BREEDING SEASON HOME RANGE PLACEMENT, ACTIVITY PATTERNS AND HABITAT USE OF THE NORTHERN SAW-WHET OWL (AEGOLIUS ACADICUS) IN THE SOUTHERN APPALACHIAN MOUNTAINS

A Thesis

by

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ABSTRACT

BREEDING SEASON HOME RANGE PLACEMENT, ACTIVITY PATTERNS AND HABITAT USE OF THE NORTHERN SAW-WHET OWL (AEGOLIUS ACADICUS) IN THE SOUTHERN APPALACHIAN MOUNTAINS. (May 2000)

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The northern saw-whet owl (*Aegolius acadicus*), the smallest owl in eastern North America, was not known to be a breeding season resident of the southern Appalachian region until chance encounters by naturalists during 1940's verified the owl's presence in the region during the spring, thus suggesting a potential for the presence of breeding populations. Almost sixty years later, the saw-whet's presence as a breeding bird in the southern Appalachians is verified from only a handful of nest records. The saw-whet is considered a habitat generalist through much of its breeding range, occupying various upland and lowland coniferous and mixed coniferous/deciduous forest types. However, in the southern Appalachians, the owl is known from accounts of vocal activity and from few nest records to breed only in a single forest type, the high-elevation boreal spruce-fir.

Relicts of the Pleistocene Ice Age, the mountaintop spruce-fir forests of the southern Appalachian Mountains are geographically isolated from other known breeding habitats of saw-whet owls in West Virginia and in the northern United States and Canada. Designated the second most threatened ecosystem in the entire southeast, these small refugia are now imperiled by human disturbances (adelgid infestation, air-borne pollutants, and global warming), endangering the very existence of the boreal spruce-fir ecosystem and placing the region's entire boreal allied flora and fauna, including the saw-whet owl, at risk of local extinction. The focus of this study is to better understand the owl's level of dependence on the boreal spruce-fir and to provide a basis for predicting impacts to regional saw-whet populations with the impending loss of habitat.

I used telemetry in combination with a geographic information system (GIS), to track and map the movements of radio-tagged saw-whet owls from three mountain ranges in the region for statistical and geospatial analysis of their activity patterns and use of habitat during the breeding season. Habitat selection was examined at two spatial scales; second order (home range placement) and third order (habitat use within home ranges). Diurnal roosts were classified by their location at either single-use sites (sites used only once) or multiple-use sites (concentrated areas of roosting which were used multiple times) for χ^2 analysis of habitat use. Night activity was grouped by two intensity levels (high- and moderate-use), based on point densities of each owl's locations, for compositional analysis of habitat use.

Home ranges of 9 of 11 radio-tagged saw-whet owls, each followed during a single spring and summer of 1993 or 1994, contained high proportions (45 - 80%, avg. 61.4%) of forest types composed (10% or greater) of spruce and/or fir trees. Saw-whets utilized forests of spruce-fir and spruce-fir/hardwood ecotone for diurnal roosting and nocturnal activity significantly more than expected compared to the proportional availability of these forest types within home ranges. Diurnal roosting patterns indicated a selection predominantly for spruce-fir when roosting at multiple-use sites. During nocturnal activity, equal preference for spruce-fir or spruce-fir ecotone was indicated within areas used intensively, delineated by the 70% utilization distribution (UD) of each owl's triangulated locations. Within areas used moderately, delineated by the 90% UD, selection of forest types was not found to be significant. However, greater than expected use of the spruce-fir associated forests was indicated at this less intensive level of use, suggesting a degree of reliance on forests containing spruce-fir during most night activity.

Seasonal differences in locations and patterns of roosting suggest that male owls, which hold breeding season territories in the boreal spruce-fir, shift to mid-elevation winter home ranges, which are adjacent to breeding season home ranges but largely out of the spruce-fir. Owls were observed making seasonal shifts away from areas they used during the breeding season from mid-July to October. Selection for spruce-fir forests principally during the breeding seasons suggests that boreal spruce-fir is the primary breeding habitat for saw-whets. These forests may provide qualities conducive for breeding that can not be found in other forest types of the region. These results indicate a level of dependence of saw-whet owls for boreal spruce-fir forests, which suggest detrimental impacts to the regional population with further declines of the spruce-fir ecosystem.

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Loving thanks to my wife, Marla, for her support through these years and for her invaluable help in preparation of the manuscript.

DEDICATION

To my parents, James R. Milling and Norma B. Milling, my wife, Marla, and my children, Ben and Hannah. What makes me most happy is that I can share this with you. I love all of you very much.

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INTRODUCTION

Background to the Study

The northern saw-whet owl (*Aegolius acadicus*) is considered to be a habitat generalist through most of its North American breeding range (Johnsgard 1988). In the northeastern U.S. and Canada (Fig. 1), the owl is found in upland areas as well as bog and riparian sites of both coniferous and deciduous forest types (Forbes and Warner 1974, Cannings 1993). At lower latitudes, the owl is primarily a montane forest dweller. In the western U.S. and Mexico, it utilizes various coniferous and mixed forest communities from elevations of 1700 to 3200 meters above sea level (Webb 1982, Hayward and Garton 1988, Binford 1989). Only in the southern Appalachian highlands (Fig. 1), the southeastern limit of the saw-whet owl's breeding range, is the owls breeding habitat thought to be restricted to a single primary forest type, the boreal spruce-fir (Simpson 1974a, Simpson 1974b, Cannings 1993).

Southern Appalachian spruce-fir forests of western North Carolina, extreme eastern Tennessee and southwestern Virginia exist as an island-like archipelago of isolated boreal ecosystems atop the region's highest mountain ranges (White 1984; Fig. 2). Covering less than 1% of the regional land-base (SAMAB 1996), these relicts of the extensive boreal forests that enveloped the southern Appalachian region during the Pleistocene Ice Age (Delcourt and Delcourt 1984) are geographically isolated from small boreal refugea on the Allegheny Plateau of West Virginia and to a greater extent from the owl's more general cold-temperate habitats farther to the north.

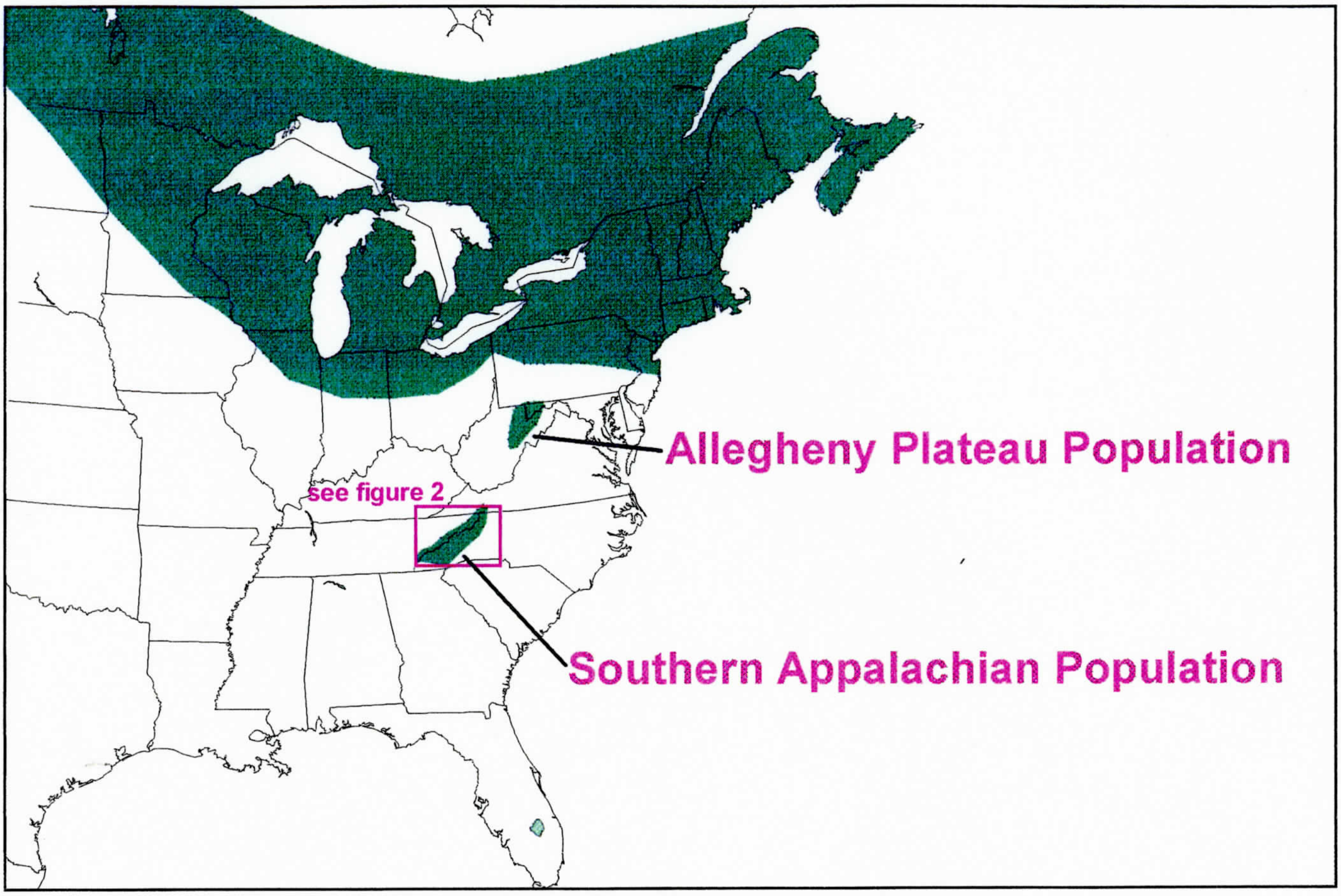

Figure 1. Eastern breeding range of the northern saw-whet owl in North America. Two disjunct populations occur along the Appalachian mountain chain south of Pennsylvania. Maroon box framing the Southern Appalachian population shows area of figure 2. Breeding distribution adapted from Cannings (1993).

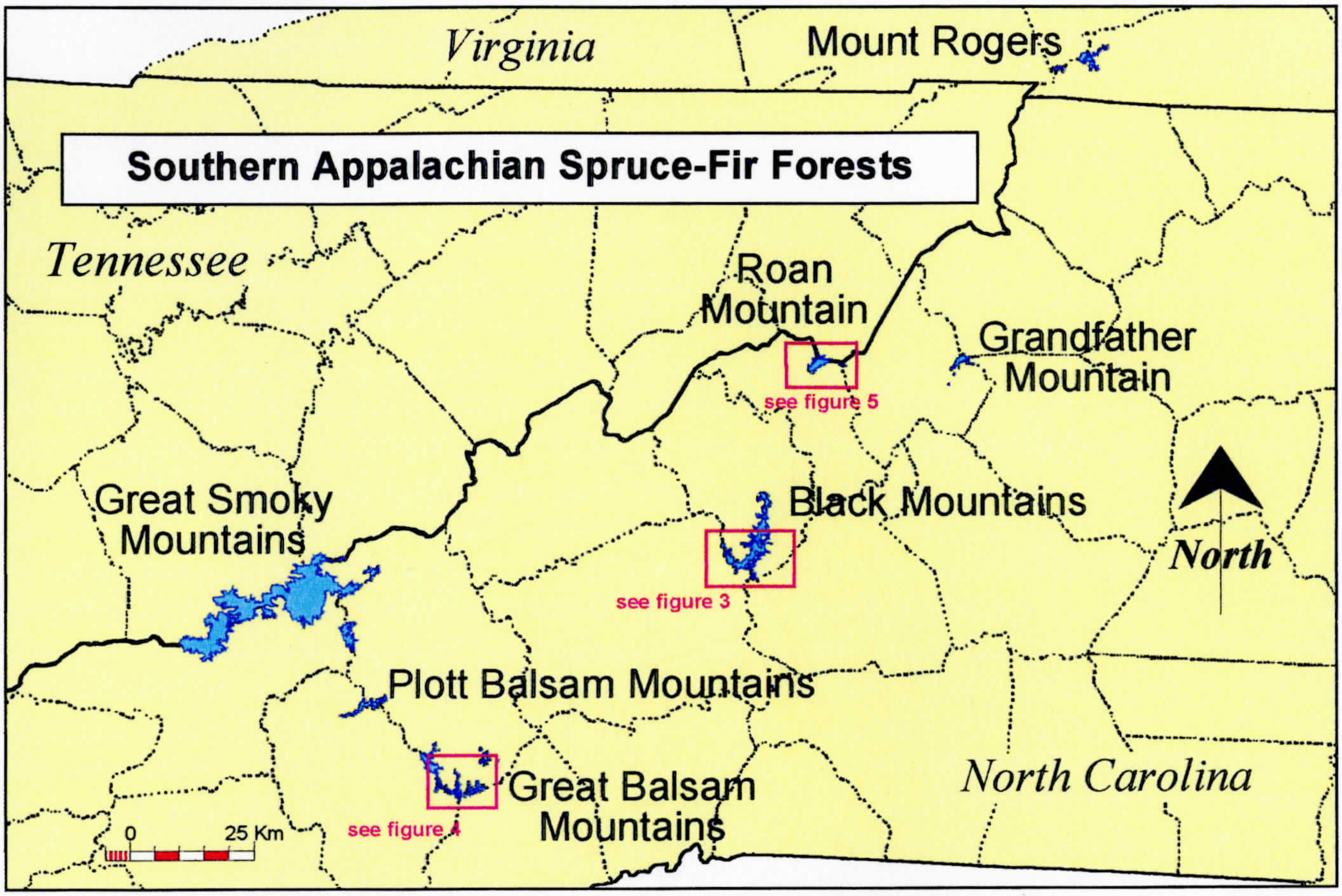

Figure 2. Southern Appalachian spruce-fir forests. Boreal spruce-fir forests of the region are distributed among seven mountain ranges. Three study areas (Great Balsam Mountains, Black Mountains and Roan Mountain) were chosen from these to census saw-whet owl breeding populations and radio-tag individuals for assessments of seasonal activity patterns and analysis of habitat use. Maroon boxes show area of figures for each study area. Distributions and extent of spruce-fir were adapted from Dull et al. (1988).

Massive "human induced" disturbances to the region's spruce-fir forests began with logging and fire at the turn of the 20th century (White 1984). Logging and slash burning became extensive in the mid- and high-elevations between 1880 and 1930. Mature spruce trees, prized as lumber for building, were essentially cleared from all regional mountain peaks, except for some small patches in the Great Smoky Mountains. Wildfires followed logging. Started from logging machinery and campfires, fires easily ignited the left over slash wood and exposed, dried carpets of needles, moss and roots in huge cut-over areas. These perturbations were devastating and long lasting in their effect. One half of the estimated pre-logging extent of the southern Appalachian spruce-fir ecosystem was eliminated (Pyle 1984). Present-day differences in species diversity and community composition among the region's mountaintop spruce-fir ecosystems have been attributed both to geologic and climatic conditions specific to each mountain and to the different disturbance histories on each mountain during this period of early logging (White 1984).

A second period of massive devastation to the spruce-fir began in the 1950s with the introduction to North America from Europe of the balsam woolly adelgid (*Adelges piceae*) and with increases of atmospheric pollutants (Eagar 1984). The adelgid is considered the principal factor in the mortality of 44-91% of mature fir and 3-14% of mature spruce on mountain tops region-wide during a period between the first regional outbreaks in the 1950s and the early 1970s (Dull et al. 1988). Today, a patchwork of conifer and hardwood stands, interspersed with open heath meadows, covers what was once the domain of the boreal spruce-fir forest (Nicholas et al. 1992).

Acid rain is implicated in critically high ground acidity levels and increased leaching of soil nutrients, causing distress in all high elevation flora (Krahl-Urban et al. 1988). In addition to the continued stresses to the spruce-fir ecosystem from the adelgid and acid deposition, abnormally high summer temperatures caused by global warming is now altering the high-elevation climate to which it has adapted (Adams and Hammond 1991).

The combined impacts to the spruce-fir from these insults (adelgid infestation, acid precipitation and global warming) have caused declines in the extent and health of the spruce-fir forest and threaten further losses and degradation in the future (Dull et al. 1988). Indeed, these continued assaults now threaten the very existence of the spruce-fir ecosystem in the southern Appalachians (Adams and Hammond 1991). If temperature increases are sustained and severe in future years, the spruce-fir ecosystem will likely be eliminated from many mountain peaks of the region, and, in so doing, cause the extirpation from those peaks of a host of spruce-fir endemic flora and fauna (Dull et al. 1988, Adams and Hammond 1991). Is this the fate of the southern Appalachian saw-whet owl?

Physiological limitation may be the mechanism that restricts saw-whets to cool montane forest communities at warmer latitudes. Researchers have suggested that saw-whet owls are intolerant of high summer temperatures (Ligon 1969, Dodge et al. 1999). But, if true, is this physiological restriction the only limitation to the saw-whet's use of habitats within the southern Appalachian region for breeding. If the owl acts as a generalist as it does elsewhere, it should randomly use all habitats within the region which provide cool forest conditions.

Within the southern Appalachian region, isolated encounters of saw-whet owls in various non-boreal forest types during the breeding season (Murdock, Rowe, Hughes pers. comm.; and unpubl. data) suggest that saw-whets might regularly use forest types other than spruce-fir for breeding. However, the owls have only been found sporadically and in very low numbers away from the boreal spruce-fir forests. Additionally, locations of owl occurrences in non-boreal habitats do not appear to be used consistently from year to year (unpubl. data), thus are not indicative of stable population centers for breeding activity.

Other accounts of saw-whets during the breeding season (Stupka 1963, Peake 1965, Simpson 1974a) support the more widely-held opinion that the spruce-fir forest is the owl's primary breeding habitat in the region. Results from two auditory censuses of saw-whet owls in forest types at high and mid-elevations (Simpson 1972, Milling et al. 1997) confirm the owl's consistent use of only the region's high-elevation boreal forests during the breeding season. Milling et al. (1997) demonstrated a three fold difference in numbers of owls heard in spruce-fir and adjoining spruce-fir ecotones compared to other high and mid-elevation forest types, and a ten fold difference between spruce-fir and other types in numbers of breeding males holding territories. Additionally, nesting activity of saw-whets has only been confirmed in forests associated with the boreal spruce-fir (Mayfield and Alsop 1992, Barb 1995, Cooper pers. comm.). If regional saw-whet owl populations are dependent on these high-elevation boreal habitats for nesting, the effects of spruce-fir decline on owl populations could be severe and irreversible.

I studied breeding season habitat use of radio-tagged saw-whet owls from three mountain ranges, to better understand how further declines or degradation of spruce-fir forest in the southern Appalachian region might affect the stability of owl populations. To investigate patterns of habitat use, movements of radio-tagged owls were examined using statistical and geospatial methods of analysis on two biological scales of habitat selection (Johnson 1980); 2nd order habitat selection - where within the geographic region do owls place their home ranges, and 3rd order habitat selection - what forest types within home ranges are preferentially selected for both night-time activity, including foraging, and for day-time roosting. Movements were analyzed with respect to short-term (within season) and long-term (between season) patterns of activity. Results are discussed with respect to habitat preferences, seasonality of activity patterns and considerations for management. The potential for assessing nesting activity remotely, through the movements of radio-tagged owls, is also discussed.

GIS in Wildlife Telemetry Studies

Telemetry error and resolutions of data representation

When triangulating owl positions, the perceived direction of the transmitter signal can be influenced by structure and terrain features of the land (Saltz and White 1990). Large positional errors, caused by deflection and reflection of the transmitter signal, can result from these influences and are a major source of systematic error in telemetry field studies (Saltz 1994). Because of this, animal positions defined as point locations possess probable spatial inaccuracies that result in the likelihood of incorrect designations of habitat type with respect to the animal's true position along habitat boundaries. The inability of remote telemetry methods (triangulation methods) to produce discrete positional data (point data) of high confidence has forced researchers studying habitat use to compromise their telemetry data to reduce the potential for Type I error. Efforts to avoid Type I error have resulted in either the removal from analysis of large numbers of animal location points that fall short of acceptable distance limits from habitat boundaries (usually 2 s.d.'s of a calculated error angle) or the generalization of habitat categories by combining habitat types into large areas of crude habitat similarity (Saltz and Alkon 1985). The elimination of points near boundaries (though positionally as accurate as the remaining points of the data set) causes small sample sizes to be further reduced (increasing the potential for Type II error) and eliminates the possibility for assessing habitat use along margins or borders of habitat types. Alternately, generalization of habitats often masks important animal-habitat relationships that could be detected if appropriate habitat complexities were used, thus causing interpretations to be grossly inadequate for use in effective management and conservation strategies.

Accepted standards used in GIS mapping and map accuracy assessment describe unverifiable positions as indefinable at discrete (point) resolutions (Merchant 1987). To conform with GIS mapping standards, data with "fuzzy" accuracies must be represented at resolutions that account for their probable error. The limitations in the accuracy of remote telemetry data strongly indicate that point data are not the appropriate resolution for representation of animal locations when using triangulation methods. Triangulated data of animal positions are no more accurate than the areal measures that estimate their probable limits of positional accuracy (Saltz and White 1990). Therefore, areal depictions of location rather than point depictions are more appropriate for representation of animal positions. Furthermore, areal representation of animal positions compensates for triangulation error of telemetry data sets by including definable portions of the estimated error distribution within the depicted area of each position (Wray et al. 1992).

Kernel density estimators, which essentially weight the distribution of animal point data by density to create frequency distributions, provide estimates of habitat use from area rather than point depictions of each triangulated fix. Frequency distributions are calculated as the addition of overlaps of each point's multivariate normal distribution estimator (smoothing estimator). A continuous surface of frequency distribution data can be created with interpolation techniques and contoured to show areas of estimated uniform density. These contoured density levels are then used to spatially define levels of use intensity or utilization distribution (UD). The combined probabilities of points in contoured areas in proportion to the entire data set provides the stability for the UD contour that surrounds a cluster of points (Wray et al. 1992). The greater the proportion of points contained within the contour with respect to the entire data set, the more spatially stable the contour becomes. Thus, greater positional accuracies are obtained based on the positional stability of clusters of points to accurately describe areas of use rather than individual points to describe locations of use (Wray et al. 1992).

Assessments of map accuracy and error propagation

Though triangulation error may be the largest source of positional error in most telemetry studies, other sources of error can influence results. Positional accuracy of registered photo images, classification and delineation of habitat types, accuracies of other spatial data sets and transformations of those data sets to map projections used in analysis all contribute to the overall map accuracy (Bolstad and Smith 1992). The disclosure of map accuracy has always been necessary in telemetry studies, in that animal positions are, by nature of the research questions, analyzed in relation to land features such as habitat types. However, the positional accuracy of land features on maps used for analysis of animal-habitat relationships has rarely been reported by researchers in previous studies. With the increasing importance of GIS in all aspects of wildlife study and management, full disclosure of spatial accuracies of land feature data sets becomes essential.

Ideally, spatial accuracies should be determined for each thematic data layer in order to evaluate animal positions in relation to any land features of interest (Bolstad and Smith 1992). However, most types of spatial error incurred when mapping each data set typically occur independently of error from other data sets and in random normal distributions (Bolstad and Smith 1992). As such, their effects are not additive. For this reason, maximum error among all sources of land feature data can be assessed from land feature maps in their final form by determining the accuracy of the data source with the greatest error potential.

For this study, the sources of greatest potential positional error in the mapping of land features come from registration of aerial photos. Errors can occur during aerial photo registration in the establishment of control points or in applying a transformation to register the photo image to the map projection (Bolstad and Smith 1992). Positional accuracy is measured by root-mean square error (RMSE) calculations, where the difference between any mapped point and its corresponding control point is measured in x and y directions.

If magnitudes of error among data sets are greatest for animal data, area representations of animal positions should adequately compensate for smaller positional errors of land features (Bolstad and Smith 1992). Nonetheless, without accuracy assessments of land feature data, magnitudes of error remain unknown and the validity of results and conclusions from habitat use analyses are little more than assumptions.

METHODS

Study Areas

A minimum of three mountain range study areas was deemed adequate to account for potential differences in habitat, thus in habitat use by owls, among mountain ranges (Fig. 2) of the southern Appalachian region. Each of the seven mountain ranges containing large proportions of the region's boreal spruce-fir support saw-whet owl populations during the breeding season (Stupka 1963, Simpson 1974b, Simpson 1976, Crutchfield 1990). From these, the Great Balsam Mountains, the Black Mountains and Roan Mountain were selected as study areas, based on travel convenience and automobile access.

