
Recent studies of the northern long-eared myotis indicate that it is a predominantly forest-dwelling species and females typically roost colonially in trees during the maternity period (Broders and Forbes 2004; Foster and Kurta 1999; Sasse and Pekins 1996). There are only limited records of roosting by northern long-eared myotis in man-made structures (Brandon 1961; Caceres and Barclay 2000; Cope and Humphrey 1972; van Zyll de Jong 1985). The timing and use of the barn as a maternity roost by bats in the Wheatley River site may provide insights into roost selection by reproductive females. That bats roosted in the barn while pregnant and lactating and in trees early and late in the season suggests that reproductive females are selecting different roosts for different requirements associated with reproduction. Intra-annual variation in roost-tree selection between reproductive and nonreproductive females has recently been demonstrated for this species (Garoway and Broders 2007) and other species (Veilleux et al. 2004).

Variation in roost selection may be due to different energetic costs associated with maintaining high body temperatures for fetal growth and during lactation, and to maintain high temperature for juvenile development (Hamilton and Barclay 1994; Kurta et al. 1990; Sedgeley 2001; Vonhof and Barclay 1996). Females may benefit energetically by selecting warm communal roosts to offset the thermoregulatory costs of maintaining a high enough body temperature for lactation (Barclay 1991; Kunz and Hood 2000; Wilde et al. 1995) or by selecting cooler roosts that may facilitate entry into torpor to delay parturition during times of environmental stress (Willis et al. 2006a). Lausen and Barclay (2006) demonstrated that juvenile big brown bats (Eptesicus fuscus) roosting in man-made structures became volant 1–2 weeks earlier than juveniles from natural roosts. In this study we could not compare thermal microclimates or differences in the timing of juvenile volancy between tree and barn roosts; 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. At least 1 confirmed pregnant female at the site initially roosted in a tree and then moved to the barn for a subsequent 2 nights. It is therefore likely that the entire colony has knowledge of both tree roosts and the barn, because information transfer about roost sites has been demonstrated in other forest-dwelling bats (Kerth et al. 2001).

Foraging areas on PEI were centered along forest-covered creeks and compared to roosting areas were more structurally cluttered and contained fewer deciduous and potential roost trees. Riparian areas are considered critical resource areas for many species of bats because they support higher concentrations of prey, provide drinking areas, and act as unobstructed commuting corridors (Downs and Racey 2006; Grindal et al. 1999; Racey and Swift 1985). No evidence was found to suggest that prey availability was greater in foraging areas than roosting areas on PEI for northern long-eared myotis, suggesting that this resource was not limiting at either site type and that bats may be selecting foraging areas that are close to creeks for reasons other than insect densities. However, the sampling design with ultraviolet-light attractant traps is inherently biased toward positively phototactic prey (Black 1974; Kunz 1988) and therefore may have been unable to detect other important nonphototactic prey consumed by northern long-eared myotis. Although water stress is often thought to be of secondary importance next to food intake in reproductively active females, 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 and Thibault 2006; Mclean and Speakman 1999; Speakman et al. 1991). Alternatively, there may be an inherent effect associated with the general composition of patches in the fragmented landscape that could explain the relationship between foraging areas and distance to water. In mapping the forests 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). Thus, it is possible that fragmented forest stands on PEI tend to contain creeks or streams and that this fact explains the apparent relationship.
Our results suggest that the availability of suitable roosts likely influences site selection on PEI. Female bats in particular face a trade-off in balancing foraging and roosting needs when reproductively active and should therefore select these areas to both capitalize on appropriate resources (i.e., suitable trees or high abundances of insect prey) and also minimize costs in travel between the 2 (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 differentiated structurally in terms of overall tree density and also in the availability of roost trees. Because prey availability did not differ between roosting and foraging areas, this suggests, in conjunction with use of the barn, that the availability of roosts appears to be a critical resource for bats in the fragmented forest landscape of PEI.

Movement and spatial dynamics.—In both study sites, movements of females were under forest cover more than expected and in open areas less than expected, indicating a strong preference for foraging and commuting within forested landscapes. Moreover, if bats were located in open areas, they were clustered to within 78 m of forest features. The capture of bats in traps positioned along forest–field edges and hedgerows also demonstrates the use of forest linear elements by bats in moving through the landscape. In particular, observations of flight paths traveled by bats emerging from the building roost indicated that given the option of following a hedgerow consisting of a narrow line of trees, female northern long-eared myotis did not cross open fields directly. These observations are similar to those of other temperate species of bats that follow linear forest features while navigating within agriculturally dominated landscapes (Downs and Racey 2006; Murray and Kurta 2004; Verboom and Huijtema 1997; Verboom and Spoelstra 1999).

Tree-lined linear features may be important for bats as navigational aids in agricultural landscapes, as protection from predators and wind, and may act to concentrate insect prey (Grindal 1996; Verboom and Spoelstra 1999). The observations of rapid and direct flights from the barn roost to forest foraging areas suggests commuting behavior along the hedgerows in the landscape (Limpens and Kapteyn 1991; Murray and Kurta 2004). The concentration of telemetry locations in open areas along forest patch edges or wooded creeks likely indicates that bats foraged opportunistically along edges in many instances (Downs and Racey 2006).

Proportionately more telemetry locations of foraging bats at the Wheatley River site were classified as being in open areas than at Greenvale. The Wheatley River site had less forest cover (18% in Wheatley River and 31% in Greenvale) and also contained more linear forest features (tree-lined hedgerows, forest–field edges, and smaller, linear forest patches). Thus, forested foraging areas are smaller and possibly limiting in the Wheatley River site and the higher proportion of commuting and foraging movements classified as open may reflect the more fragmented nature of the study area. There may have been some misclassification error in locating bats on linear features because of a combination of error in telemetry triangulations and from the resolution of the geographic information system forest-cover data. However, the clustering of open locations near forest features suggests that movements by northern long-eared myotis occur 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 could reflect tracking more lactating females at this site if lactating females tended to regularly return to roost trees during the night, presumably to nurse juveniles (e.g., Henry et al. 2002).