Southern Great Balsam Mountains

The ridge line of the Balsams divides the North Carolina counties of Haywood to its north from Transylvania to its southeast and Jackson to its southwest and west. The point where the three counties meet is the location of the southern-most stands of spruce-fir forest in eastern North America. The Great Balsam Mountains are centrally located within the southern Blue Ridge Mountain physiographic region, with prominent ranges of the Great Smoky Mountains to its northwest, the Nantahala Mountains to its southwest and the Blue Ridge Mountains to its south and east. The two peaks of highest elevation in the Great Balsam Range are Black Balsam Knob (1894 m) and Richland Balsam (1954 m). Valley areas surrounding the mountain range typically vary in elevation from 650 to

750 m. Spruce-fir forests of the Great Balsams cover 5601 A (2267 ha), 10 percent of the region's total spruce-fir (Dull et al. 1988).

Black Mountains

Yancey and Buncombe Counties in North Carolina are partitioned by the high ridge of the Black Mountains. The Black Mountains are the most prominent component of the Blue Ridge mountain range complex, which separates the southern Appalachian and Piedmont physiographic regions in North Carolina and delineates the eastern Continental Divide. The Blacks are home to Mt. Mitchell, 2037 m (6684 ft), the highest peak in eastern North America. Other high peaks include Mount Gibbes (1987 m) and Celo (1928 m). The southeastern slopes of the Black Mountains drop to valleys in the upper Piedmont of North Carolina (400 m). Valleys to the east, north and west of the mountain range are mountain valleys of the Blue Ridge complex and range in elevation from 750 to 880 m. Spruce-fir covers 7221 A (2922 ha), approximately 11 percent of the total in the region (Dull et al. 1988). The range's steeply rising eastern slopes are scoured by landslides that divide sections of spruce-fir with large talus and bedrock gullies which terminate within the hardwood forests below.

Roan Mountain

Roan Mountain is part of the Unaka Mountain range, which separates the southern Blue Ridge Mountain physiographic region to its east from the Ridge and Valley physiographic region to its west. County and state lines between Carter County, Tennessee and Mitchell

County, North Carolina traverse the ridgeline of Roan Mountain. High peaks of Roan Mountain are Roan High Bluff (1912 m) and Roan High Knob (1916 m). Valleys surrounding "The Roan" range in elevation from 640 to 950 m. The spruce-fir forests of Roan mountain cover 1699 A (688 ha), accounting for two percent of the region's total spruce-fir forests (Dull et al. 1988).

Southern Appalachian High and Mid-elevation Forest Types

Floristic zonation is a natural occurrence along elevational gradients in the southern Appalachians (White et al. 1993). Variability in micro-climatic and edaphic conditions of mountain landscapes, however, result in indistinct zonal boundaries. Therefore, broad overlaps in elevation can occur between zones on a regional level. Forest types of two vegetational zones, the high-elevation montane boreal zone (4500 - 6684 ft) and the mid-elevation mixed forest zone (3000 - 5500 ft), are described below. Historically, most breeding season observations of saw-whet owls have been from forests of these two zones (Stupka 1963, Peake 1965, Simpson 1972, Crutchfield 1990), though occurrences of owls outside of spruce-fir forests of the boreal zone are occasionally reported (Simpson 1972, Simpson 1974a, Milling et al. 1997).

Forests of the Boreal Zone

Spruce-Fir and Spruce-Fir Ecotone

Dominated by red spruce (*Picea rubens*) and fraser fir (*Abies fraseri*), boreal forest remnants only occur on the seven highest mountain peaks and ranges of the region

(Fig. 2; Dull et al. 1988). An eighth mountain (Whitetop Mountain, Virginia) of the region is topped with small stands of spruce but no fir. The montane boreal zone (spruce-fir zone) becomes relatively continuous at around 1600 to 1700m (5300 to 5500 ft) and higher (White et al. 1993). While these two species occur individually and together as small pure stands, mixed stands of these with northern hardwood species also occur at most elevations of the boreal zone. Fraser fir trees typically reach their greatest densities at higher elevations and are sparse to absent at the lower limits of the boreal zone. Red spruce trees are more broadly distributed in elevation than fir and can be found in mixed stands with non-boreal species or in pure stands from the lower elevations of the zone to many high peaks. At the lower limit of this zone, spruce forms small pure stands or mixes with tree species associates of mid-elevation forest types (hemlock cove, northern hardwood and red oak and pine ridges) to create ecotones down to 1400m (4500ft). Deciduous species common to the montane boreal zone are yellow birch (*Betula lenta*), mountain ash (*Sorbus americana*) and mountain maple (*Acer spicatum*). Heath shrubs, primarily rhododendron (*Rhododendron maximum and R. catawbiense*), may occur as a dense or scattered vegetation layer in these forests.

Forests of the Mid-Elevation Zone

Eastern Hemlock Coves

Hemlock coves are found in mid-elevation sheltered areas of concave topography producing mesic to wet-mesic soil conditions. Hemlock coves are less common on southern facing slopes than on slopes of other aspects. This forest type, typified by the presence of eastern hemlock (*Tsuga canadensis*), is rarely found in pure (single dominant canopy species) stands. Hemlock mixes with spruce-fir at the highest reaches of mountain stream headwaters. At lower elevations, it integrates down slope with rich cove forest species including red maple (*Acer rubra*), yellow birch (*Betula lutea*), American beech (*Fagus grandifolia*) and yellow poplar (*Lirodendron tulipifera*). Hemlock becomes less dominant at lower elevations. A second conifer, white pine (*Pinus strobus*), is also associated with mid-elevation mesic to wet-mesic forest conditions, mixing with hemlock cove forest at the lower limits of this zone. However, white pine is not as restricted to cove conditions as is eastern hemlock and can be found in other forest types. An evergreen shrub layer of rhododendron is common in hemlock cove forests, which can persist as dense, unbroken thickets for many hectares.

Northern Hardwood

Northern hardwood forests occur at mid- to high-elevation coves, slopes and flats of mesic, well-drained soils. Dominant tree species include American beech (*Fagus grandifolia*), yellow birch (*Betula lenta*), sweet birch (*Betula allegheniensis*), red maple (*Acer rubra*), sugar maple (*Acer saccharum*) and yellow buckeye (*Aesculus flava*). White pine mixes with this forest type at some mid elevation localities. Forests of this type can contain an evergreen shrub layer of rhododendron or mountain laurel (*Kalmia latifolia*), which can be sparse to dense in cover.

Northern Red Oak

Northern red oak forests occur on moderately exposed mid- to high-elevation ridges with mesic to dry-mesic soils. The dominant species is northern red oak (*Quercus rubra*). This forest type also occurs at mid-elevations with chestnut oak (*Quercus prinus*) and on some high elevation mountain tops where spruce-fir is absent. Forests of this type can contain a sparse to dense evergreen shrub cover of mountain laurel or rhododendron.

Pine Ridge

Pine ridge forests occur at mid-elevations, along exposed ridges with dry-mesic soils. The dominant species can be table mountain pine (*Pinus pungens*), Virginia pine (*Pinus virginiana*) or pitch pine (*Pinus rigida*), one of which typically persists as the lone conifer species in the stand. Near pure stands to stands mixed with xerophilic hardwood species are found. Forests of this type often contain an evergreen shrub component of mountain laurel, or less commonly, rhododendron. Pine ridge forests are most prevalent on southern facing slopes.

Field Techniques and Spatial Analysis

Study animals were trapped with mist nets at the three study areas during spring and early summer of 1993 and 1994 (Milling et al. 1997). Owls were sexed, using the wing-mass discriminate function available from Project Owlnet (Brinker unpubl. manusc.). This method uses a combination of body mass and wing-cord length to determine sex. Owls were then fitted with, backpack-style (Smith and Gilbert 1981), a transmitter (Wildlife Materials Inc., Carbondale, Illinois, model SOPB2070LD) using elastic, degradable strapping. The weight of each transmitter plus harness was no more than 3.5 grams, <5% of the average weight of owls that were trapped. Each owl was followed for only a single breeding season.

Telemetry

Owl positions were obtained during diurnal (roosting) and nocturnal (active) periods. During diurnal periods, owls were tracked to their roost sites where exact locations could be plotted and forest types/condition could be verified. Coordinates of roost sites were taken with a Magellan Field Pro V, Global Positioning System (GPS). Observations of stand vegetative structure and measurements of topography were recorded, and each roost site was flagged for later vegetative-plot sampling. During nocturnal periods, owl locations were obtained through triangulation. Simultaneous bearings were taken of an owl's position using two to three mobile receivers. Bearings were taken from designated receiver stations along roads and trails that were locatable on aerial photographs and afforded good vantage points of the surrounding terrain. Bearings were taken at a minimum interval of 15 minutes using the null method (Kenward 1987). Bearing takers at the receiver stations synchronized triangulations with hand-held two-way radios. A single owl was tracked per night.

Steps were taken to minimize telemetry error caused by signal bounce, narrow bearing angle, or observer bias. While triangulating, signal variability and strength were recorded. Bearings of low signal strength, or triangulations with bearing angles that were near parallel (<20 degree difference) or near opposite (between 160 and 200 degree difference) were eliminated from analysis. Bearing takers noted possible signal deflection (bounce). Those bearings were eliminated from analysis if the correct direction of the owl could not be determined by changing the receiver location (Saltz and White 1990). These eliminations of potentially erroneous data caused reductions in each owl's data set. All analyses were performed on "corrected" data sets after these revisions were made.

To account for observer error and bias, the error angle was calculated using beacon transmitters (Saltz and White 1990). To duplicate field conditions, beacon transmitters were placed at various locations within a tagged owl's home range. All crew members took estimates of the signal bearing from multiple receiver stations to 4 different beacon transmitters, which were placed at distances from receiver stations that were typical of actual receiver-to-owl distances during the study. The error angle was found by calculating the difference between the averaged bearings taken by all observers and actual bearings to beacon transmitters located by GPS (error < 5 meters) (White and Garrott, 1990). When tested, crew members were unaware of beacon locations.

Mapping

Maps of forest types were prepared from USGS 1988-89 high altitude infrared aerial photographs (scales from 1:69,400 to 1:75,750). Photos were digitally scanned at 400dpi (producing a pixel size of 3 to 4 meters - allowing individual trees to be recognized and stand boundaries to be accurately digitized). Forest types were classified directly from the photo originals using grid count methods (Avery 1978). The scanned photo images were registered to USGS 7.5 minute topographic maps using ERDAS Imagine (ERDAS 1998) and boundaries of forest types were digitally traced from the computer monitor. All maps and spatial data sets were set to Universal Transverse Mercator (UTM) projection.

Triangulated owl locations were generated using Telem 88 home range software (Coleman and Jones 1988). For calculations of owl home range size, routines in Telem 88 were used to determine the minimum convex polygon (MCP). Kernelhr software (Seaman and Powell 1991) was used to delimit areas of usage at moderate and high use levels (based on density of triangulated owl positions) using fixed kernel methods with least squares cross validation smoothing on a 100 meter interval grid (Seaman and Powell 1996). MapMaker software (Dudley and Forbes 1999) was used to overlay owl spatial data sets onto the registered images and digitized forest stand layers for analysis of habitat use and activity patterns.

Classification of Habitat Types

Habitat types within each owl's home range (defined as the minimum convex polygon (MCP) for 100% of each owl's diurnal and nocturnal positions obtained during the breeding season) were classified by forest type to determine preferences of owls among available high- and mid-elevation forests. Forest types were classified by their component percentage of conifer. Four classes were identified: high-elevation boreal forest (> 70% spruce and/or fir), high-elevation boreal ecotone forest (10 to 70% spruce and/or fir), mid-elevation deciduous forests (< 10% any coniferous species) and mid-elevation conifer forests composed predominantly of conifer species other than spruce or fir (> 10% conifer). Non-forested (open) areas of <20% woody cover were separated into two categories based on ground cover type; vegetated (thick ground layer vegetation) and non-vegetated (altered or exposed soil). The "open vegetated" category primarily refers to mountain meadows and heath balds, whereas "open non-vegetated" refers to areas of human-altered condition, where ground cover is disturbed or converted to pavement.

For this study, forest stands of the montane boreal zone composed predominantly (> 70%) of spruce and/or fir trees are designated as spruce-fir. Spruce-fir ecotone (10 to 70% spruce and/or fir) with hardwood types is designated as spruce-fir ecotone. Spruce-fir ecotone with other conifer types is designated either as spruce-fir or other conifer, based on the dominant tree species of the stand. Forests composed of 90 to 100% of deciduous species are designated as hardwood. And finally, areas lacking woody vegetation (> 80% free of tree and shrub cover) are collectively referred to as open. Habitat types were ground checked to correct inconsistencies in aerial photo interpretation.

Observations and Measurements at Roost Sites

Intra-stand conditions were recorded while observing owls at roost sites. Physical and vegetative measurements were taken and micro-habitat conditions around roosts were described. Measurements included elevation, determined using an (ALTIPLUS - K2 digital altimeter) altimeter; slope and aspect, using a (Silva - ranger) compass with inclinometer; and height of forest vegetation layers, determined using the Silva compass and a 30 meter tape. Prominent vegetation layers of the forest stand at each roost site were visually identified and their heights were determined by calculating the tangent of the vertical angle from the observer to a tree top at the mean height for each vegetation layer, then multiplying the result by the distance of the observer, on level slope, from the base of the same tree. In addition to measurements, visual estimates and descriptions of the vegetative characteristics at the roost sites were recorded. The forest structure around roosts was described and the percent closure of each forest layer was estimated. These data are used to assess differences of roosting conditions between two observed roosting patterns (single-use sites, locations of isolated roosts used only once vs. multiple-use sites, locations of roosting clusters).

Analysis

Accuracy assessments of maps

Positional accuracy on two-dimensional map or image surfaces is measured by root-mean square error (RMSE) calculations, where the difference between any mapped point and its corresponding control point is measured both in x and y directions:

$$\mathrm{RMSE} = [(ex^2+ey^2)/n]^{1/2}$$

where: ex is error measured in x direction

and: ey is error measured in y direction

and: n is the number of points considered.

Home range assessments

To determine the placement of home ranges, minimum criteria were created for determining which tagged owls remained in locations for a suitable period of time to indicate territorial establishment. Owls were considered to be holding territories if they were present in an area during 3 or more roost checks and 2 or more nights of tracking.

Though data for day roosting activity extended for some owls into the fall of each year, data for nocturnal movements and foraging activity ended in August. For the proposes of this study, data sets were intended to cover only periods of the breeding season prior to natal dispersal. Therefore, triangulation of nocturnal activity was halted one month after the latest known seasonal record of nesting activity, an unusually late nesting on June 29, 1992 (Mayfield and Alsop 1992). As incubation in saw-whet owls runs 27-29 days and fledging occurs 28 days after hatching (Cannings 1993), this August ending period likely more closely corresponds with the post-fledging period and the beginning of dispersal in most years. In fact, seasonal changes, beginning in July and August, were observed in patterns of roosting for 5 of the radio-tagged adult owls, suggesting the beginning of the post-breeding season. Estimates of home range size must include the spatial use of habitat for both roosting and foraging activities. Therefore, I limit my home range estimates strictly to periods from March/April (depending on the trapping date of each owl) to August, the span of time when data for both night activity and roosting were taken. Only those roosts which were located prior to post-breeding activity of each owl (operationally defined as the point in time when each owl's observed seasonal roosting pattern changed) were used in home range estimates.

Observed changes in seasonal roosting patterns occurred asynchronously among owls, starting as early as mid-July and ending as late as mid-October. Therefore, final dates of roost data included in home range analyses differed for each owl and involved the elimination of all post-July roosts which were out of the breeding season roost area (the breeding season roost MCP) by greater than the mean distance between each owl's roosts for the breeding season period. One roost location was obtained per observation date of each owl.

For analyses of home range characteristics and habitat use, the home range is defined as the 100% minimum convex polygon (MCP) after the previously mentioned triangulation data corrections. One of the owls analyzed (owl 856) made an apparent permanent movement away from the area in which it was trapped mid-way through the breeding season. For this owl, only data of post-translocation roosting and foraging positions were used in these analyses.

To show differences in areas used for roosting and foraging, MCPs for these activities were mapped separately. Overlaps of roosting and foraging MCPs for each owl were calculated using the formulas in Jacobsen and Sonerud (1987):

$$O = 2(AuB)/(A+B)$$

where A is the cumulative nocturnal MCP and B is the cumulative diurnal MCP of owl positions during the breeding season and AuB is the area common to both.

To determine whether sample sizes per owl were sufficient for estimating breeding season home ranges, cumulative area was calculated for each activity and plots of cumulative area to number of dates of data were analyzed for asymptotic condition (Harris et al. 1990).

Seasonal movement patterns

In order to examine changes in movement patterns across seasons, a suitable data set was needed that spanned all periods of observation. Nightly foraging data were collected only during the beginning and mid portions of each yearly observation period (ending in August). Roosting data were collected throughout the observation period and thus represent the best data set for analysis of activity patterns in relation to seasonal changes.

To determine if observed patterns of roosting activity represented a significant difference between breeding and post-breeding seasons, center points of seasonal roost activity were calculated for each owl. All roosting locations were included to calculate breeding and post-breeding roost center points (defined as the harmonic mean of all day roost positions for each period). It should be noted these calculated centers of roosting activity do not correspond with any specific locations of roosting and are only used as markers of central tendency for analysis of seasonal change.

Nesting activity patterns

As previously mentioned, each yearly period of observation extended beyond the known seasonal breeding and nesting periods for saw-whet owls in the southern Appalachian region (accounts of nesting from the southern Appalachian meta-population; Boynton pers. comm., Mayfield and Alsop 1992, Barb 1995). Therefore, assuming any owls in the study nested, data sets of owls likely included records corresponding with the activities and movement patterns of breeding, nesting and post-fledging periods. In order to analyze movements with respect to possible breeding activity, indices of breeding periodicity were identified (based on known periods of breeding activity for saw-whet owls in the southern Appalachian metapopulation). I used the dates of seasonal change in vocal activity, identified through auditory census (Milling et al. 1997), as indices of the estimated nesting period for analysis of movement patterns and identification of possible nesting activity of owls during that period.

Vocal activity early in the breeding season has been identified in other populations as the territorial and mate attraction calls of males (Cannings 1993). From accounts of the nesting behavior of individual males, heavy vocal activity has been recorded up to the time of the hatching of nestlings (Farbotnik 1977, Palmer 1987). Vocal data from our auditory censuses (Milling et al. 1997), conducted on the same mountaintop populations and during the same period as this study, showed general increases in vocal activity until May 26-27 and May 11-14 of 1993 and 1994, respectively. Vocal activity declined dramatically after these dates, implying dates of hatching for those years. Further evidence of nesting periodicity comes from among the few accounts of nesting for the southern Appalachian metapopulation. A nest box study, conducted independently of this project, determined dates of hatching for three saw-whet nests on Roan and Unaka Mountains in 1994 to be from May 15 to 22 (Barb 1995). These hatching dates match closely the 1994 dates of decline in vocal activity observed in our census work (Milling et al. 1997). Though dates of nesting and hatching in a given year likely vary to a greater extent among nesting pairs of the regional metapopulation than are indicated by these two studies, the dates of nesting periodicity from these studies are likely to be an accurate approximation of the nesting period.

Parental activities of males during the post-hatching period consists of feeding nestlings or newly fledged young (Cannings 1993). If owls nested during the year each was tagged, nocturnal movements should show repeated trips to a single location, the site of a nest tree, where the adult male would periodically bring prey items to the nest. Overlays of nightly MCP's that overlap at a single area would be suggestive of this paternal behavior, indicating the possible location of a nest tree. This technique of overlaying nightly activity polygons was used to show the location of an active nest of a Tengmalm's owl (*Aegolius funereus*), a cavity-nesting close relative of the saw-whet (Sonerud et al. 1986). Conversely, if overlays of nightly MCP's indicate no area of repeated use, it is less likely that the male had successfully nested and was engaged in tending a nest of nestlings. Polygynous males might be feeding nestlings at two nests simultaneously (Marks et al. 1989). Though feeding rates may be lower at each nest of polygynous males than those of monogamous males, a study showed that polygynous male Tengmalm's owls typically brought prey to each nest multiple times in a given night

(Carlsson et al. 1987). If the same is true for polygynous saw-whets, parental behavior should still be discernible at one or both of the owl's nests from overlays of nightly MCP's.

Analysis of habitat use

The manner in which owls utilized available habitats was determined differently for periods of nocturnal activity and diurnal roosting. Habitat use for periods of nocturnal activity was analyzed by compositional analysis (Aebischer et al. 1993) using the kernel density estimator (Seaman and Powell 1996). Seaman and Powell (1996) determined that 50 fixes of each animal's location were adequate for minimizing positional variability of core areas about their centers. So, I set acceptable criteria for owl data sets used in compositional analysis to contain at least 5 nights of tracking, which included 50 or more owl positions after triangulation error corrections were made to each data set. The frequency distribution of each owl's night-time locations, computed with Kernelhr software, was used to describe each owl's estimated utilization distribution (UD). Probability contours, which estimate areas of equal probability from the density distribution of points of each data set, were applied to each owl's UD at 10% intervals. These contours define areas at different levels of point density, and in so doing, delimit areas at different estimated intensities of use. Higher probability UD contours (contours of larger area) contain greater percentages of points from each data set. Therefore, using higher probability contours decreases the likelihood of positional error with respect to each owl's true area of use. This bears importance given the positional uncertainty of triangulation data. Additionally, resolutions used for analyses should match resolutions of data sets used to describe and delineate habitats (Merchant 1987). For areas of usage in this study, the size of higher probability UD's more closely matches areas of forest type units (stands) delineated from aerial photos. Therefore, higher probability contours are more appropriate as designators of area utilized by owls in this study.

The percent probability contour, determined from among owl UDs, closest to the mean of points of inflection of contour lines when plotting their size against their percent probability was used to define high-use areas (core areas) of owl night-time activity (Woollard and Harris 1990). This was determined to be the 70% UD contour. To determine if habitat preferences found in high-use core areas hold true at lower intensity levels of use (higher probability contours), a second level of usage was selected to define areas of moderate use. This moderate-use level, though rather arbitrarily based, was identified from among owl UD's as a suitable median area of use between home range MCPs and core area sizes of each owl. This was determined to be the 90% UD.

Usage of forest types for diurnal roosting was analyzed with "conventional" point location methods. Frequencies of owl locations (point data) in each habitat type were used to estimate usage, while proportions of habitat types within each owl's home range MCP were used to estimate availability (White and Garrott 1990). Roosting data sets (7 to 14 roosts per owl) were too small to produce usable utilization distributions for compositional analysis, based on a 30 data-point minimum necessary for detection of core areas (Wray et al. 1992). Therefore, cluster analysis was used to delineate clusters of roosts (areas of concentrated roosting activity) versus scattered roosts (isolated roost locations only used once) for separate analysis of each pattern of roosting (Kenward 1987). Clusters of roosts were formed by initially joining the three roosts of each owl with the shortest mean distance between them into a cluster, then adding roosts based on the nearest-neighbor distance to the cluster. If the mean distance between three other (non-clustered) roosts is less than the distance of the first cluster to its nearest neighbor, than a second cluster is formed by the three. This process continues until a predetermined percentage of roosts for each owl are clustered.

Identification of the forest type at each roost site was determined from overlays of geo-referenced roost data onto the registered aerial photo images. These were checked against habitat descriptions from direct, observational data at roost sites. Roost data sets were too small to run analyses on each owl separately, so roost data were pooled among owls. Proportions of roosts from all owls in each habitat type were compared to averaged proportions of habitat types in all owl home range MCPs combined. The χ^2 statistic was used to determine if forest types were used in proportion to their availability (Neu et al. 1974).

Calculations

Differences in usage vs. availability were analyzed by the Wilks' Lambda (Λ) statistic, which allows comparison of differences for multiple habitats simultaneously (Aebischer and Robertson 1992). The first step in statistical procedures for compositional analysis is a log-ratio transformation of the proportional habitat data to render the data independent:

$$d = \ln(Yu1/Yu2) - \ln(Ya1/Ya2)$$

where d is the difference in the log-ratio of the utilized proportion of habitat 1 (Yu1) divided by the utilized proportion of habitat 2 (Yu2) and the log-ratio of the available proportion of habitat 1 (Ya1) divided by the available proportion of habitat 2 (Ya2). These calculations are determined for all habitat combinations for each owl. The difference (d) in the log-ratio values of each pairwise comparison indicates whether the habitat type in the numerator was used more or less than expected compared to the habitat type in the denominator. If forest types are used randomly, d nears 0, (Yu~=Ya). Positive values indicate greater than expected use. Likewise, negative values indicate less than expected use.

The Wilks' lambda (Λ) statistic is described in Stevens (1996) as:

$$\Lambda = |W|/|T| = |W|/|B+W|, \quad 0 <= \Lambda <= 1$$

where |W| and |T| are determinants of the within and total sum of squares and cross products (SSCP) matrices of habitat type variables. W is the multivariate generalization of the sum of squares and cross products within groups (SSCPw), and thus, is a measure of within-group (individual owl) variability for each variable (forest type). B is the among groups sum of squares and cross products matrix (SSCPb), and thus, is a measure of difference in treatment effects on the set of dependent variables (forest types). T is the multivariate expression of observations in each group about the grand mean (among owls) for each variable (SSCPt).

To calculate multivariate generalizations of within, between and total SSCP, matrices are constructed of all pairwise usage/availability log-ratioed differences for each owl, with determinants of each matrix pooled among owls. Lambda (Λ) is the product of (SSCPw) divided by (SSCPt). The smaller Λ is, the more significant centroid differences are among groups (owls).

Next, lambda is compared to chi-square to determine significance. The F-value is approximated because groups (owls) are greater than 3 and variables (forest types) are greater than 2. The formula for the approximation is taken from Aebischer and Robertson (1993):

$$V = -N \ln\Lambda$$

where V is the F-value (approx.) from Λ, N is the number of groups (owls). The natural log of Λ is found and multiplied by the negative (-) sign of total groups.

Following Wilks' Λ calculations, habitat preferences were ranked for each owl using matrices of all pairwise differences between usage and availability of each forest type. Proportions of forest types within each owl's 70% UD contour and 90% UD contour were compared to those within its corrected 100% home range MCP.

RESULTS

Fifteen owls were radio-tagged during the two-year study, with some data of roosting and/or foraging activity obtained from each (Table 1). The yearly period of telemetry observation (the yearly period of telemetry data capture) spanned from May 17 to December 5 of 1993 and from March 12 to September 9 of 1994. Data taking on individual owls varied within each yearly period (Table 1). For all owls combined, data were obtained from 65 nights of triangulation (totaling 227.25 hours of tracking) and 142 day roosts. Day roost positions were obtained no less than two hours after sunrise or before sunset. Night triangulation typically commenced one half hour after sunset, though sometimes earlier if initial evening bearings of the owl's position (taken to locate the owl before dark and determine the best locations for observers to be positioned for triangulation) indicated that the owl was already active and moving. The time span of each night's tracking period varied. Hours of nightly data taking ranged from 1 to 8.25 hours, averaging 3.75 hrs per night, with fixes of owl positions obtained on some nights during all hours of the night.

Criteria for Analysis of Owl Data Sets

Very limited data were obtained on 4 owls (101, 132, 223, 278; Table 1) of the 15 owls due to a variety of causes. One owl died from apparent predation, one died of unknown causes, one shed its transmitter and one left the area or had transmitter failure shortly after being trapped and tagged. Data from these individuals were dropped from

Table 1. Data of transmittered saw-whet owls. The table shows sex, study area of each owl and periodicity of data obtained from each owl. A question mark in "sex" signifies that morphometric measurements fell within a overlapping range for both sexes, indicating uncertainty as to the owl's gender.

owl radio frequency	^ sex	Mtn. Range	date of initial radio-tagging	date of last record form owl	date span of data (days)	total # day roosts	# triangulation nights
*067/203	M	Blacks	3 Jun 1993	5 Dec 1993	186	19	5
101	M?	Roan	27 May 1993	11 Jun 1993	15	2	0
114	M	Blacks	30 May 1993	18 Sep 1993	111	18	8
132	?	Blacks	2 Jun 1993	6 Jun 1993	4	1	1
176	M	Blacks	3 Jun 1993	15 Aug 1993	73	9	7
185	M	Blacks	12 Mar 1994	2 Jun 1994	82	13	6
223	F	Blacks	3 Jun 1994	11 Aug 1994	69	3	1
260	M	Blacks	2 Apr 1994	14 Apr 1994	12	5	2
278	M	Blacks	19 Aug 1993	11 Nov 1993	84	9	0
*725/880	?	Balsams	22 May 1994	27 Aug 1994	97	18	9
747	M?	Blacks	3 Jun 1994	12 Aug 1994	70	8	9
767	M?	Balsams	28 May 1994	3 Sep 1994	98	5	3
856	M	Balsams	16 Apr 1994	5 Aug 1994	111	13	5
859	M	Roan	23 May 1993	29 Aug 1993	98	12	7
926	M	Roan	17 May 1993	8 Jul 1993	52	7	2
total						142	65

* two owl frequency numbers indicate the owl was retagged with a new transmitter part-way through the data taking period, first number is used to identify owl in text

^ sex determined using the wing-mass DF available from Project Owlnet (Brinker unpubl. manusc.)

statistical analyses and are only discussed in a descriptive manor to indicate any possible conformity or departure from patterns observed in the other owls. Data sets for the remaining 11 owls included 3 or more roost locations and 2 or more nights of triangulation data, which provided minimum criteria for the verification of territorial establishment. These owls were used in descriptive analyses of 2nd order habitat use (home range placement). Of these, data sets of three owls (260, 767, 926) were only of adequate size and duration to indicate home range placement. Data sets for each of the remaining 8 owls spanned all or a major portion of the saw-whet owl's breeding and nesting periods, thus providing information for analysis of seasonal activity patterns. For assessments of home range size and 3rd order habitat use (habitat use within home ranges), roosting and foraging data sets were analyzed separately. Because of this, only 7 owls satisfied the 5 night/50 data point criteria for foraging data alone, thus one of the 8 (owl 067) was subsequently dropped from these analyses.

Map Accuracy and Spatial Data Error

The total root-mean square error (RMSE) of registered aerial photo images ranged from 2.3 to 7.5 pixels. With pixel dimensions of 3 to 4 meters, maximum ground scale error of land feature data was 22.3 to 30.0 meters.

Telemetry error was measured as the difference in angle degrees of observer estimated bearings and true (calculated) bearings to the transmitter. The error angle (i.e., averaged difference between observer estimated bearings and true bearings to beacon transmitters) was 8.97 degrees (1 s.d.= 8.04 degrees). The 95% confidence error polygon

(2 s.d. of the error angle in both directions from the (calculated) true bearing) covered 32.16 degrees. Average distance of receivers to triangulated owl locations was 363m (calculated from bootstrap subset techniques). So, with dual receiver methods at triangulation angles of 40, 93, and 140 degrees (providing a range of the triangulation angles used during the study), the error polygons for average receiver-to-transmitter distances in the study were calculated to be 14.1 ha, 4.19 ha, 6.82 ha, respectively. Given these, the average distance of the calculated transmitter location (intersection of the two bearing lines at the geometric center of the error polygon) to the four corners of the error polygon was 210, 149, and 405 m, for each polygon respectively. The average of these (254.6 m) is the mean maximum linear distance error, a generalized estimate of maximum positional error for triangulated telemetry data in the study.

Home Range and Patterns of Movement

Home Range Placement

Eleven owls, each from one of the three study areas, were tracked during nocturnal activity periods on at least two nights and were observed at diurnal roost sites on three or more occasions. Seven of the 11owls (067, 114, 176, 185 and 747) from the Black Mts. (Fig. 3), owl 725 from the Great Balsam Mts. (Fig. 4), and owls 859 from Roan Mt. (Fig. 5), remained within the area each was trapped, indicating that these owls were well established in their breeding season territories by the time they were radio-

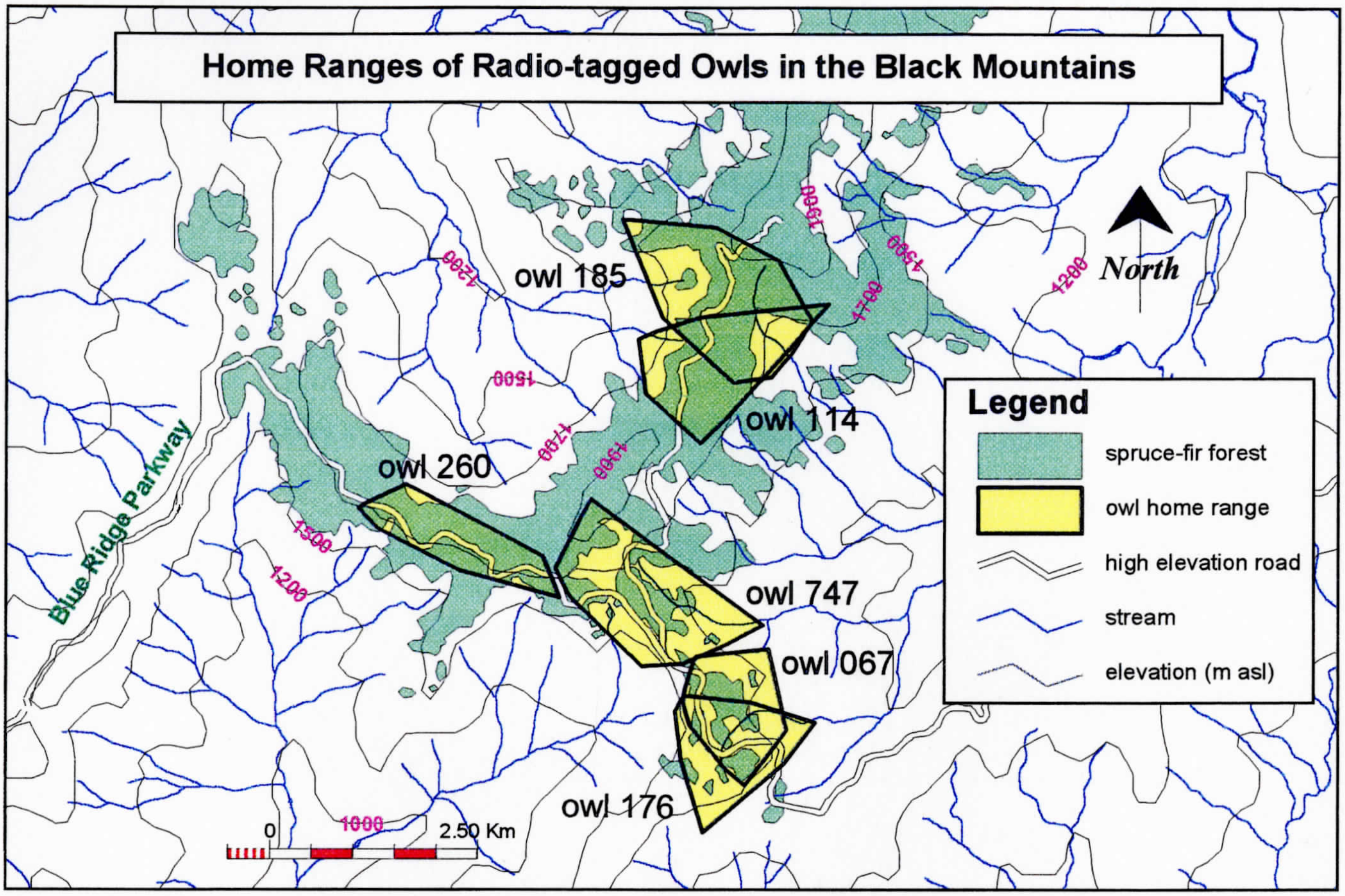

Figure 3. Home ranges of radio-tagged owls in the Black Mountains. Yellow, dark-bordered polygons indicate the 100% minimum convex polygon (MCP) of each owl's movements during the breeding season, the total extent of night activity and day roosting. Owls tracked during 1993 are 067, 176 and 114. Owls tracked during 1994 are 185, 260 and 747. Distributions and extent of spruce-fir (light green) were adapted from Dull et al. (1988). The figure shows the exclusive use of high elevation terrain and the apparent limitation of each owl's movements to areas near spruce-fir forests.

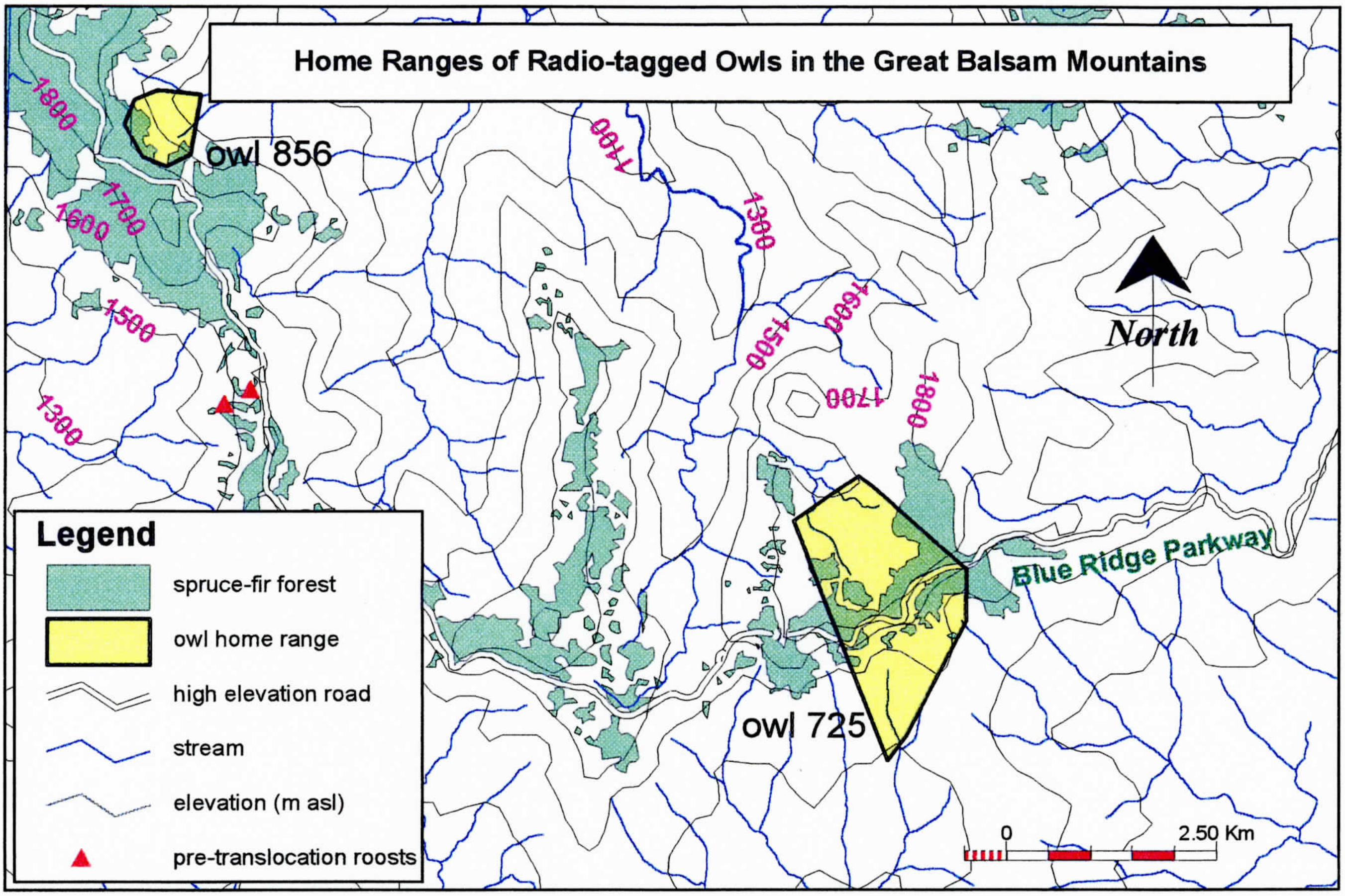

Figure 4. Home ranges of radio-tagged owls in the Great Balsam Mountains. Yellow, dark-bordered polygons indicate the 100% minimum convex polygon (MCP) of each owl's movements during the breeding season, the total extent of night activity and day roosting. Both owls were tracked during 1994. Distributions and extent of spruce-fir (light green) were adapted from Dull et al. (1988). Red triangles identify roost sites of owl 856 before translocation to its final home range (yellow polygon in north west corner of figure). Owl 725 had the largest and owl 856 had the smallest breeding season home ranges of the owls tracked in this study (see table 2). The figure shows the exclusive use of high elevation terrain and the apparent limitation of each owl's movements to areas near spruce-fir forests.

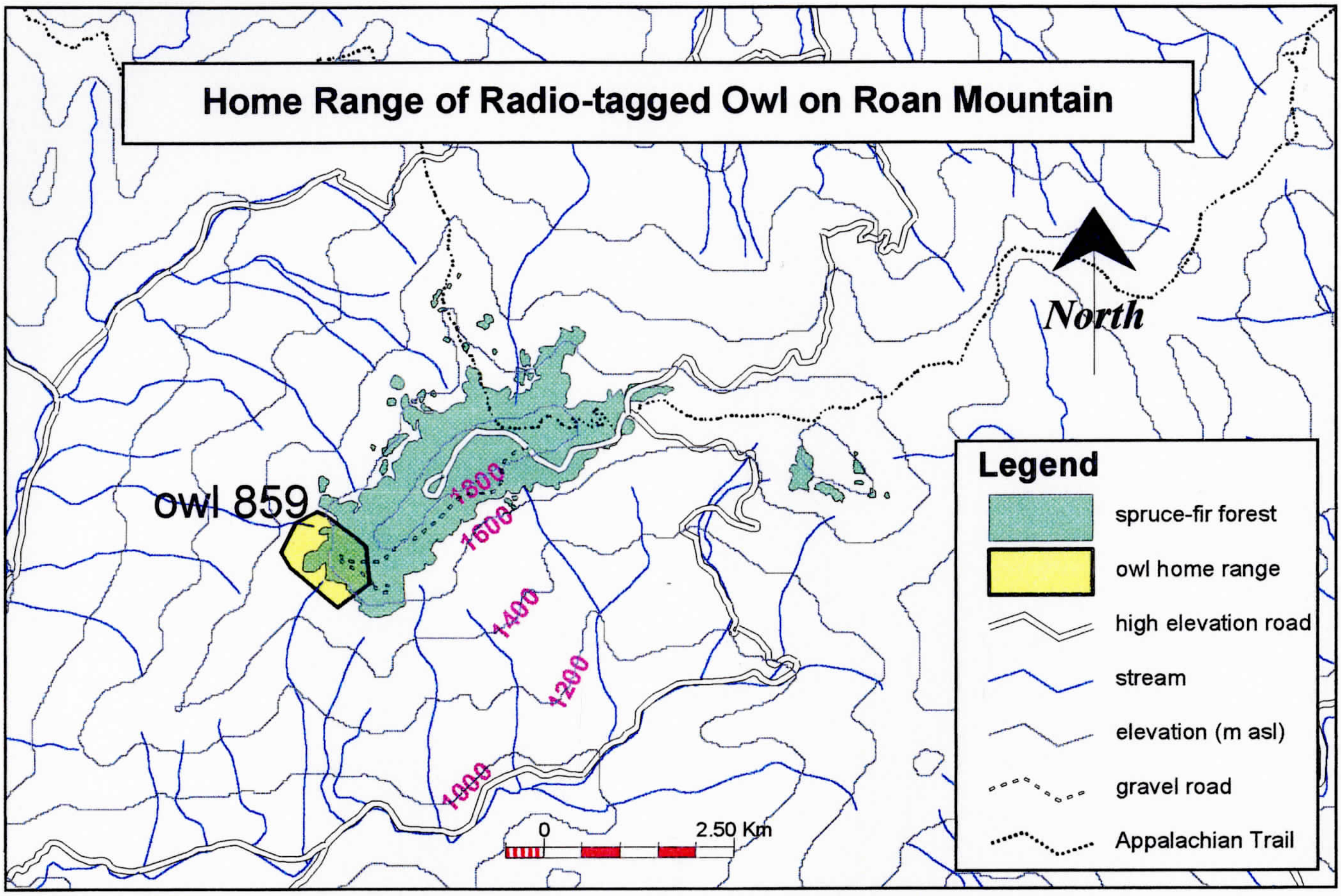

Figure 5. Home range of radio-tagged owl on Roan Mountain. Yellow, dark-bordered polygon indicates the 100% minimum convex polygon (MCP) of owl 859's movements during the breeding season, the total extent of night activity and day roosting. This owl was tracked during 1993. Distributions and extent of spruce-fir (light green) were adapted from Dull et al. (1988). The figure shows the exclusive use of high elevation terrain and the apparent limitation of the owl's movements to areas near spruce-fir forests.

tagged. In support, our census data showed that territories of these owls had been occupied for one to four weeks prior to trapping (Milling et al. 1997). Four of the 11 (owls 767 and 856 from the Balsam Mts., 260 from the Black Mts. and 926 from Roan Mt.) moved away from the area in which each was trapped within a few weeks after the trapping date. The new territories of three of these owls were eventually located.

Home ranges of all 11 owls (including data before and after territorial shifts from translocated owls) were situated at the upper reaches of valley to high ridge elevations of each mountain study area (Fig. 6). Maximum and minimum elevations of home range MCPs for these owls averaged 1775.2 m (range: 1953 m - 1565 m) and 1399.1 m (range: 1592 m - 1225 m), respectively, placing the home ranges of these owls within the upper third of valley to high peak elevations for each mountain range. The range of elevations recorded during nocturnal activity periods defined the elevational limits for 10 of 11 owl home ranges during the breeding season. Elevations of roosts for these owls were generally contained as subsets within the elevations of nocturnal activity. Maximum and minimum roost elevations averaged 1718.8 m (range: 1917 m - 1492 m) and 1510.5 m (range: 1725 m - 1320 m), respectively.

The movements of each owl typically reached the high ridge of the mountain range where the owl was located. In fact, owls in adjacent territories were found to call simultaneously near the crest of high ridge lines during the early part of the breeding season (Milling et al.1997), suggesting that competition among owls for high ground may limit each owl to a short section of ridge line that overlooks its territory. Home ranges typically covered a section of the high ridge and one, but sometimes two, high elevation head water coves (Figs. 3, 4, 5). Minimum roost elevations appeared to be linked to the minimum elevation of boreal forest types within each owl's home range (Fig. 6). While data of night-time movements indicate that most owls moved moderate distances below the spruce-fir zone on some nights, elevational minimums of roosts remained very close to the estimated lower elevational limits of forest stands dominated by spruce within the home range of each owl. Roosting patterns of owls 767 and 926 appear to be exceptions. Activity patterns of these two owls are discussed in later sections (see "Cases of atypical habitat use" in Discussion).

Home Range Size

Home range analyses were conducted for all six owls that had established territories prior to trapping and for one of the four that translocated (owl 856). Data obtained from the other three translocated owls did not meet the data set criteria (5 nights / 50 data points).

Home range size (100% MCP of day roost and night activity data combined) averaged 193.7 ha (range 60.49 ha to 382.8 ha; Table 2). The total area used by each owl for night activity and foraging during the breeding season (night activity MCP) was larger than the total area used by each during the same period for day roosting (roost MCP). Night activity MCPs averaged 175.2 ha (range: 49.62 ha to 382.8 ha) and roosting MCPs averaged 44.6 ha (range 20.51 ha to 103.6 ha). However, roost MCPs were completely contained within the night MCPs for only two of the seven owls. For

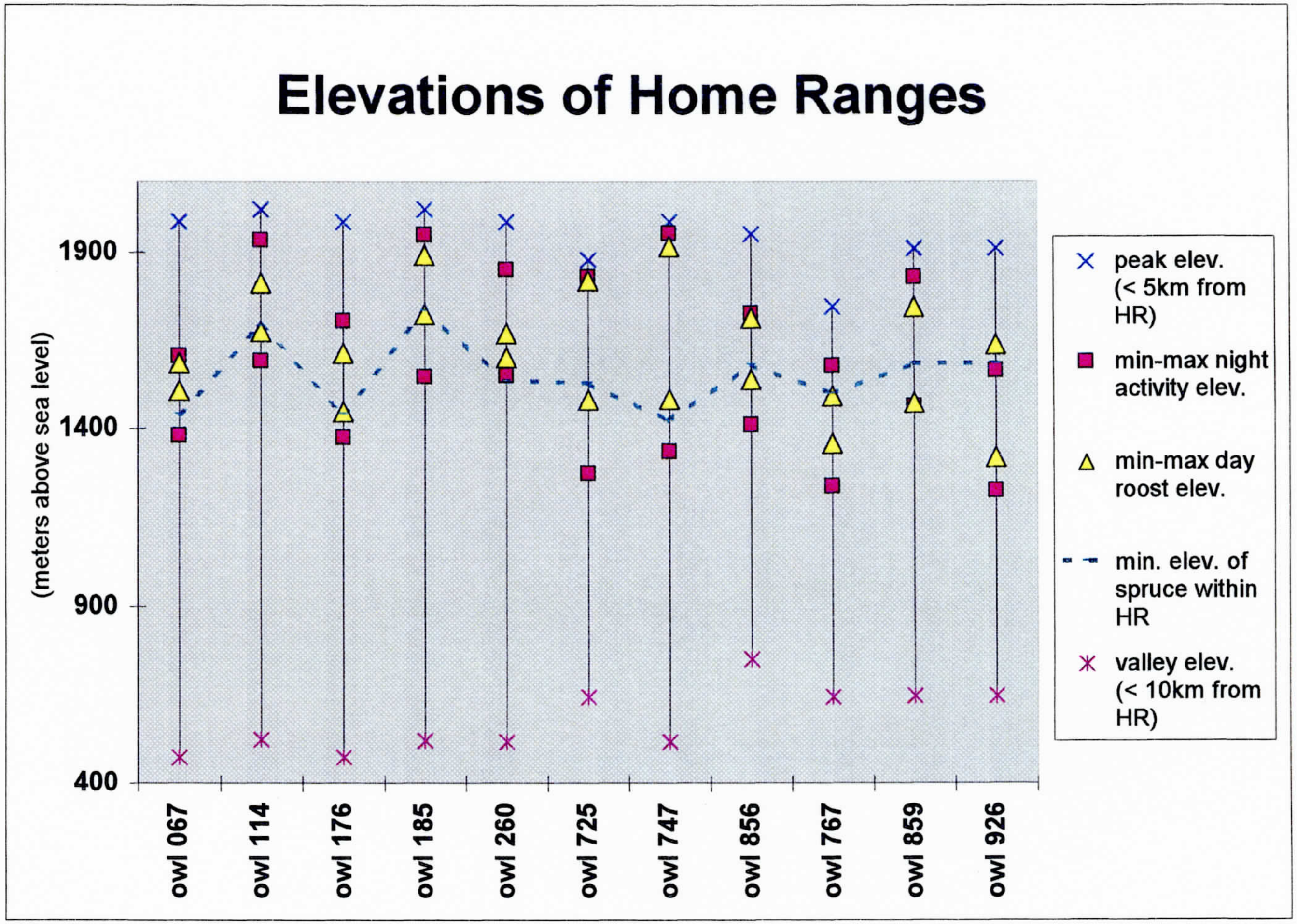

Figure 6. Elevations of breeding season home ranges of radio-tagged owls. The maroon squares indicate the highest and lowest elevations attained by each owl during night-time activity. The yellow triangles show elevational limits of each owl's day roosts. Elevations of highest peaks less than 5 km and of valley areas less than 10 km from each owl's home range are shown by crosses above and below each home range, indicating that breeding season movements of territorial male saw-whets are restricted to the upper half to third of elevations available to them within the southern Appalachian region. Lowest elevations of spruce stands in each owl's home range are indicated by the dashed jagged horizontal line. While night activity for most owls appears to occasionally drop below lower limits of stands composed predominantly of spruce and/or fir, lowest elevations of roosts for most owls were more closely associated with the lower limits of spruce-fir stands. Two owls (767 and 926) were exceptions.