Spatial use of the landscape by females likely reflects the constraining force of the fragmented forest landscape on the mobility and resource selection of bats. Movement distances between capture and the 1st located roost (285 m ± 121 SD) were smaller than those found for northern long-eared myotis in forested landscapes (1,001 m in New Brunswick [Broders et al. 2006] and 602 m in New Hampshire [Sasse and 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 those on PEI (6.0 ha). Overall, the magnitude of movements exhibited by females on PEI were most similar to those found for a maternity colony of northern long-eared myotis in a similar agriculturally dominated landscape in Michigan (Foster and Kurta 1999). Together with the work in Michigan, this suggests that if forest cover is reduced in an area, then the activities of northern long-eared myotis may be constrained in landscapes where areas of suitable forest cover are limiting. If this is true, then on PEI this may mean that female northern long-eared myotis perceive forest fragmentation at a small “patch-level” scale where bats are not using a network of multiple forest patches in the greater landscape. Differences in the spatial dynamics exhibited in forested and forest–agricultural studies of the species also imply plasticity in resource use and subsequent movements relative to the local landscape.

### Table 2

Mean (SD) plot-level forest characteristics and component loadings of principle components assessed to compare the forest structure of roosting and foraging areas of female *Myotis septentrionalis* on Prince Edward Island, Canada.

<table>
<thead>
<tr>
<th></th>
<th>Foraging plots</th>
<th>Roosting plots</th>
<th>Component 1&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Component 2&lt;sup&gt;a&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dominant canopy height (m)</td>
<td>19 (4)</td>
<td>21 (3)</td>
<td>0.664</td>
<td>0.193</td>
</tr>
<tr>
<td>No. deciduous trees</td>
<td>24 (15)</td>
<td>33 (12)</td>
<td>0.880</td>
<td>0.075</td>
</tr>
<tr>
<td>No. coniferous trees</td>
<td>37 (28)</td>
<td>9 (12)</td>
<td>-0.199</td>
<td>0.940</td>
</tr>
<tr>
<td>Density of trees (total trees)</td>
<td>61 (35)</td>
<td>42 (11)</td>
<td>0.294</td>
<td>0.929</td>
</tr>
<tr>
<td>No. potential roost trees</td>
<td>2 (2)</td>
<td>10 (5)</td>
<td>0.763</td>
<td>-0.434</td>
</tr>
<tr>
<td>Distance to creek (m)</td>
<td>43 (33)</td>
<td>153 (81)</td>
<td>0.649</td>
<td>-0.521</td>
</tr>
</tbody>
</table>

<sup>a</sup> Loadings in boldface type are those identified as having significant effects in differentiating between foraging and roosting vegetation plots.
The findings of this study and the Michigan study (Foster and Kurta 1999) provide a contrast to studies of *M. septentrionalis* in more contiguous forested landscapes, which may imply that a forest specialization may limit the vagility of this species in a forest–agricultural landscape. On PEI, movements of northern long-eared myotis were strongly associated with forest features and foraging areas were centered along forest-covered creeks. Bats roosted in the forest interior, although females in the more fragmented study area (Wheatley River) used a building during pregnancy and lactation, which suggests an alternative strategy by the colony to persist in a landscape that may have had fewer roost tree resources. The importance of woodlands in agricultural landscapes for bats is stressed by studies that document higher activity and captures of bats in woodlands or along wooded linear features (Bernard and Fenton 2003; Bianconi et al. 2006; Bontadina et al. 2002; Russ and Montgomery 2002; Walsh and Harris 1996; Wickramasinghe et al. 2003). This study emphasizes that forest-dwelling bats are affected by forest fragmentation. Further long-term studies examining movements, resource selection, and social structure of forest-dwelling bats before and after a forest fragmentation event would provide valuable insight into the mechanisms and specific impacts of forest fragmentation on such a species.

**ACKNOWLEDGMENTS**

We are especially grateful to the landowners in the communities of Wheatley River and Greenvale who granted us access to their land. We thank C. Garroway, T. Herman, K. Patriquin, J. Lundholm, R. McCulla, T. Kunz, and K. Safi for helpful comments and reviews that greatly improved this manuscript. J. Poissant, E. Hennessey, P. Hiço, and A. Burns provided excellent assistance in the field. Funding was provided by Parks Canada; the Prince Edward Island Model Forest Partnership Network; Prince Edward Island Department of Energy, Environment and Forestry; a Discovery Grant to HGB from the Natural Science and Engineering Research Council of Canada; and student awards to LEH from Bat Conservation International and the American Society of Mammalogists.

**LITERATURE CITED**


PRINCE EDWARD ISLAND. 2000. PEI corporate resource inventory. Resource Inventory and Modeling Section, Department of Agriculture and Forestry, Charlottetown, Prince Edward Island, Canada.


APPENDIX I

Data for individual female northern long-eared myotis (*Myotis septentrionalis*) radiotagged during the study.

<table>
<thead>
<tr>
<th>Bat</th>
<th>Colony</th>
<th>Reproductive status</th>
<th>Body mass (g)</th>
<th>Transmitter % of body mass</th>
<th>No. different roosts located</th>
<th>No. foraging locations</th>
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<tr>
<td>1</td>
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<td>Nonreproductive</td>
<td>5.5</td>
<td>6.4</td>
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<td>6.3</td>
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<td>4.6</td>
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