Table 2. Measurements of Home Range Size, Area of Usage and Movement. Table shows parameters of each owl's breeding season home ranges.

	Area of Home Range (ha)				Distance (m)			Elevation (m asl)			Area of Usage (ha)			
owl frequency #	home range size (100% MCP of night and day locations combined)	cumulative night activity area (MCP of night fixes)	cumulative roost area (MCP of roost locations for breeding season)	% of HR used for both activities	avg. dist. between breeding season roosts to (^) roost MCP center	avg. dist. between post-breeding roosts to (^) roost MCP center	dist. between breeding & post-breeding roost centers	breeding season roost center (roost MCP center)	post-breeding roost center (harm. mean of roosts from period)	difference in elevation between breeding and post-breeding roost centers	area of moderate use (90% UD contour)	percentage of home range area covered by moderate use area	area of high use (70% UD contour)	percentage of home range area covered by moderate use area
owl 067	140.1	137.6	40.37	45.25	468	541	1079	1539	1431	-108	*	*	*	*
owl 114	198.5	135.8	37.3	22.58	481	296	894	1744	1846	102	56.2	28.3	16.8	8.5
owl 176	158.3	126.1	40.3	19.25	380	*	*	*	*	*	49.4	31.2	9.3	5.9
owl 185	266.8	241.6	103.6	51.36	540	*	*	*	*	*	177.1	66.4	62.9	23.6
owl 260	*136.7	*131.5	*9.09	*11.48	*	*	*	*	*	*	*	*	*	*
owl 725	382.8	382.8	58.2	26.39	524	715	1254	1657	1403	-254	48.9	12.8	9.5	2.5
owl 747	251.3	251.3	48.6	32.41	474	216	1234	1619	1540	-79	150	36.6	57	13.9
owl 767	*	*	*	*	*	*	*	*	*	*	*	*	*	*
owl 856	60.5	49.6	20.5	39.17	190	*	*	*	*	*	64.2	106.1	37.9	62.6
owl 859	91.4	76.8	32.5	51.21	358	*	1307	1670	1276	-394	42.5	46.5	12.6	13.8
owl 926	*	*	*	*	*	*	*	*	*	*	*	*	*	*
average	193.7	175.2	44.57	33.23	426.875	442	1153.6	1645.8	1499.2		84.04286	46.8	29.42857	18.7

* data set inadequate for measurement

^ roost MCP center - refers to the harmonic mean of roosts from the breeding season the other five owls, the proportion of each owl's day roost MCP which overlapped its night activity MCP ranged from 39.7% to 99.7% (average 79.8%). Additionally, of total area used by each owl (combined areas of roost and night activity MCPs for the breeding season), only 19% to 51% (average 33%) was common to both activities. In the case of this latter comparison (common area of roost and night polygons), the low proportional area in common to both activities suggests that different habitat conditions are selected by owls for roosting vs. foraging.

Activity patterns of owl 856 (the owl with the smallest home range) were unusual for the group. This owl had translocated to its final home range mid-way through the breeding season (see figure 4) and produced very tight foraging and roosting patterns once on the new home range. Explanations for this owl's unusual activity patterns are presented later in this section (see "Patterns of Movement with Respect to Activity" and "Patterns of Movement with Respect to Nesting").

Though the average home range size for owls in this study appears to be similar to breeding season home ranges of two saw-whet owls in British Columbia, Canada (142 and 159 ha; Cannings 1987), results among owls in this study varied widely. To determine if sample sizes were, indeed, adequate for home range estimates, the cumulative areas used by each owl for diurnal roosting and nocturnal activity were plotted separately against number of data taking events (number of nights of triangulation and number of days that roosts were located; Figs. 7 and 8, respectively). The cumulative area of night activity for owls 067, 176, and 114 asymptoted (indicated on the graphs as a leveling off of the cumulative area line of each owl for a minimum of three consecutive

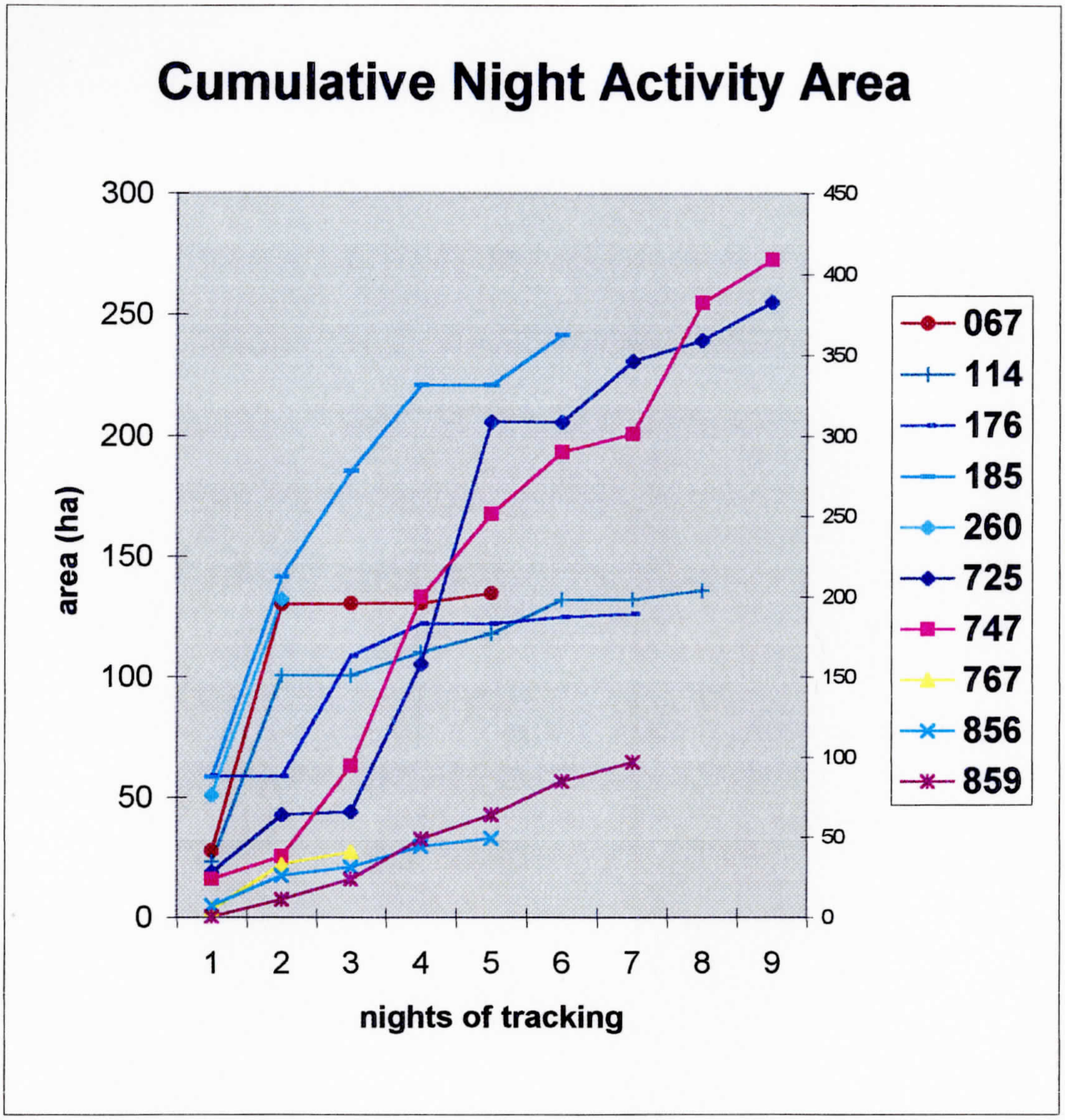

Figure 7. Cumulative area of night activity. Each owl's nightly movements are sequentially combined into a total area of movement through the internal each owl was tracked. Areas used by three owls (067, 176, 114) stabilized after 4 to 7 nights, while areas continued to increase for four other owls (185, 725, 747, 859) after 6 to 9 nights of tracking. Actual seasonal home range sizes only appear to be reached by the former owls. However, data of late season movements from the two owls with the largest cumulative areas (725 and 747) suggest these owls were engaged in post-season movements away from their breeding season home ranges when tracking was halted, thus likely used smaller areas than are indicated during the breeding season alone.

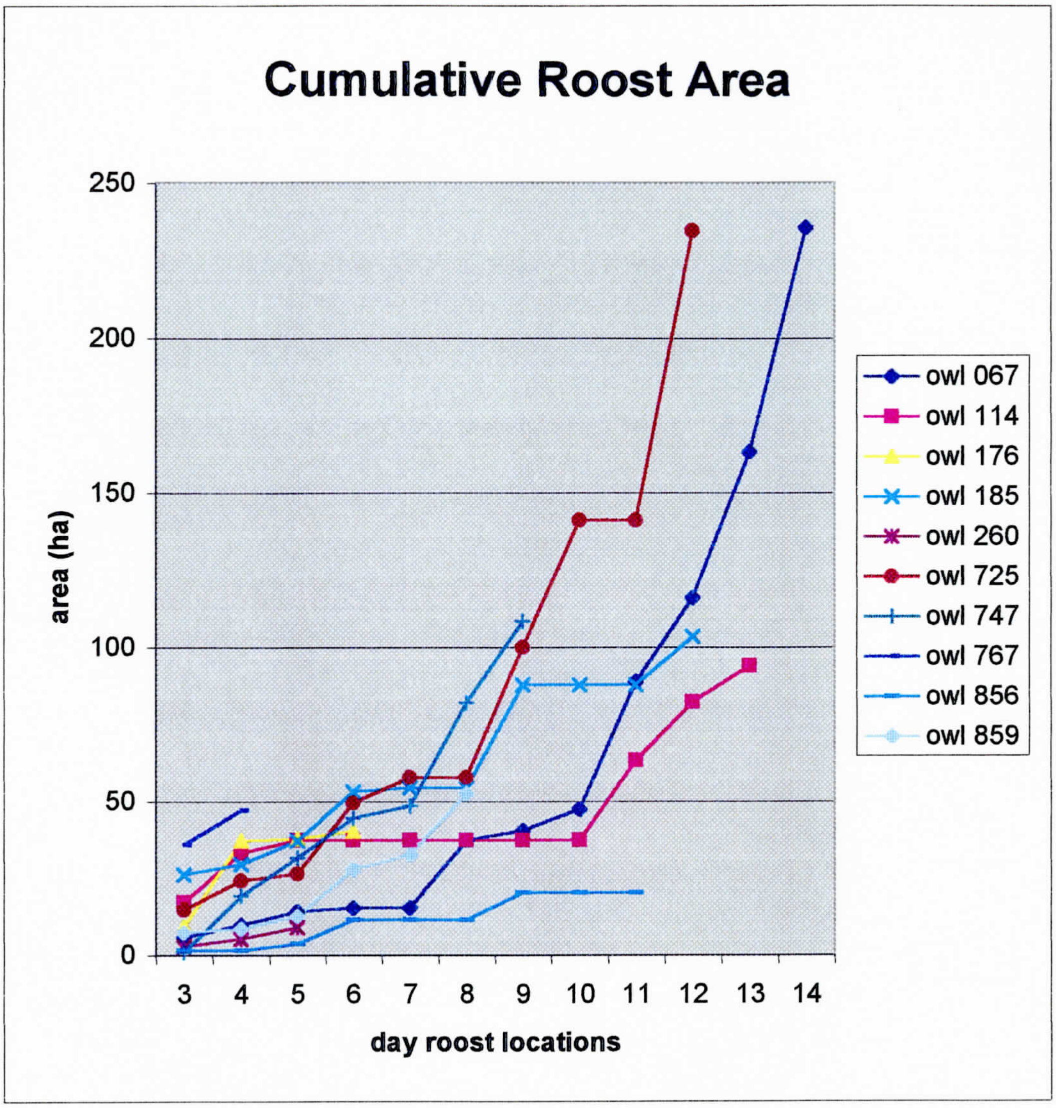

Figure 8. Cumulative area used for roosting. Each owl's roost locations are sequentially combined into a MCP of the area used for roosting through the interval each owl was tracked. Seasonal areas of use do not appear to be reached for most owls. However, data of late summer and fall roost locations suggest owls were engaged in post-season movements and patterns of roosting away from their breeding season home ranges when tracking was halted. Most notably, roosting areas for two owls (067 and 725) tracked into the late summer and fall were exceptionally large compared to roosting areas of owls only tracked from spring to mid summer (176, 185, 856).

data taking events) after two, four, and six nights, respectively. Conversely, the cumulative area of three other owls (owls 185, 725, and 747) showed false initial asymptotes after four to six nights which later increased with additional nights of triangulation. The cumulative area of night activity for two additional owls (856 and 859 - those with the smallest cumulative areas of the group) increased gradually but did not show noticeable asymptotes after five and seven nights, respectively. The roost data essentially reiterated what the night activity data demonstrated (Fig. 8). Asymptotes of cumulative area used for roosting were reached by owl 176 after plotting 4 roost locations and owl 856 after plotting 9 roost locations. False asymptotes occurred for owls 067, 114, and 185, with later increases in roost area with additional roosts. Consequently, the cumulative area graphs give no clear indication that total home range area was reached for either activity by most owl data sets.

Biological periods of mating, nesting, and post-fledging were, as previously mentioned, estimated based on observed changes in calling activity. These biological periods generally correspond with early (March-April), mid (May-July), and late (August) calendar periods of the breeding season. Differences in owl activity among these periods are indicated from night activity patterns (Figs. 9 and 10). Early spring MCPs of nightly activity tended to be larger and extended farther from the center of roosting activity (avg. area = 45.85 ha and avg. distance per night from roost center = 854.3 m; n = 8) than did those of late spring – early summer (avg. area = 21.51 ha and avg. distance per night from roost center = 487.6 m, respectively; n = 40). Nightly activity MCPs of late summer were smaller than those of previous periods, but varied

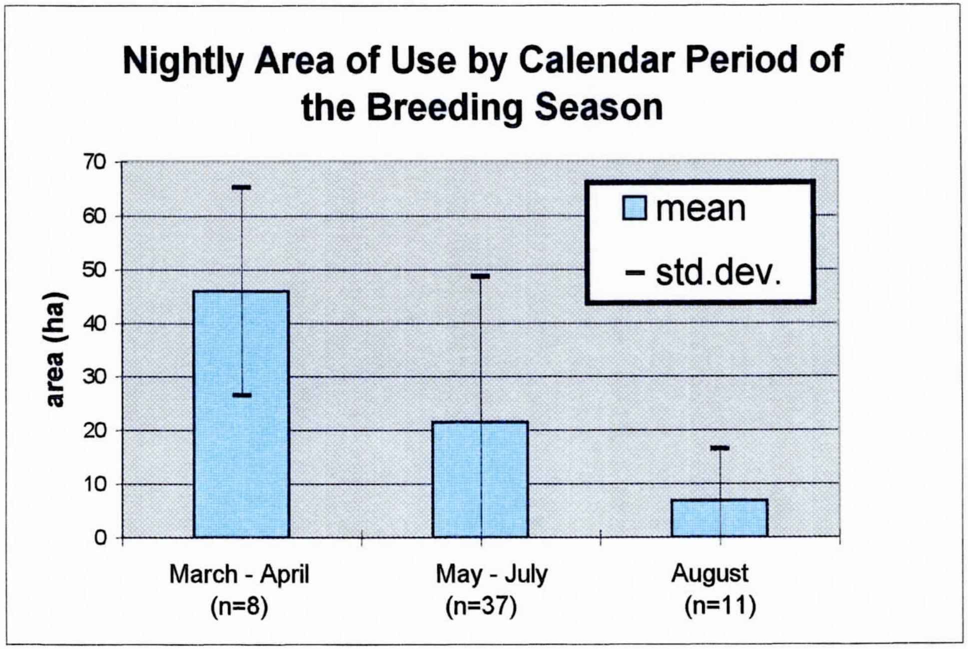

Figure 9. Nightly area of use by calendar period of the breeding season. Comparison of average areas used during nightly activity for calendar periods of the breeding season, which roughly correspond to biological stages (mating, nesting and post-fledging) as indicated by territorial male vocal activity (Milling et al. 1997) and nesting records (Barb 1995).

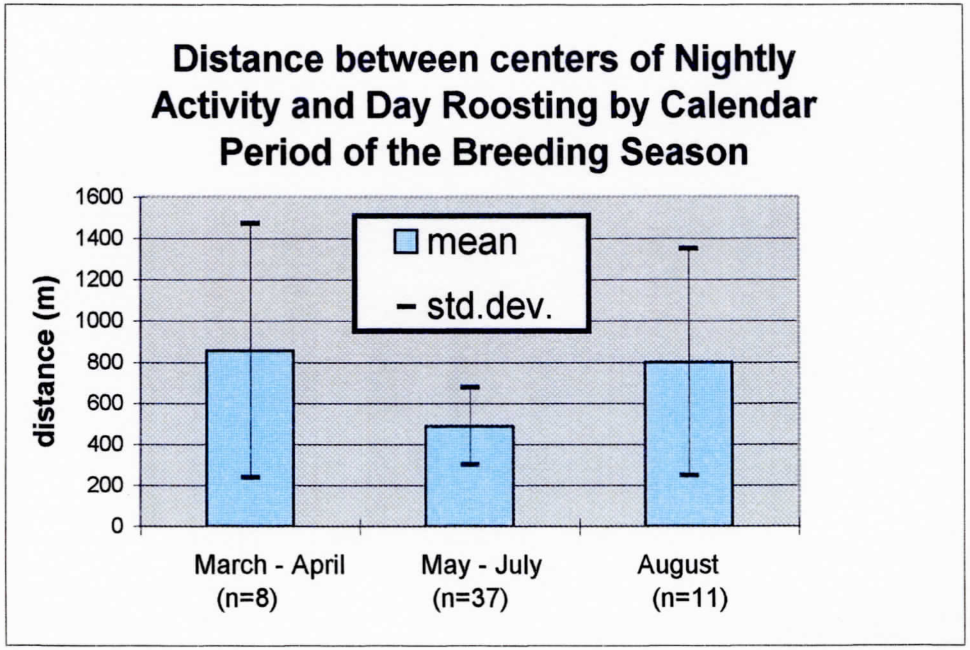

Figure 10. Distance between centers of nightly activity and day roosting by calendar period of the breeding season. Comparison of average distances from areas of night activity to breeding season roosting centers for calendar periods of the breeding season, which roughly correspond to biological stages (mating, nesting and post-fledging) as indicated by territorial male vocal activity (Milling et al. 1997) and nesting records (Barb 1995).

among owls in their distance from the breeding season center of roosting (avg. 6.77 ha and avg. distance 798.7 m, n = 12). Thus, for owls with sufficiently long data sets, differences in patterns of activity among biological periods of the breeding season may have caused cumulative home range sizes to initially asymptote and then later increase as activity patterns changed.

Patterns of Movement with Respect to Activity

Diurnal roost patterns

Initial observations of roosting patterns suggested that owls roosted randomly within their home ranges, apparently lacking any tendency toward a specific stand or area of the home range (Figs. 11 A-H). For example, an owl observed on successive roost searches might be found at opposite ends of its breeding season roost polygon (the roost MCP). Then, on the next roost search, the owl might be found at a site not previously used, or back at or near a site used previously. This is visible from the "criss-cross" pattern of sequential roost locations (Figs. 11 A-H). Distances between roosts on successive searches (2 calendar days apart) ranged from 26 to 1,140 m. By comparison, roosting activity of three saw-whet owls in Idaho showed a similar (scattered) pattern during the breeding season, with a maximum distance between roosts on successive days of 1.8 km (Hayward and Garton 1984). However, for all 8 owls in this study for which roost data covered major portions of the breeding season, patterns of repeated use at one or two stand-sized locations (< 4 ha) became apparent as more roosts of each owl were found during the season.

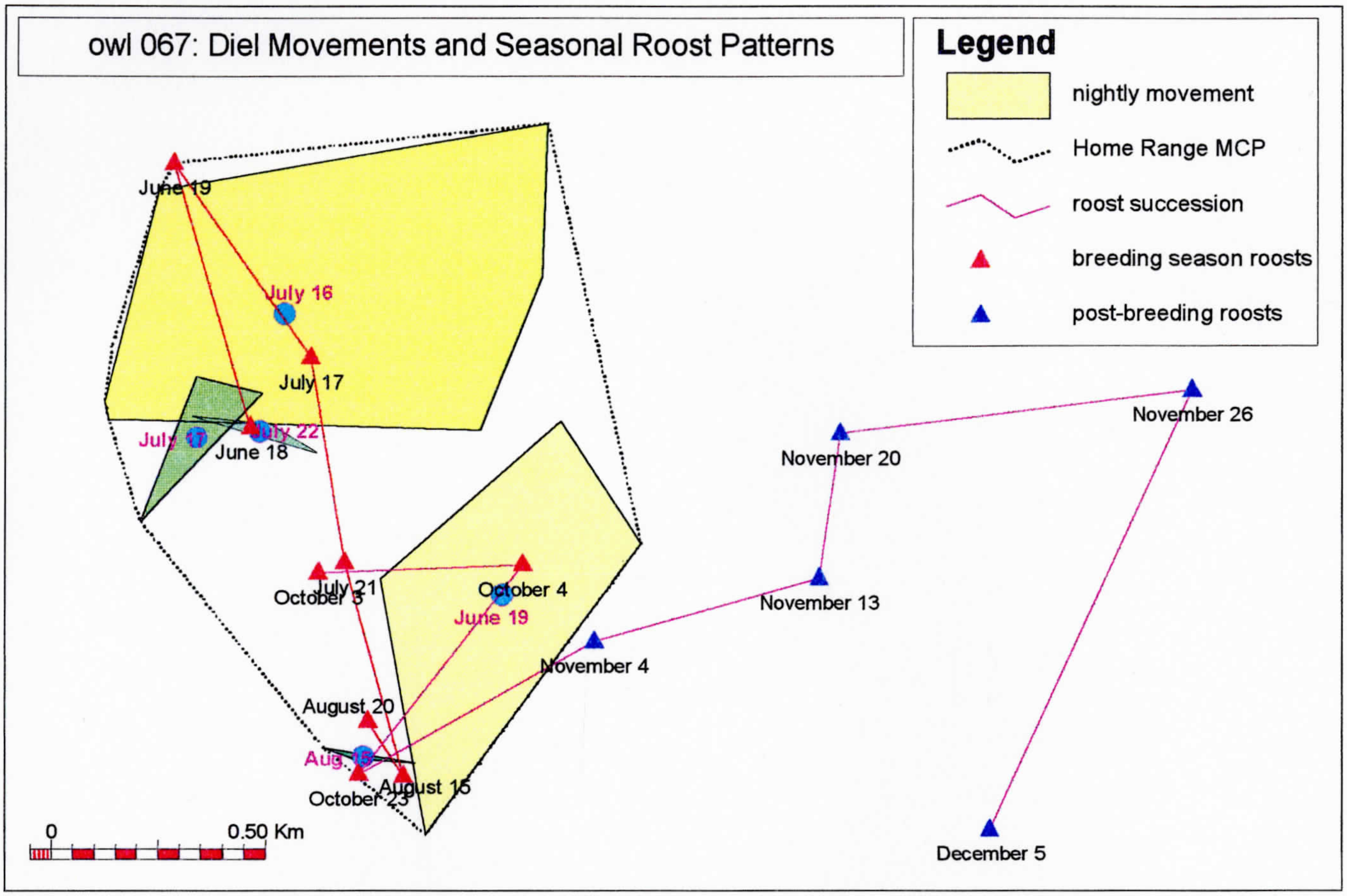

Figure 11 A. Daily movements and seasonal roost patterns of owl 067. The position of day roosts (individual roosts represented by a red, breeding season, or a blue, post-breeding season, triangle) and areas of night activity (individual nights represented by different colored polygons) are displayed in relation to the breeding season home range (represented by a dotted line connecting outer most locations of the owl's seasonal activity). Roosts are connected in chronological sequence by a maroon line. Dates of roosts (black type) and nightly activity polygons (maroon type) are shown.
Owls 067 only met minimum criteria for home range analyses and seasonal movements (see criteria in methods). Thus, maps are not included for this owl in figure sets 12 or 13.

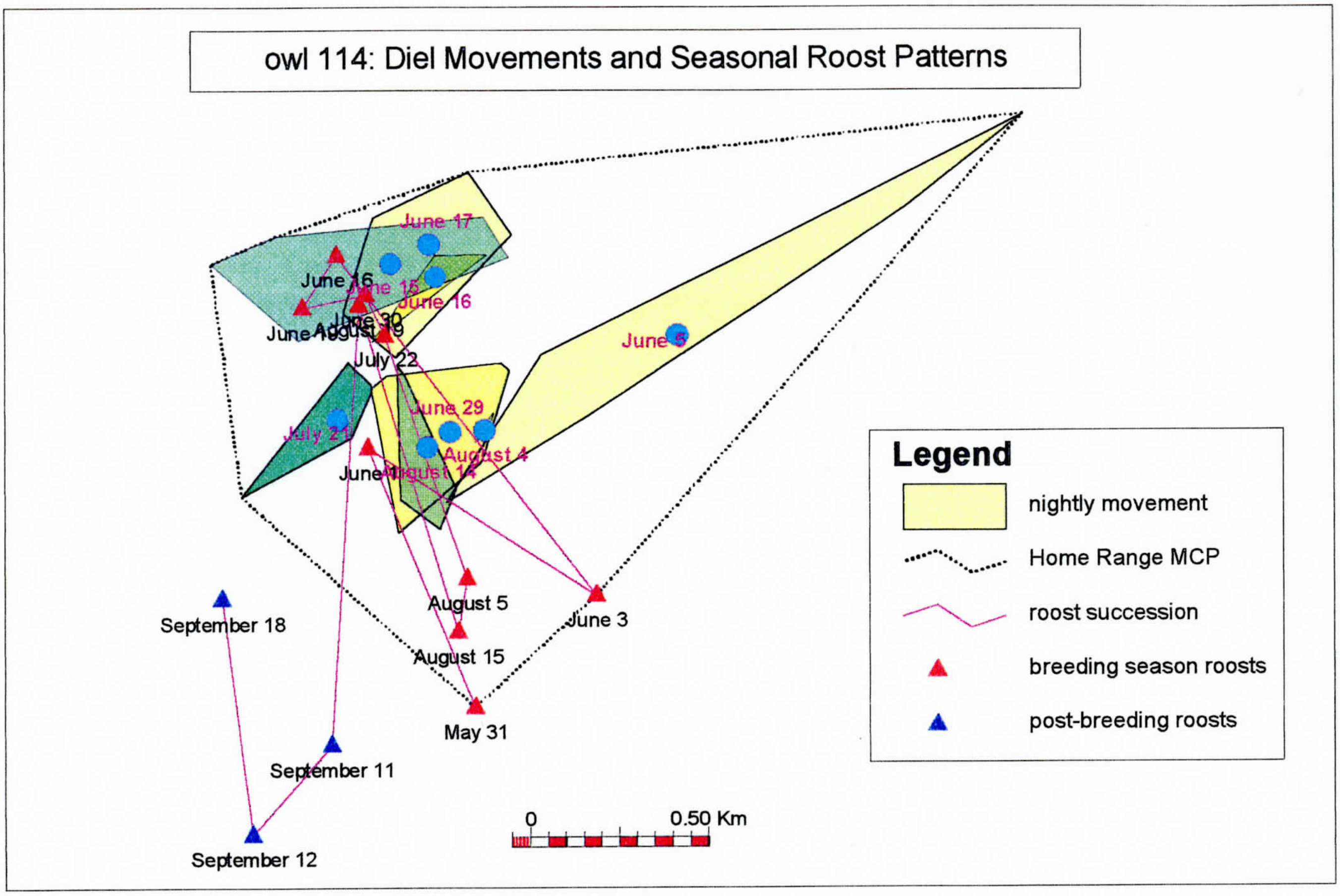

Figure 11 B. Daily movements and seasonal roost patterns of owl 114. The position of day roosts (individual roosts represented by a red, breeding season, or a blue, post-breeding season, triangle) and areas of night activity (individual nights represented by different colored polygons) are displayed in relation to the breeding season home range (represented by a dotted line connecting outer most locations of the owl's seasonal activity). Roosts are connected in chronological sequence by a maroon line. Dates of roosts (black type) and nightly activity polygons (maroon type) are shown.

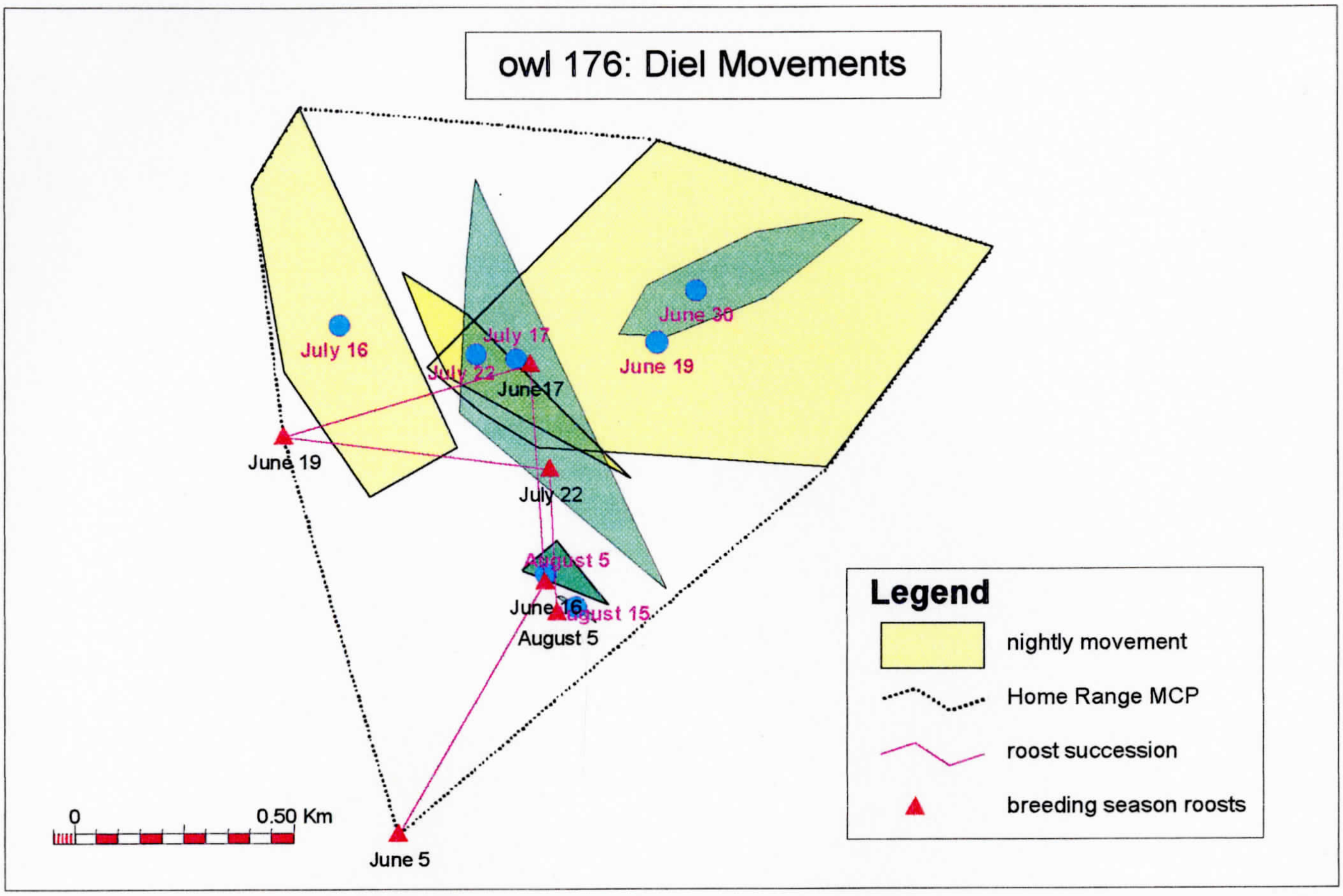

Figure 11 C. Daily movements and seasonal roost patterns of owl 176. The position of day roosts (individual roosts represented by a red, breeding season, or a blue, post-breeding season, triangle) and areas of night activity (individual nights represented by different colored polygons) are displayed in relation to the breeding season home range (represented by a dotted line connecting outer most locations of the owl's seasonal activity). Roosts are connected in chronological sequence by a maroon line. Dates of roosts (black type) and nightly activity polygons (maroon type) are shown.

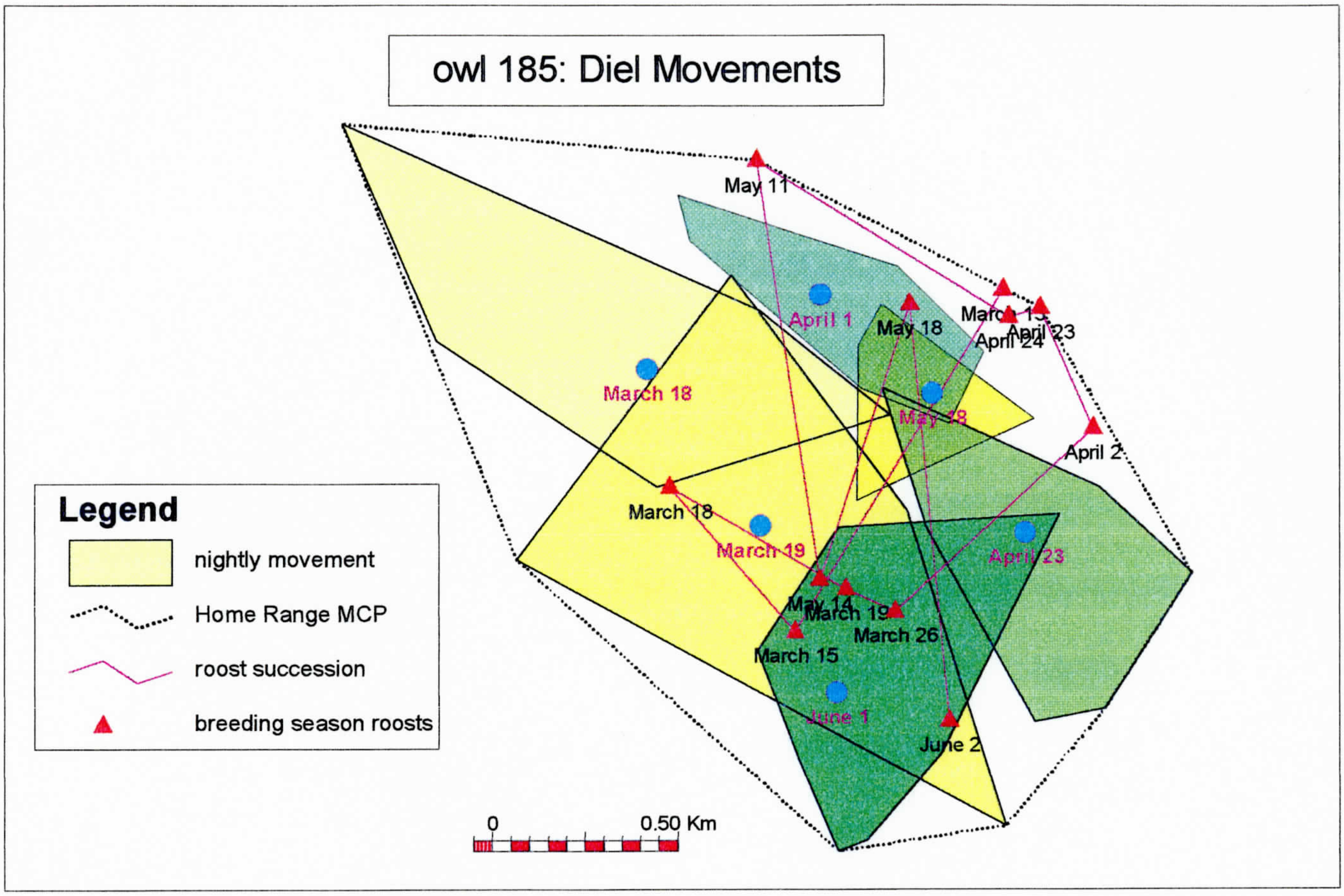

Figure 11 D. Daily movements and seasonal roost patterns of owl 185. The position of day roosts (individual roosts represented by a red, breeding season, or a blue, post-breeding season, triangle) and areas of night activity (individual nights represented by different colored polygons) are displayed in relation to the breeding season home range (represented by a dotted line connecting outer most locations of the owl's seasonal activity). Roosts are connected in chronological sequence by a maroon line. Dates of roosts (black type) and nightly activity polygons (maroon type) are shown.

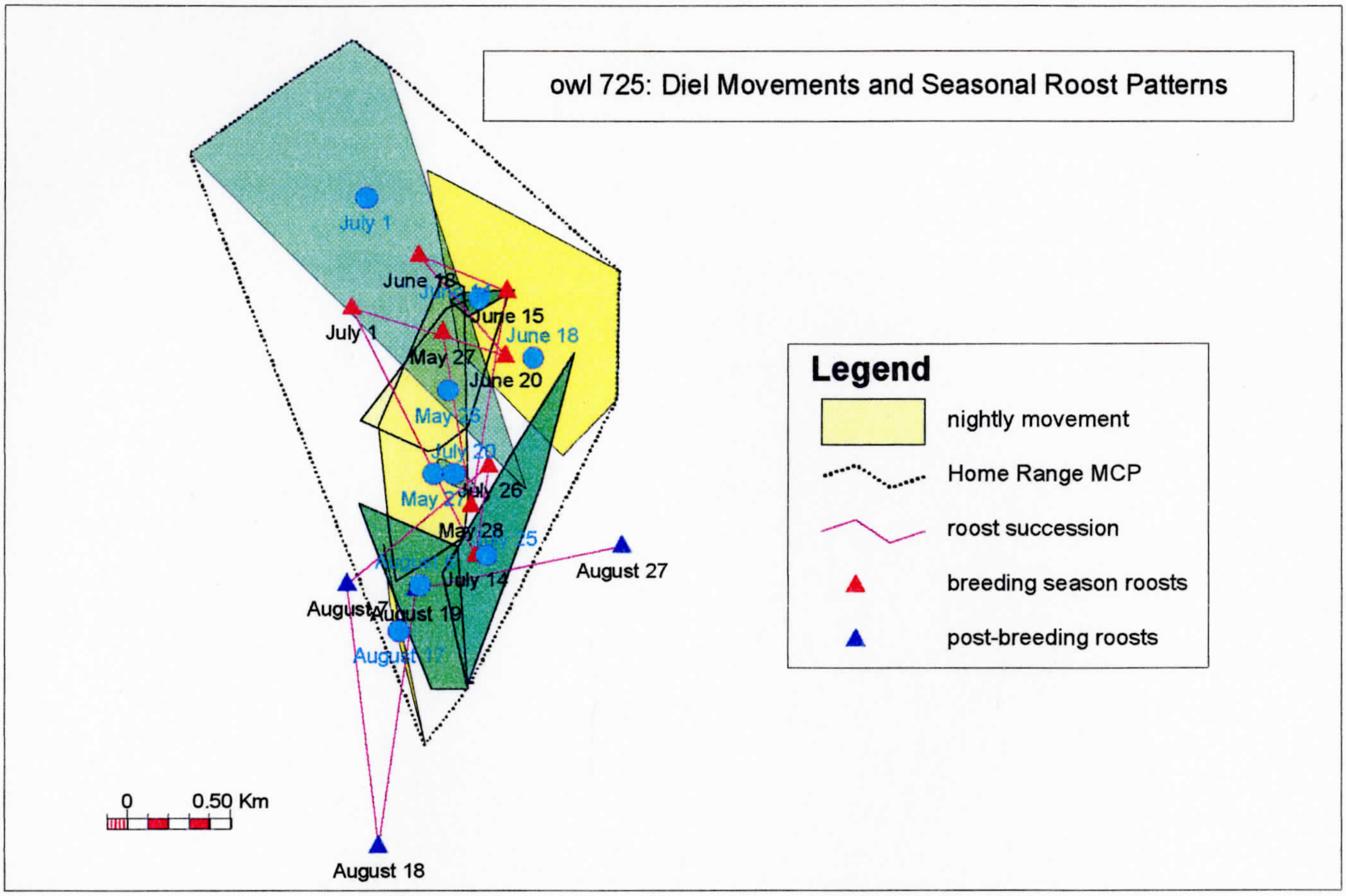

Figure 11 E. Daily movements and seasonal roost patterns of owl 725. The position of day roosts (individual roosts represented by a red, breeding season, or a blue, post-breeding season, triangle) and areas of night activity (individual nights represented by different colored polygons) are displayed in relation to the breeding season home range (represented by a dotted line connecting outer most locations of the owl's seasonal activity). Roosts are connected in chronological sequence by a maroon line. Dates of roosts (black type) and nightly activity polygons (maroon type) are shown.

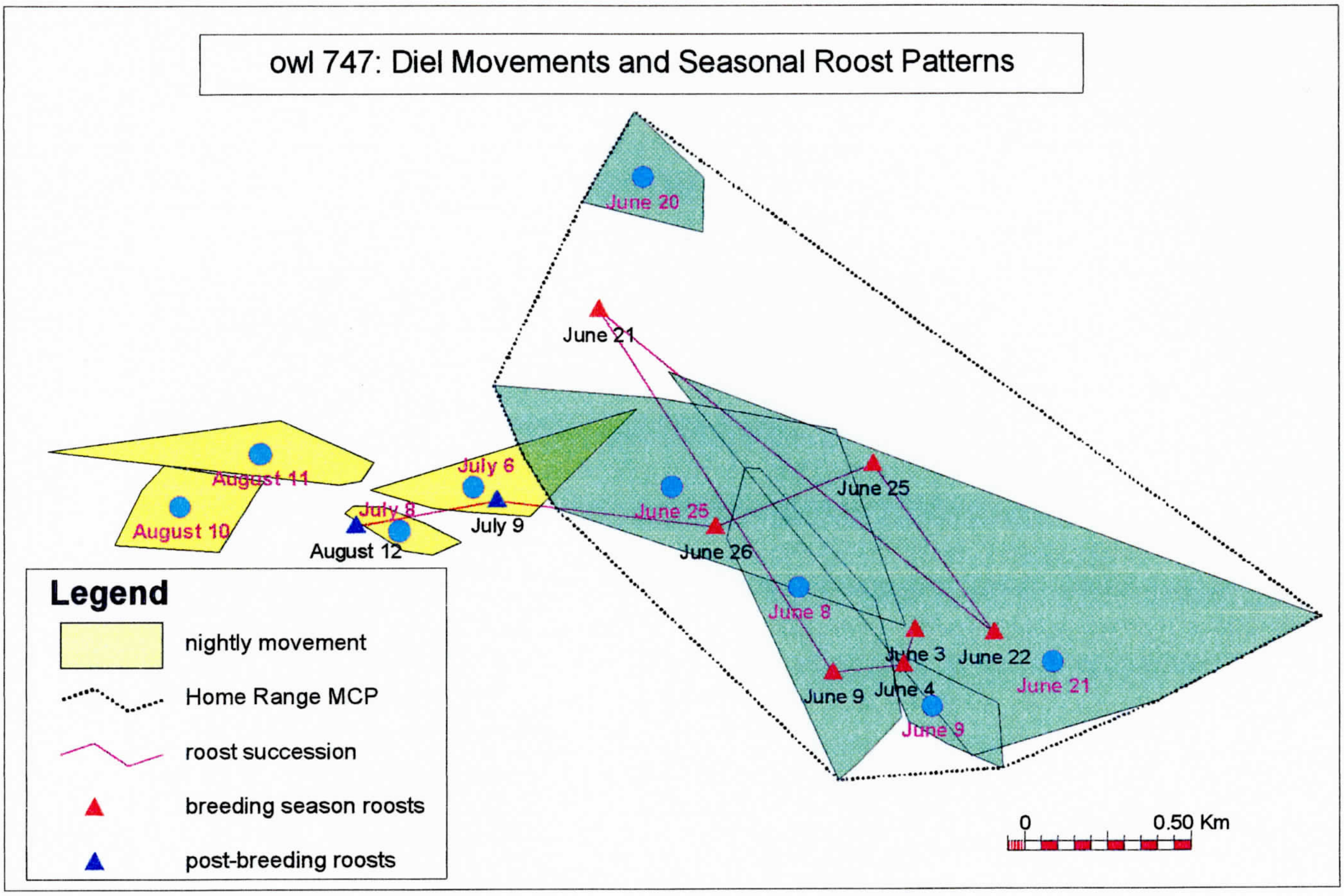

Figure 11 F. Daily movements and seasonal roost patterns of owl 747. The position of day roosts (individual roosts represented by a red, breeding season, or a blue, post-breeding season, triangle) and areas of night activity (individual nights represented by different colored polygons) are displayed in relation to the breeding season home range (represented by a dotted line connecting outer most locations of the owl's seasonal activity). Roosts are connected in chronological sequence by a maroon line. Dates of roosts (black type) and nightly activity polygons (maroon type) are shown.
A post-breeding season shift was observed in both roosting and night foraging activity of this owl, where locations of activity for July and August moved into the home range of a neighboring owl (260; see figure 3). For this owl, night activity polygons in green identify nights before and in yellow nights identify after the post-season shift began.

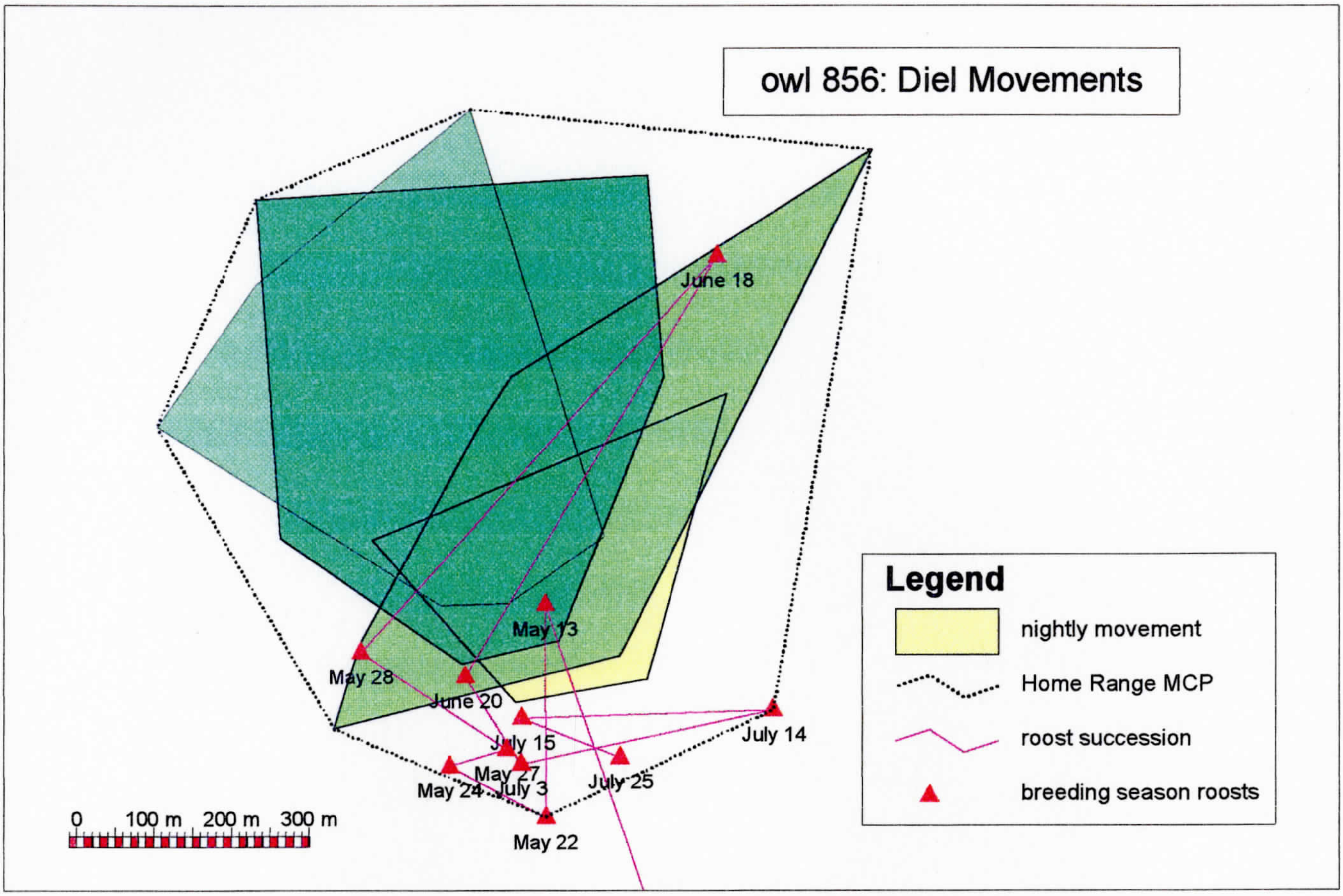

Figure 11 G. Daily movements and seasonal roost patterns of owl 856. The position of day roosts (individual roosts represented by a red, breeding season, or a blue, post-breeding season, triangle) and areas of night activity (individual nights represented by different colored polygons) are displayed in relation to the breeding season home range (represented by a dotted line connecting outer most locations of the owl's seasonal activity). Roosts are connected in chronological sequence by a maroon line. Dates of roosts (black type) and nightly activity polygons (maroon type) are shown.

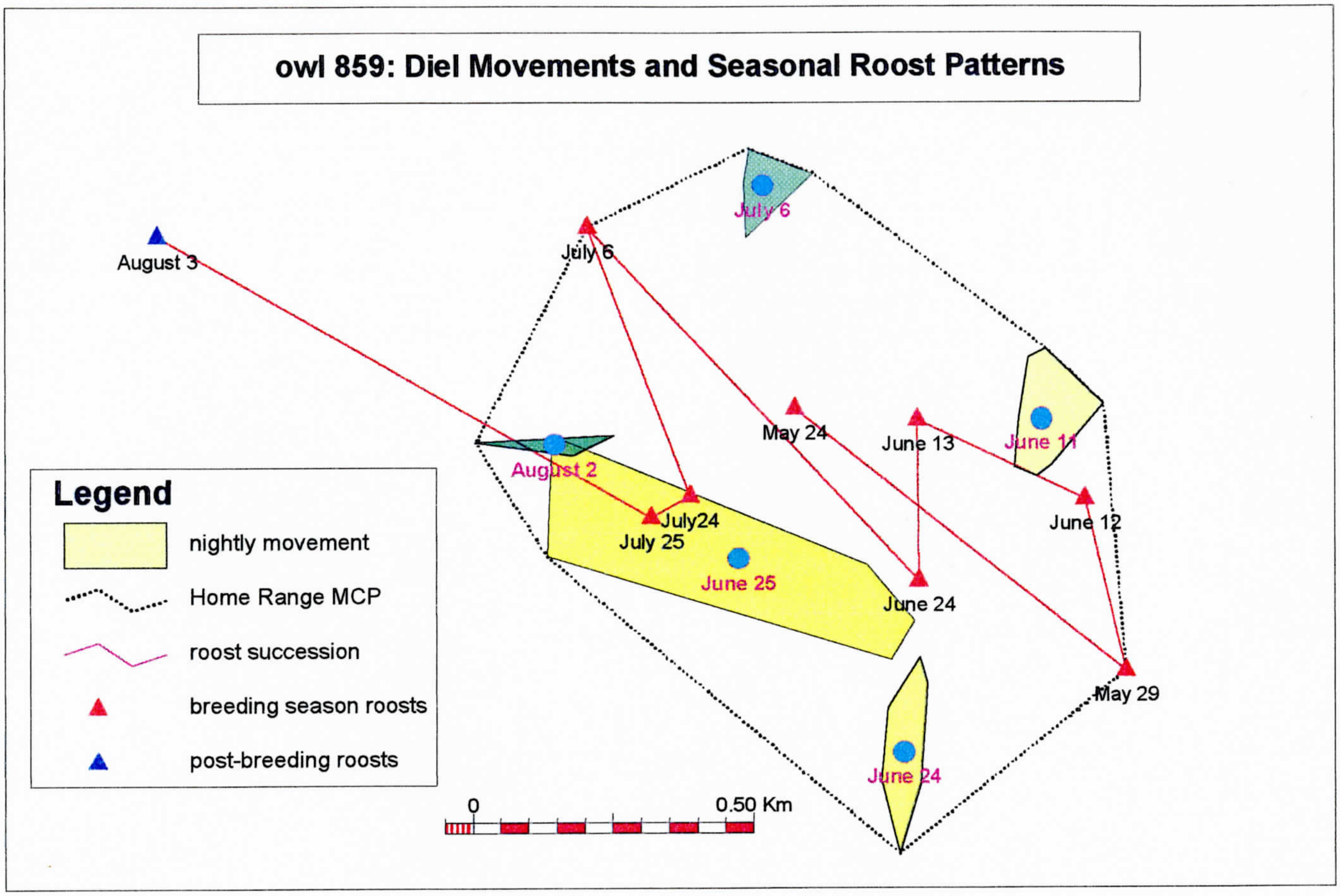

Figure 11 H. Daily movements and seasonal roost patterns of owl 859. The position of day roosts (individual roosts represented by a red, breeding season, or a blue, post-breeding season, triangle) and areas of night activity (individual nights represented by different colored polygons) are displayed in relation to the breeding season home range (represented by a dotted line connecting outer most locations of the owl's seasonal activity). Roosts are connected in chronological sequence by a maroon line. Dates of roosts (black type) and nightly activity polygons (maroon type) are shown.

The most common spatial pattern of roosting observed among owls during the breeding season was that of multiple roost site use, with frequent use of one to two, occasionally three, separate forest stands. These areas of frequent use ("multiple-use" roost areas) apparently afforded each owl the most suitable roosting conditions within its home range. Chronology of roosting activity indicated that owls alternated their use of "multiple-use" areas with roost sites used infrequently or only once (Figs. 11 A-H). For example, figure 11D shows that owl 185 used multiple-use roost areas in the upper right and lower middle portions of its home range on dates (March 13, 15, 19, April 23, 24 and May 14) while roosting at single-use sites on dates (March 18, April 12, May 11 and June 2). single-use sites were typically scattered randomly through the home range, with occasional isolated roosts well away from areas commonly used for roosting and foraging (Figs. 12 A-G).

Distances between roosts at multi-use sites (identified from cluster analysis as 50% of each owl's roosts with the shortest nearest-neighbor distances) averaged 66.4 m (range 2 to 160 m). In contrast, roosts identified as "single-use" sites (identified from cluster analysis as 50% of each owl's roosts with the farthest nearest-neighbor distances) were widely scattered through much of the home range and were often situated farther from areas of concentrated night activity (high-use areas) than were multiple-use sites. Distances between roosts of single-use sites averaged 518 m (range 225 to 786m).

Roosting activity for 7 of the 8 owls (owls 067, 114, 176, 185, 725, 747, 859) followed this multiple site pattern, indicating the absence of a single primary location of

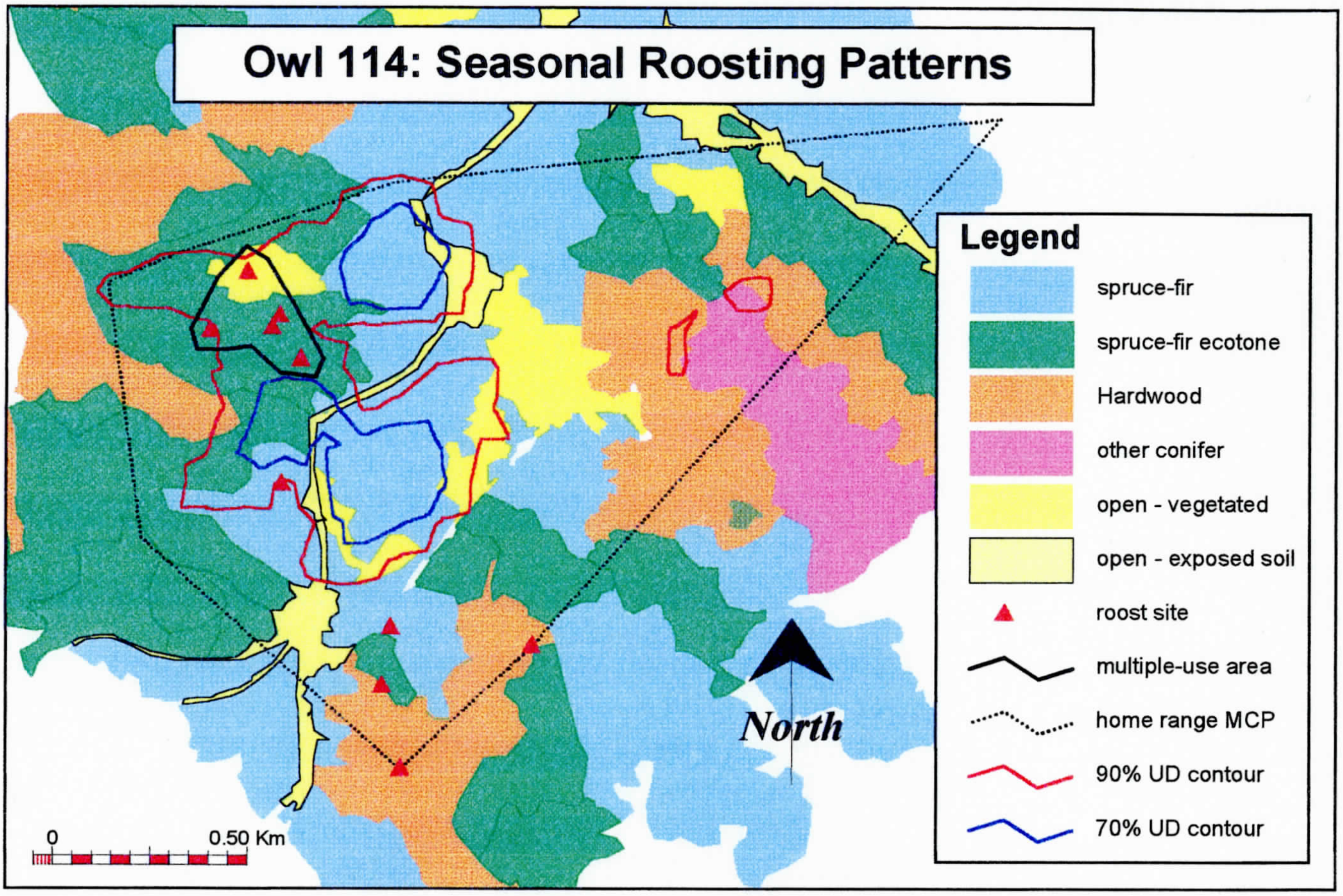

Figure 12 A. Seasonal roosting patterns of owl 114. During the breeding season, owls used 1 to 2 areas multiple times for roosting (area of clustered roosts, red triangles, delineated by a thick black line). Roosts of multiple-use areas were associated with stands of spruce-fir or spruce-fir ecotone with dense lower vegetation layers where owls would commonly perch. Other roost locations (single-use sites, red triangles located outside of delineated multiple-use areas) were more isolated and randomly distributed among forest types within home ranges (dotted black line). Multiple-use roost areas were typically located adjacent to areas used regularly during night activity (high- and moderate-use areas delineated by blue and by red contours, respectively), whereas single-use sites were often found greater distances from areas of night activity.

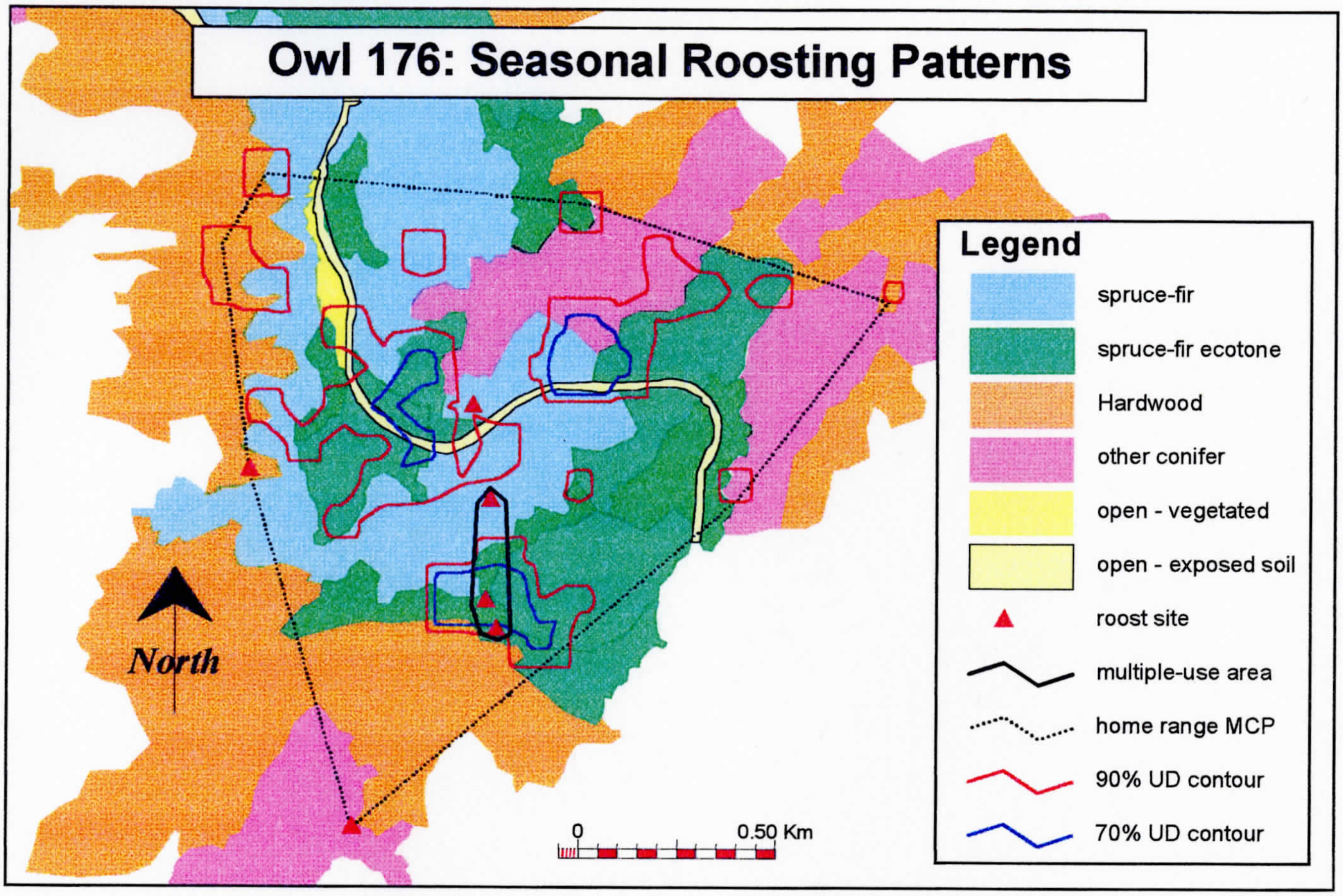

Figure 12 B. Seasonal roosting patterns of owl 176. During the breeding season, owls used 1 to 2 areas multiple times for roosting (area of clustered roosts, red triangles, delineated by a thick black line). Roosts of multiple-use areas were associated with stands of spruce-fir or spruce-fir ecotone with dense lower vegetation layers where owls would commonly perch. Other roost locations (single-use sites, red triangles located outside of delineated multiple-use areas) were more isolated and randomly distributed among forest types within home ranges (dotted black line). Multiple-use roost areas were typically located adjacent to areas used regularly during night activity (high- and moderate-use areas delineated by blue and by red contours, respectively), whereas single-use sites were often found greater distances from areas of night activity.

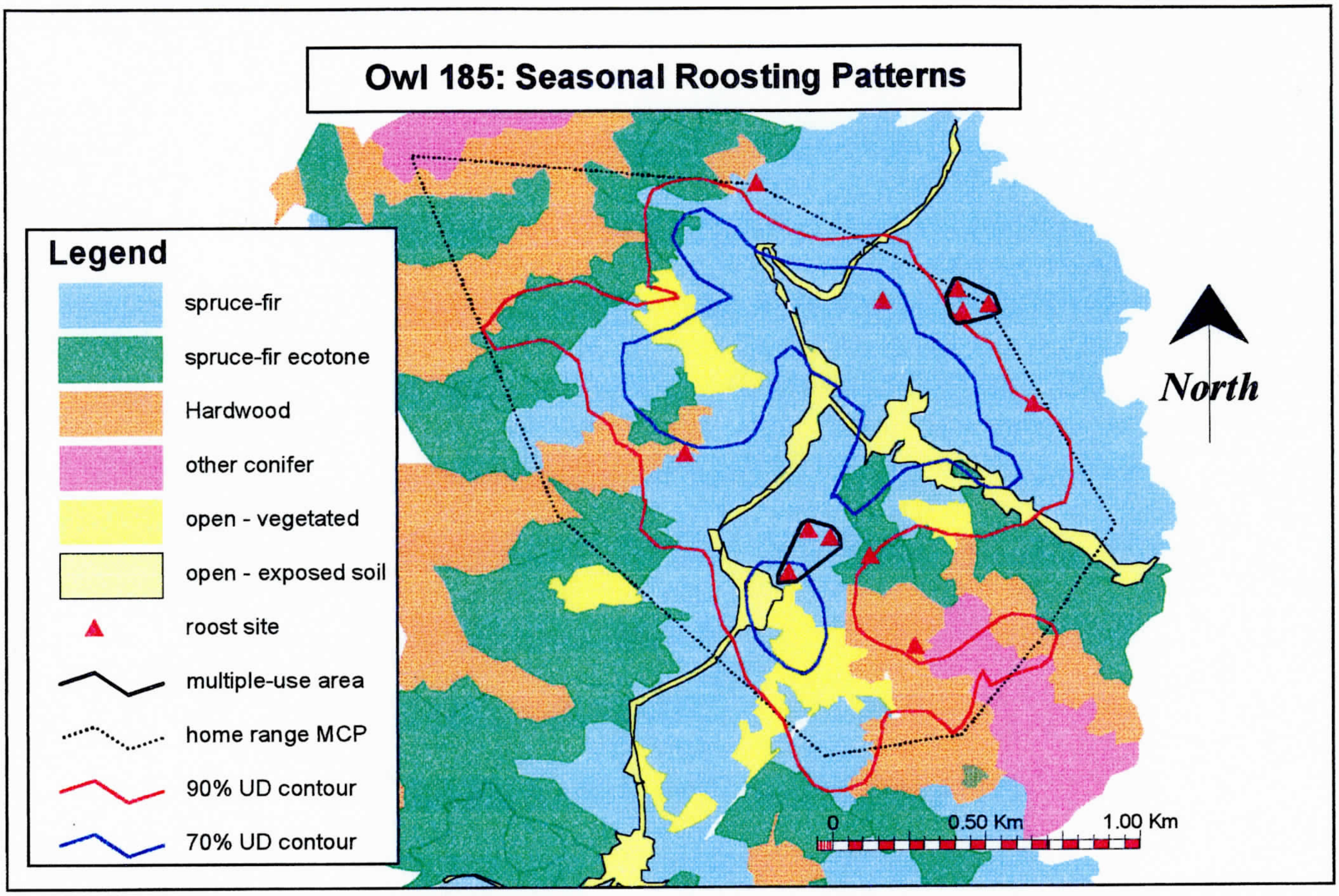

Figure 12 C. Seasonal roosting patterns of owl 185. During the breeding season, owls used 1 to 2 areas multiple times for roosting (area of clustered roosts, red triangles, delineated by a thick black line). Roosts of multiple-use areas were associated with stands of spruce-fir or spruce-fir ecotone with dense lower vegetation layers where owls would commonly perch. Other roost locations (single-use sites, red triangles located outside of delineated multiple-use areas) were more isolated and randomly distributed among forest types within home ranges (dotted black line). Multiple-use roost areas were typically located adjacent to areas used regularly during night activity (high- and moderate-use areas delineated by blue and by red contours, respectively), whereas single-use sites were often found greater distances from areas of night activity.

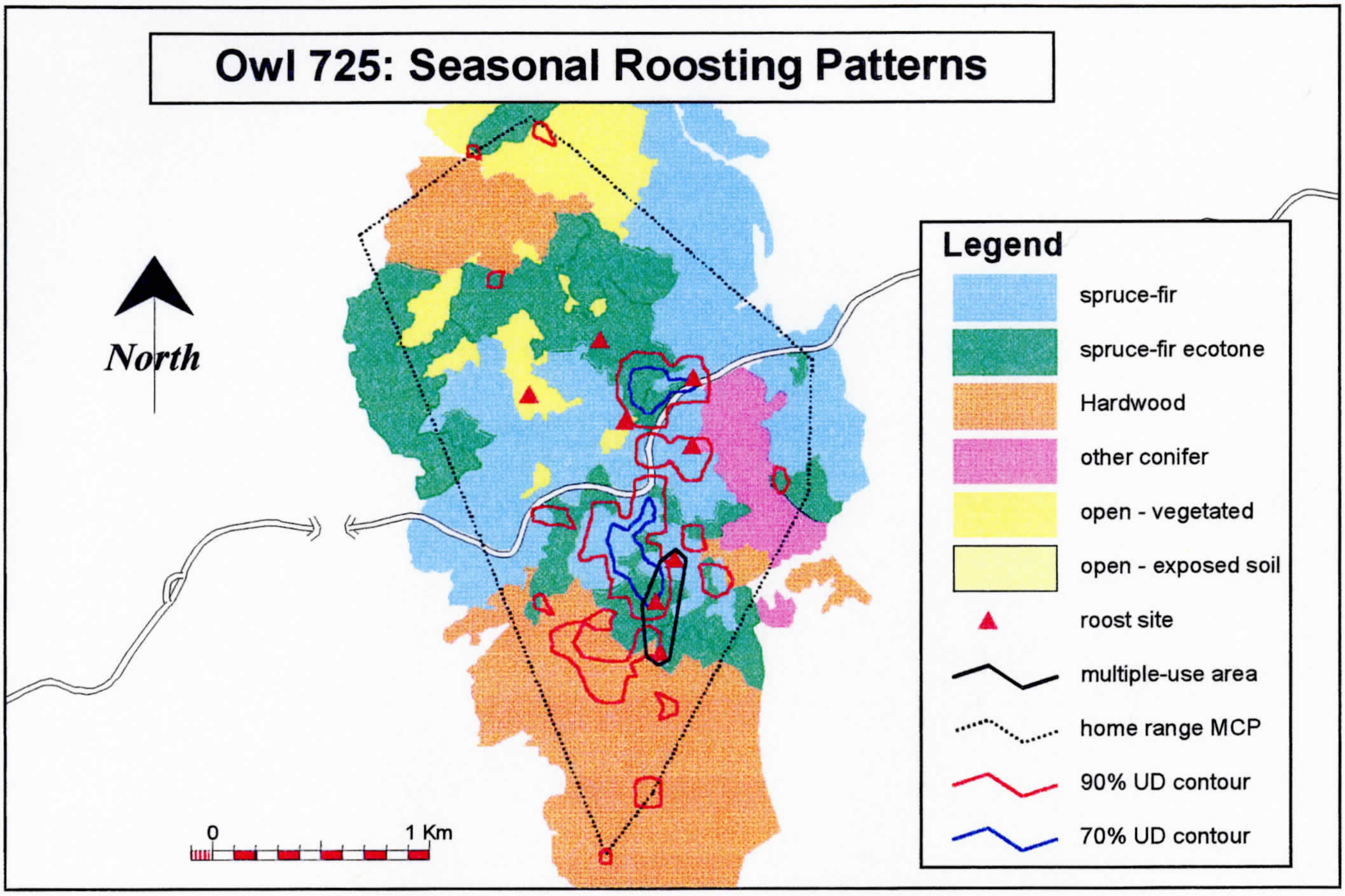

Figure 12 D. Seasonal roosting patterns of owl 725. During the breeding season, owls used 1 to 2 areas multiple times for roosting (area of clustered roosts, red triangles, delineated by a thick black line). Roosts of multiple-use areas were associated with stands of spruce-fir or spruce-fir ecotone with dense lower vegetation layers where owls would commonly perch. Other roost locations (single-use sites, red triangles located outside of delineated multiple-use areas) were more isolated and randomly distributed among forest types within home ranges (dotted black line). Multiple-use roost areas were typically located adjacent to areas used regularly during night activity (high- and moderate-use areas delineated by blue and by red contours, respectively), whereas single-use sites were often found greater distances from areas of night activity.

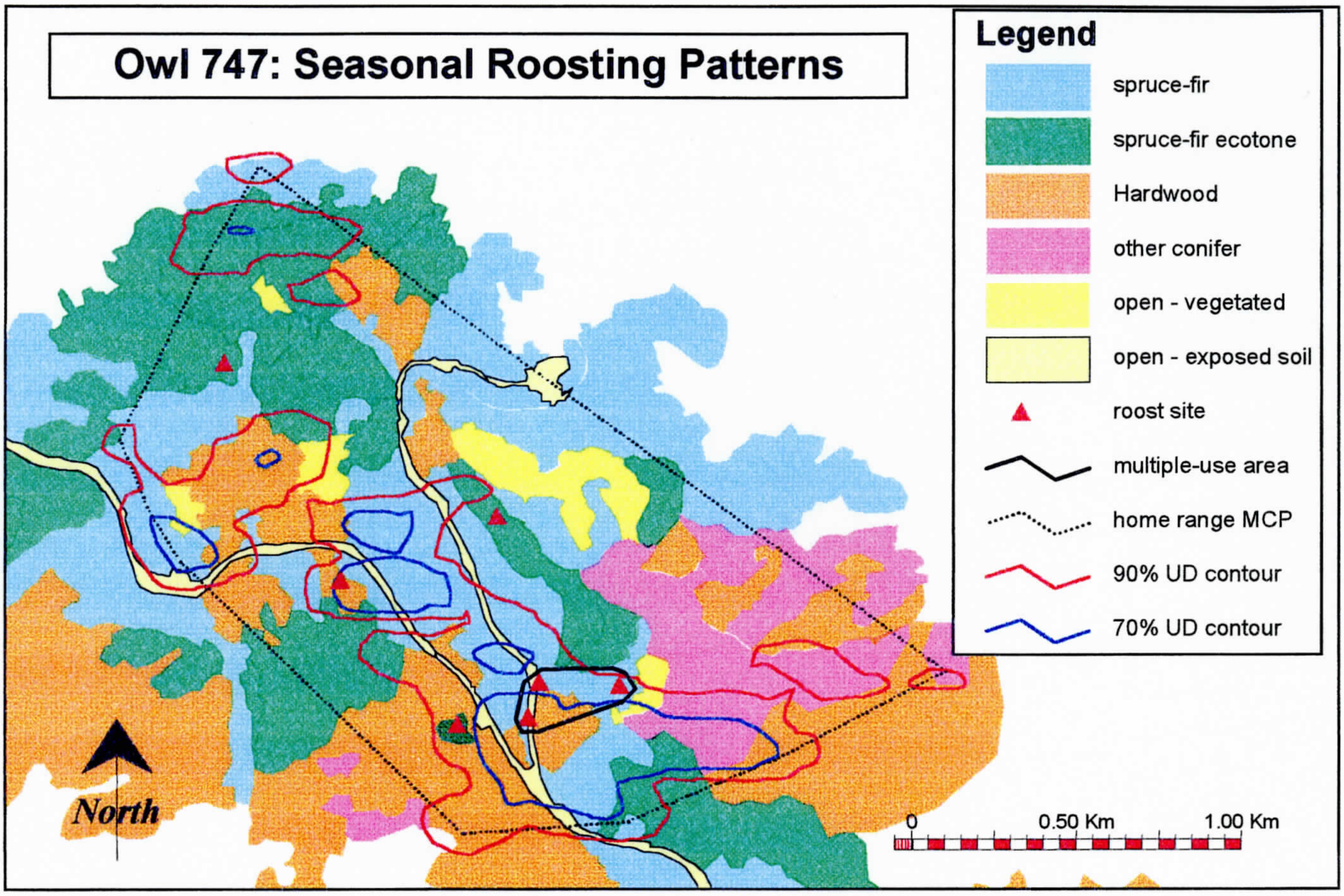

Figure 12 E. Seasonal roosting patterns of owl 747. During the breeding season, owls used 1 to 2 areas multiple times for roosting (area of clustered roosts, red triangles, delineated by a thick black line). Roosts of multiple-use areas were associated with stands of spruce-fir or spruce-fir ecotone with dense lower vegetation layers where owls would commonly perch. Other roost locations (single-use sites, red triangles located outside of delineated multiple-use areas) were more isolated and randomly distributed among forest types within home ranges (dotted black line). Multiple-use roost areas were typically located adjacent to areas used regularly during night activity (high- and moderate-use areas delineated by blue and by red contours, respectively), whereas single-use sites were often found greater distances from areas of night activity.

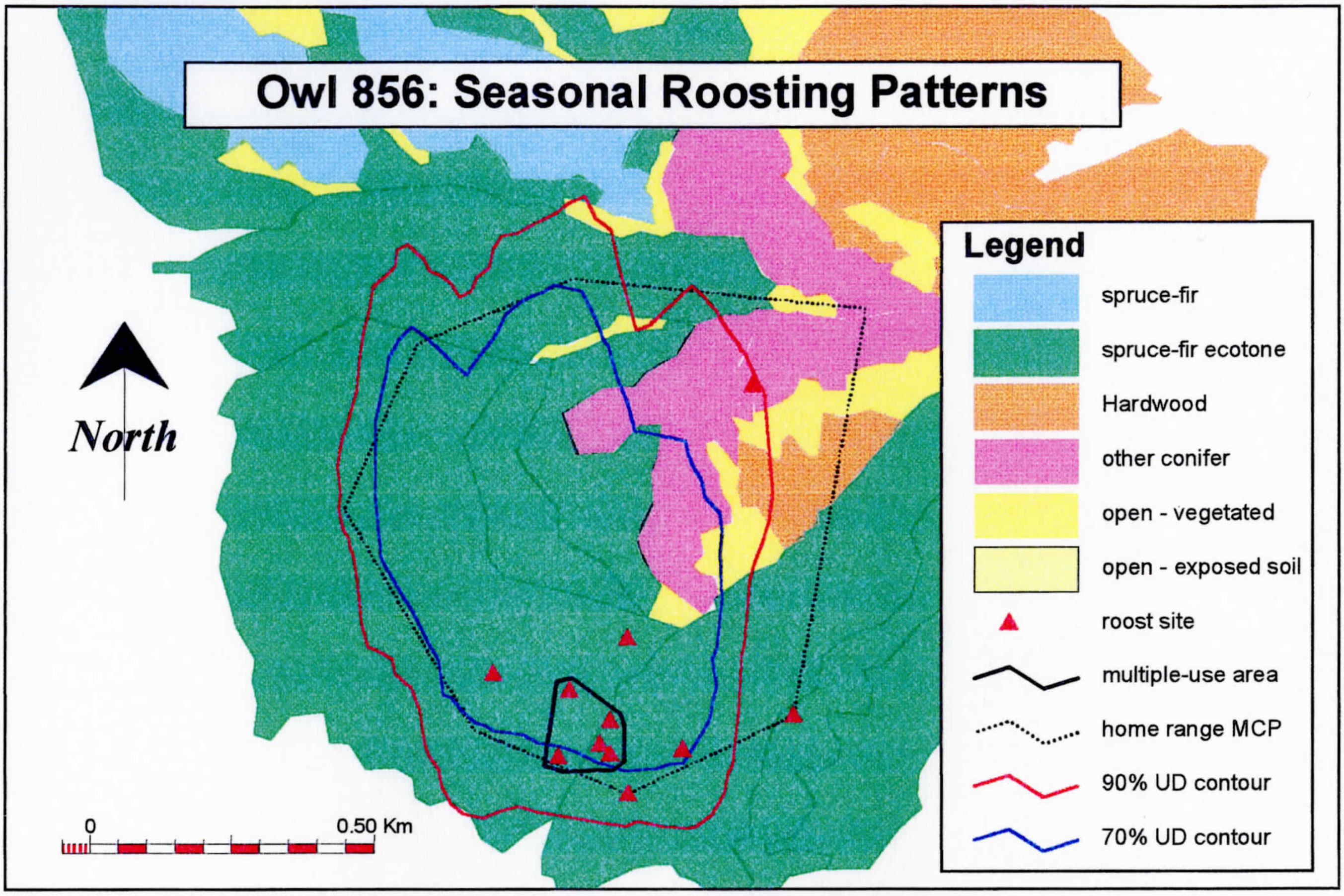

Figure 12 F. Seasonal roosting patterns of owl 856. During the breeding season, owls used 1 to 2 areas multiple times for roosting (area of clustered roosts, red triangles, delineated by a thick black line). Roosts of multiple-use areas were associated with stands of spruce-fir or spruce-fir ecotone with dense lower vegetation layers where owls would commonly perch. Other roost locations (single-use sites, red triangles located outside of delineated multiple-use areas) were more isolated and randomly distributed among forest types within home ranges (dotted black line). Multiple-use roost areas were typically located adjacent to areas used regularly during night activity (high- and moderate-use areas delineated by blue and by red contours, respectively), whereas single-use sites were often found greater distances from areas of night activity.

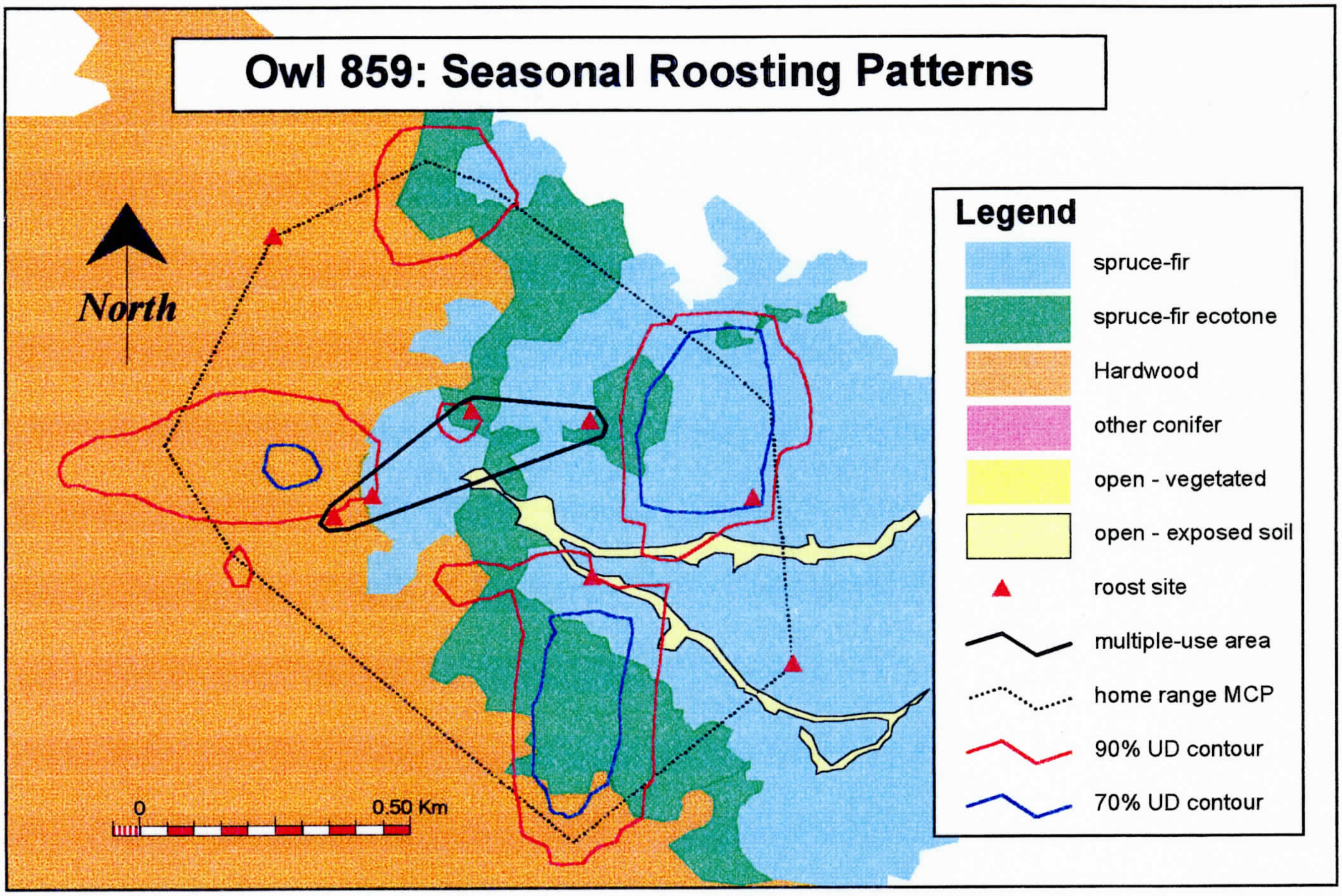

Figure 12 G. Seasonal roosting patterns of owl 859. During the breeding season, owls used 1 to 2 areas multiple times for roosting (area of clustered roosts, red triangles, delineated by a thick black line). Roosts of multiple-use areas were associated with stands of spruce-fir or spruce-fir ecotone with dense lower vegetation layers where owls would commonly perch. Other roost locations (single-use sites, red triangles located outside of delineated multiple-use areas) were more isolated and randomly distributed among forest types within home ranges (dotted black line). Multiple-use roost areas were typically located adjacent to areas used regularly during night activity (high- and moderate-use areas delineated by blue and by red contours, respectively), whereas single-use sites were often found greater distances from areas of night activity.

activity such as would be presumed of nesting. Conversely, roosting patterns of one owl (owl 856) exhibited a regular pattern for the use of a single roost area over consecutive days and weeks (Fig. 11 G). All but one roost of this owl (n=11) were contained within a 7.75 ha area.

Nocturnal activity patterns

The total area used during each nightly activity period (each nightly MCP) varied greatly among nights (0.07 ha to 84.14 ha; Figs. 11 A-H). This variability is likely the result of multiple factors, including seasonal and weather-related responses of the owls (e.g., reduced activity in response to rain events) which have been found to influence distances and rates of movement (Forbes and Warner 1974), as well as non-standardized nightly sampling periods. Because climatic data were not analyzed in relation to owl activity and the nightly period of owl tracking was not standardized, possible reasons for the variability in areas used nightly should be treated with some caution.

Patterns of night activity show that owls typically use 2 to 4 areas of their home range on a heavy or frequent basis (Figs. 13 A-G). These areas of high use (core areas, delimited by the 70% UD contour) were typically located close to areas of concentrated roosting (multiple-use roost areas), suggesting a concentrated pattern of foraging activity near areas used frequently for roosting but not necessarily within the same forest stands (Figs. 12 A-G). The movements of owls within core areas (presumed to be those of normal foraging activity), were typically composed of short, infrequent or sporadic movements within a limited area for periods of one to four hours (Figs. 14). As with other eastern forest owls, saw-whets are perch-and-pounce type hunters that wait on low perches for small mammals to expose their locations (Cannings 1993). While hunting, owls move only short distances between perches. The comparatively long intervals of time per bout owls spent at core areas and the minimal movement (comparative distance between successive triangulation fixes of owl positions within and outside of core areas; Figs. 14) while at these areas suggests that owls were primarily foraging at these high-use areas. Hayward et al. (1987) came to the same conclusion from very similar night activity patterns of boreal owls (*Aegolius funereus*).

In contrast to foraging patterns of movement, some owls were observed, primarily early in the breeding season, ranging far from normal centers of activity during brief but highly mobile bouts. Movements of owls while on these highly mobile bouts (extended forays) were quicker and covered more distance between triangulation fixes than did movements presumed to be those of normal foraging (Figs. 14). Of three owls, for which at least one night of radio tracking indicated an extended foray, distances between consecutive triangulation fixes during apparently normal foraging activity averaged 137.5 m (n=75). Distances between triangulation fixes while owls were on forays averaged 518.2 m (n=28). Additionally, average distances of nightly activity centers (harmonic mean of each night's triangulation fixes) from the home range center (the harmonic mean of each owl's roosting locations within the breeding season roost MCP) were different between the two activities. The average distance from roost center to nightly activity centers for nights of normal foraging was 388.1 m (n=18), while the average distance for nights when forays were observed was 850 m (n=3).

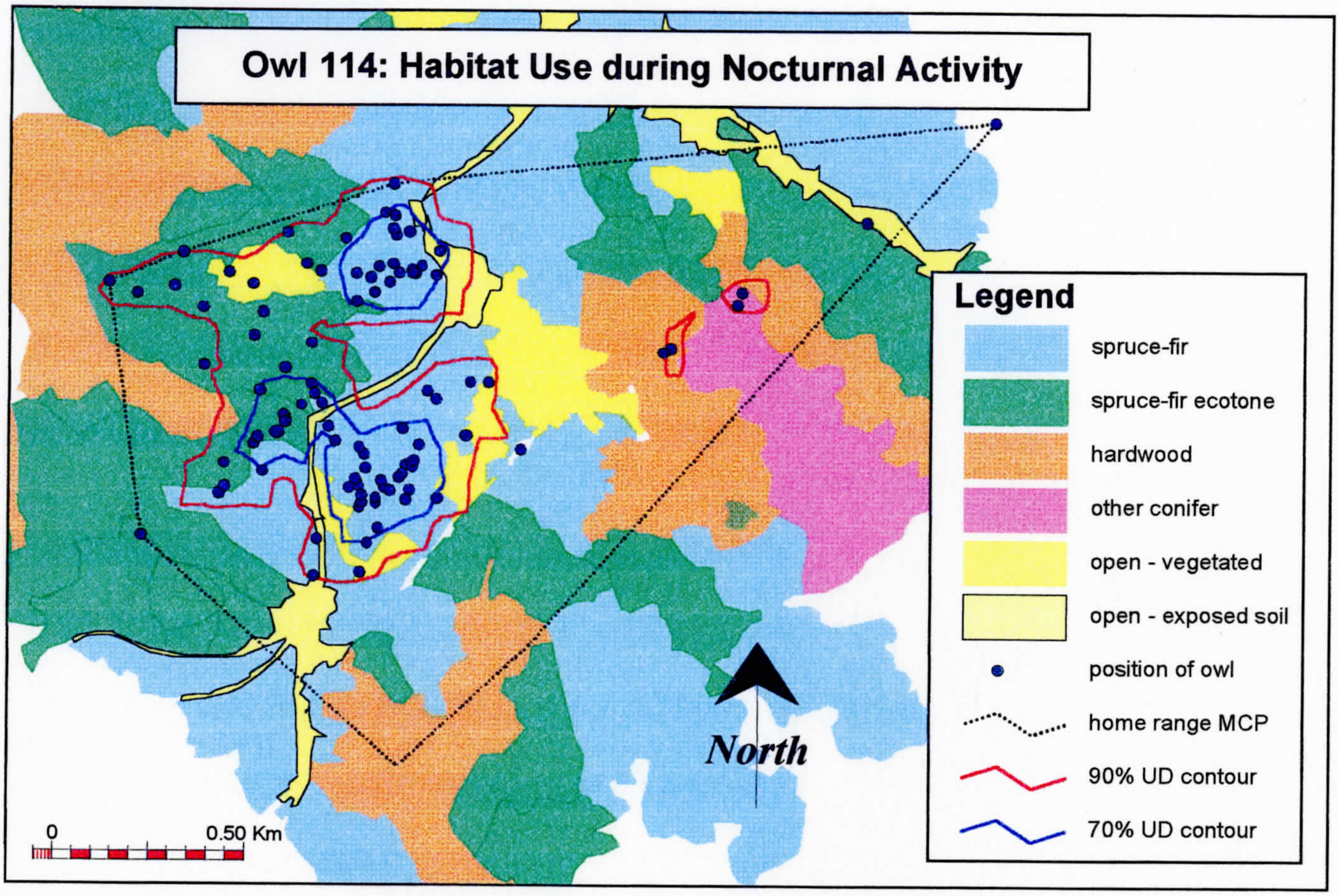

Figure 13 A. Habitat use during nocturnal activity of owl 114. The use of habitat types within the home range (dotted line indicating home range MCP) is depicted by a moderate-use level (red bordered polygons delineating 90% utilization distribution (UD) areas) and a high-use level (blue bordered polygons delineating 70% UD areas). Owl positions, recorded during night tracking, are indicated by small dark dots. The varying density of dots indicates spatial usage as a function of time spent in each area.

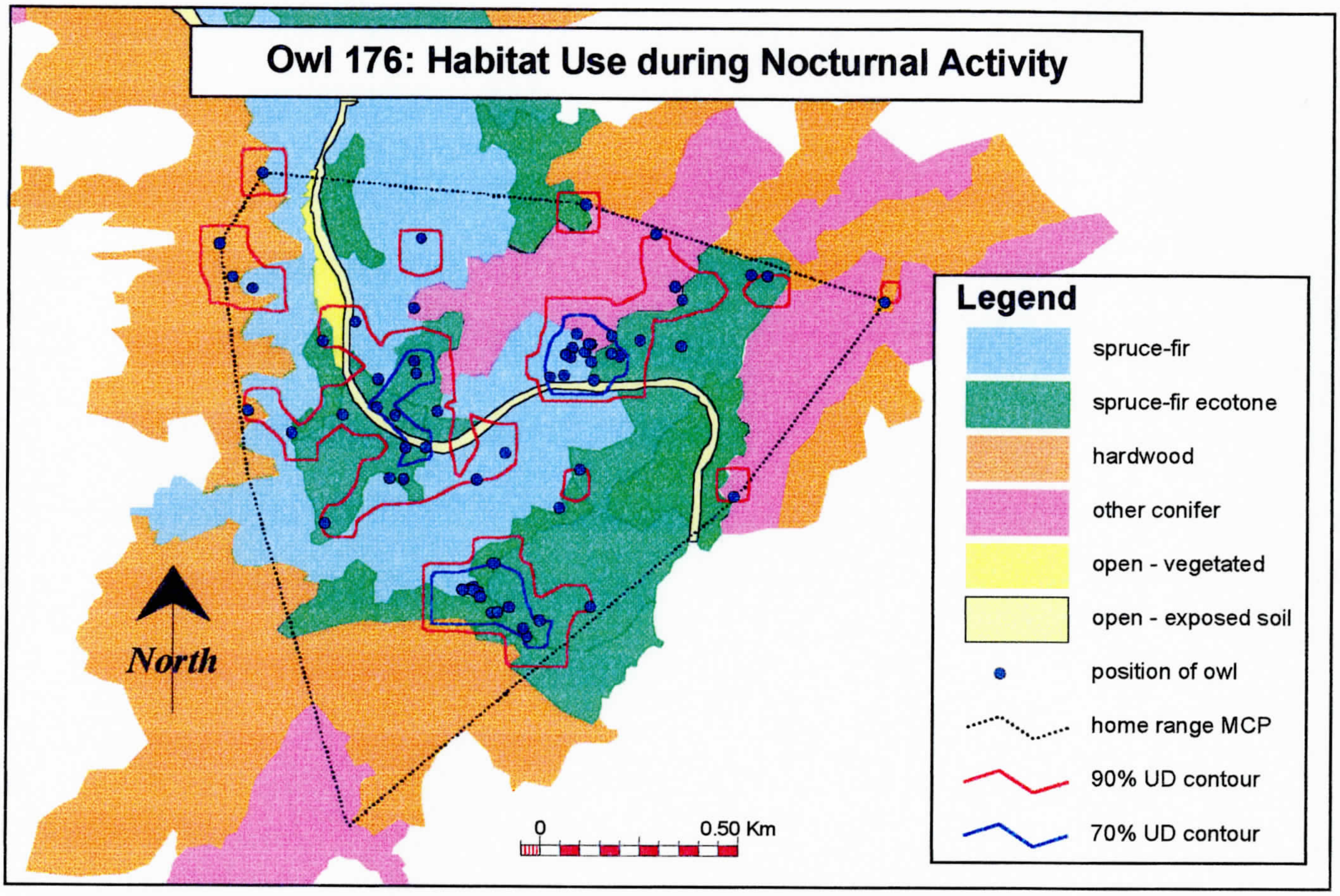

Figure 13 B. Habitat use during nocturnal activity of owl 176. The use of habitat types within the home range (dotted line indicating home range MCP) is depicted by a moderate-use level (red bordered polygons delineating 90% utilization distribution (UD) areas) and a high-use level (blue bordered polygons delineating 70% UD areas). Owl positions, recorded during night tracking, are indicated by small dark dots. The varying density of dots indicates spatial usage as a function of time spent in each area.

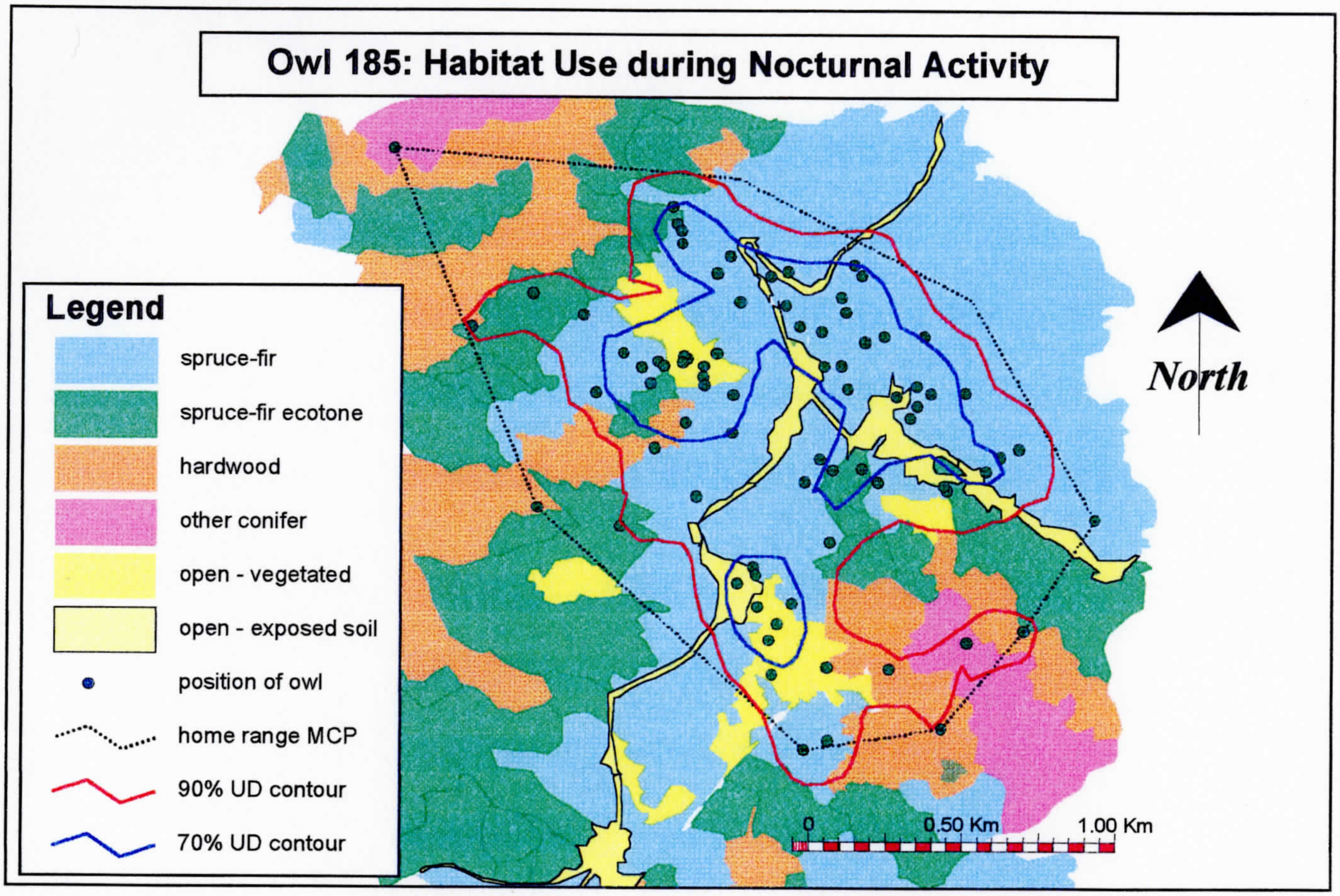

Figure 13 C. Habitat use during nocturnal activity of owl 185. The use of habitat types within the home range (dotted line indicating home range MCP) is depicted by a moderate-use level (red bordered polygons delineating 90% utilization distribution (UD) areas) and a high-use level (blue bordered polygons delineating 70% UD areas). Owl positions, recorded during night tracking, are indicated by small dark dots. The varying density of dots indicates spatial usage as a function of time spent in each area.

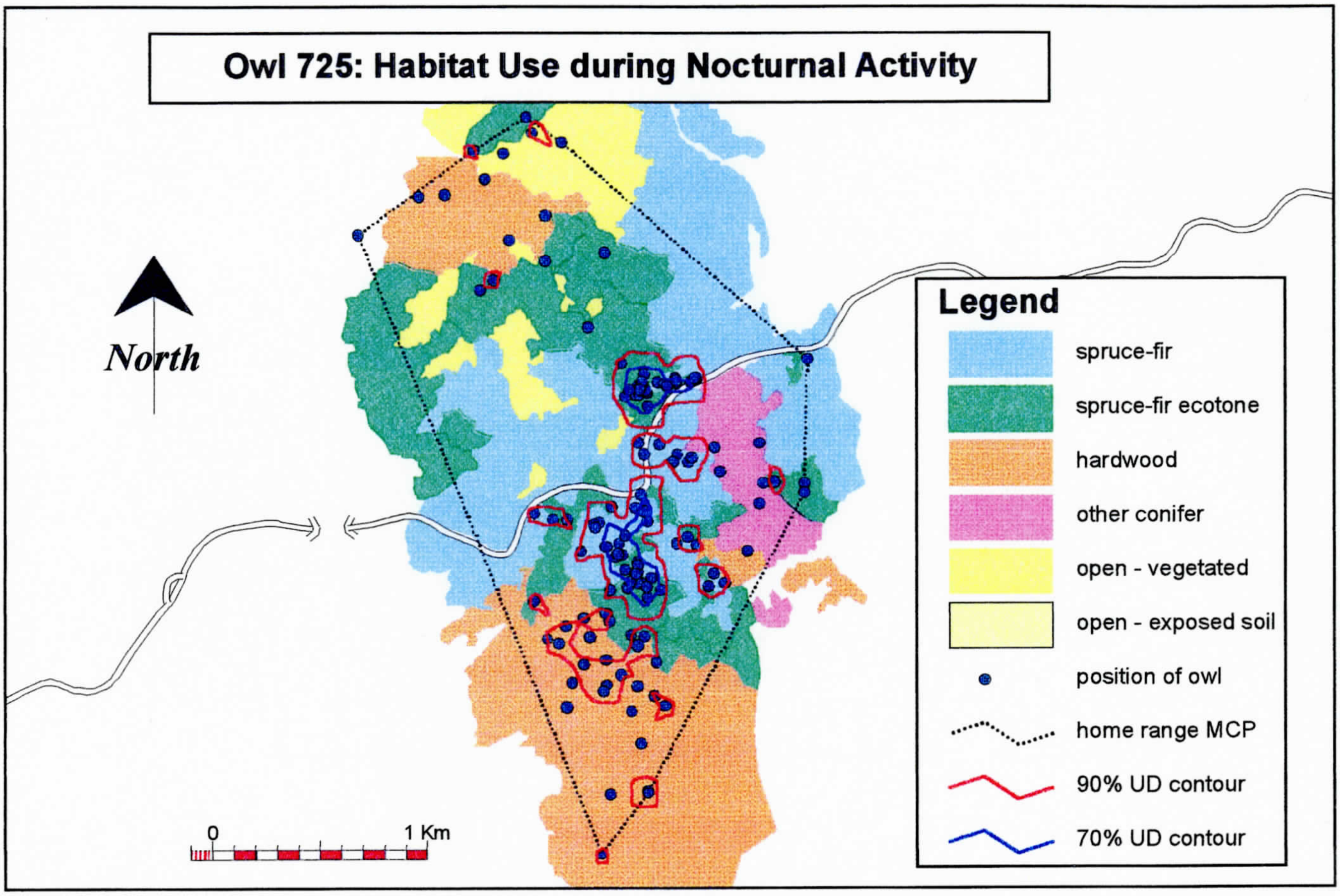

Figure 13 D. Habitat use during nocturnal activity of owl 725. The use of habitat types within the home range (dotted line indicating home range MCP) is depicted by a moderate-use level (red bordered polygons delineating 90% utilization distribution (UD) areas) and a high-use level (blue bordered polygons delineating 70% UD areas). Owl positions, recorded during night tracking, are indicated by small dark dots. The varying density of dots indicates spatial usage as a function of time spent in each area.

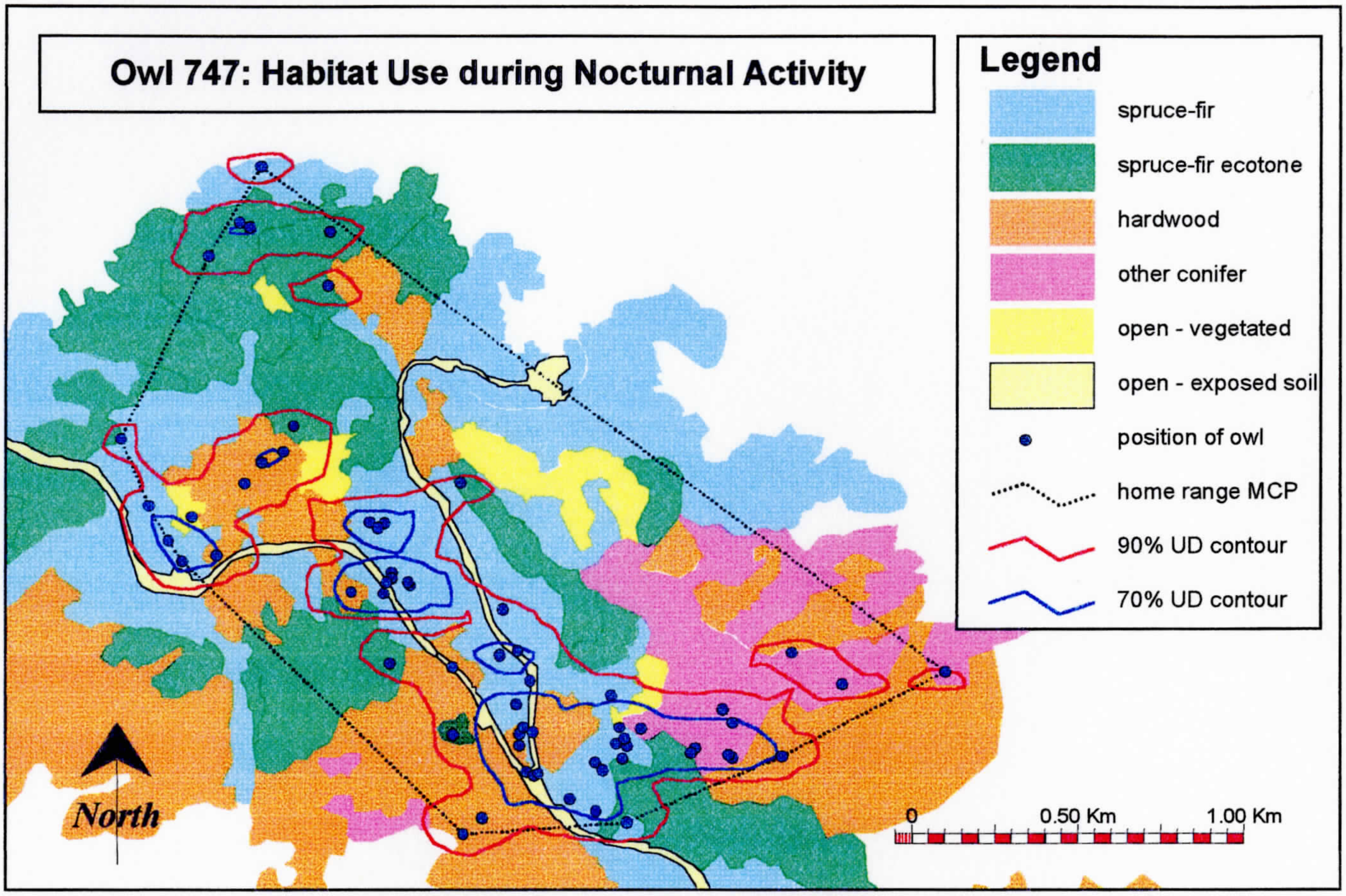

Figure 13 E. Habitat use during nocturnal activity of owl 747. The use of habitat types within the home range (dotted line indicating home range MCP) is depicted by a moderate-use level (red bordered polygons delineating 90% utilization distribution (UD) areas) and a high-use level (blue bordered polygons delineating 70% UD areas). Owl positions, recorded during night tracking, are indicated by small dark dots. The varying density of dots indicates spatial usage as a function of time spent in each area.

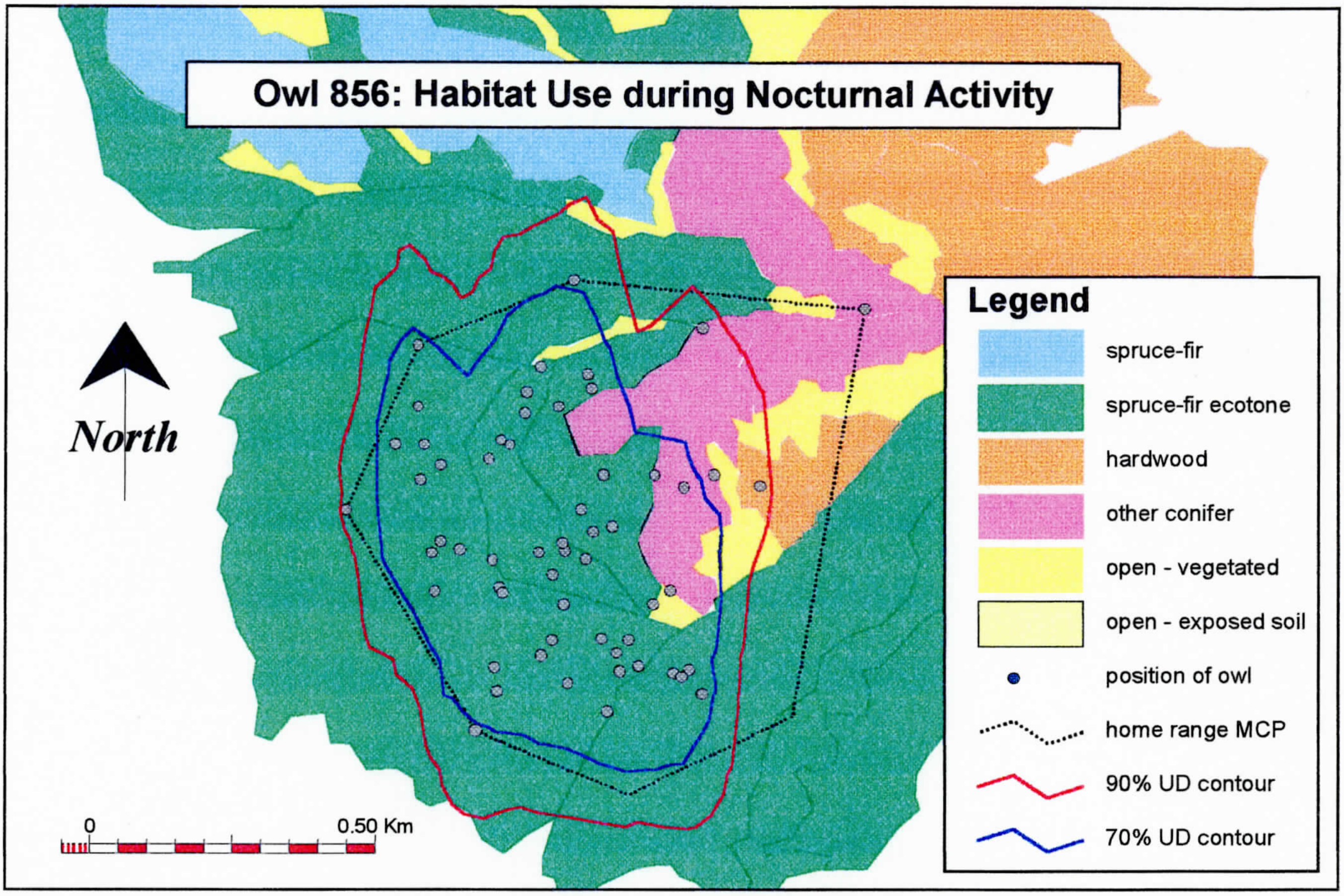

Figure 13 F. Habitat use during nocturnal activity of owl 856. The use of habitat types within the home range (dotted line indicating home range MCP) is depicted by a moderate-use level (red bordered polygons delineating 90% utilization distribution (UD) areas) and a high-use level (blue bordered polygons delineating 70% UD areas). Owl positions, recorded during night tracking, are indicated by small dark dots. The varying density of dots indicates spatial usage as a function of time spent in each area.

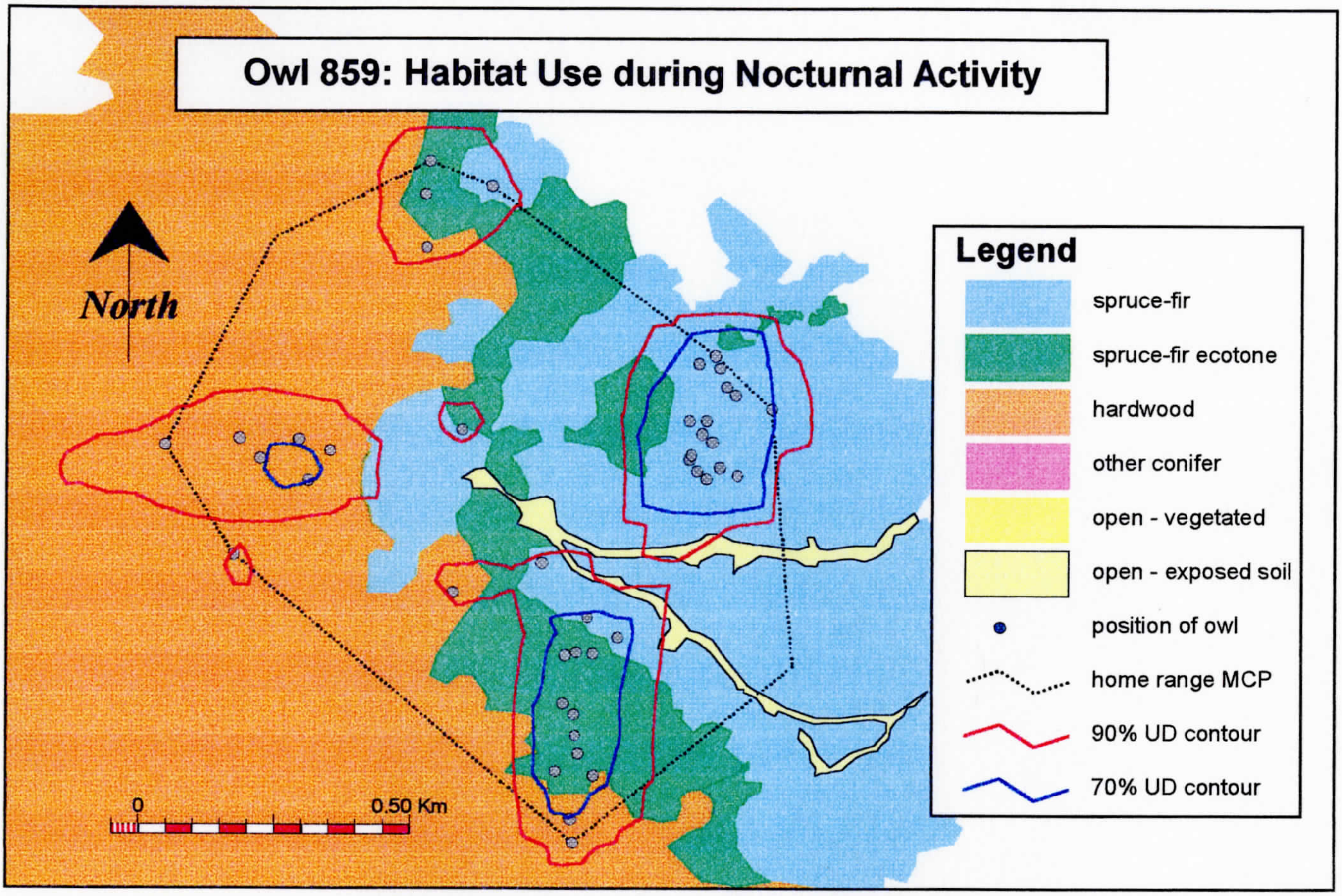

Figure 13 G. Habitat use during nocturnal activity of owl 859. The use of habitat types within the home range (dotted line indicating home range MCP) is depicted by a moderate-use level (red bordered polygons delineating 90% utilization distribution (UD) areas) and a high-use level (blue bordered polygons delineating 70% UD areas). Owl positions, recorded during night tracking, are indicated by small dark dots. The varying density of dots indicates spatial usage as a function of time spent in each area.

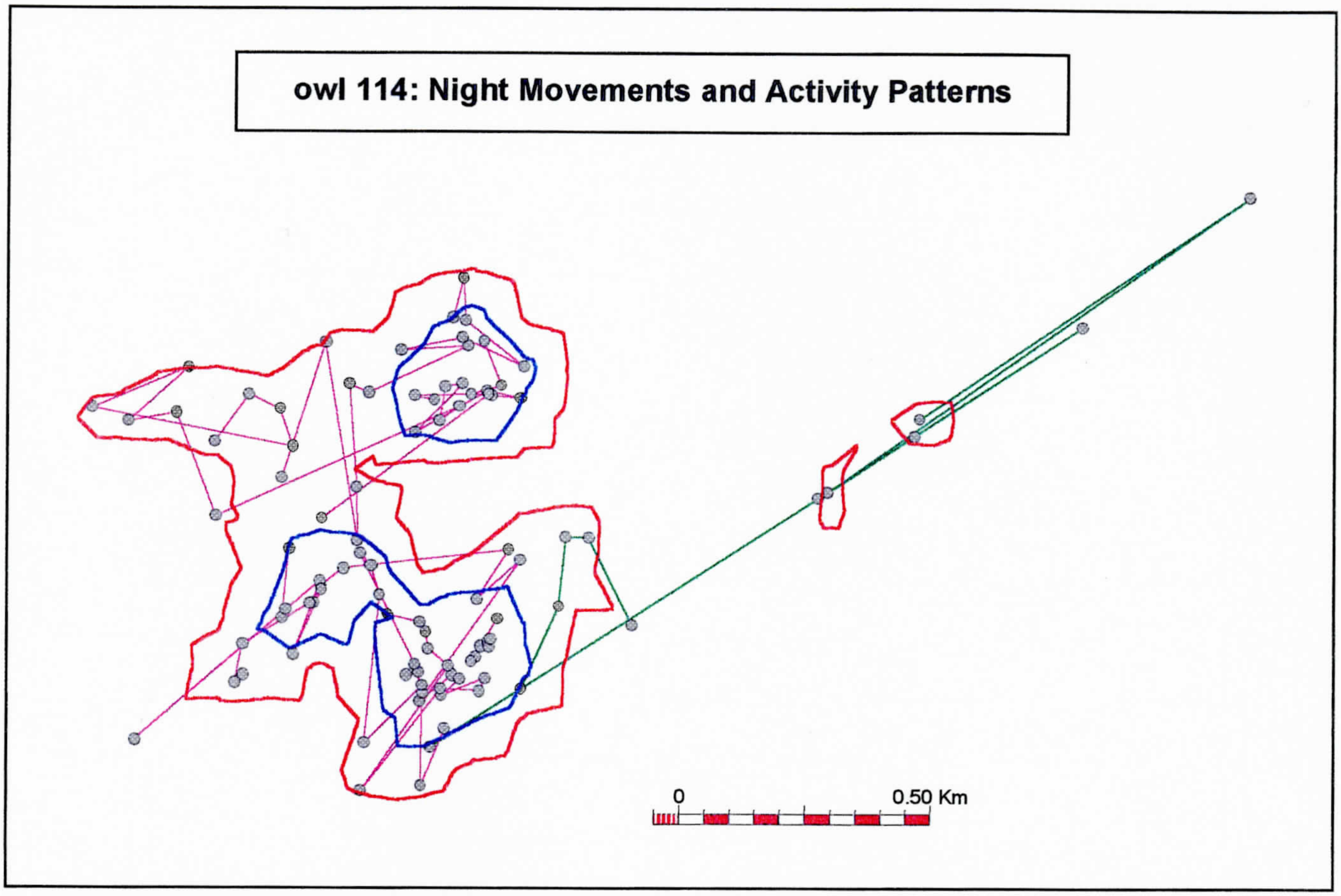

Figure 14 A. Night movements and activity patterns of owl 114. Above is an example of types of nocturnal activity observed of saw-whets during the breeding season. Individual fixes of the owl's position are indicated by dots which are linked in sequence by a line connecting only those fixes from the same night of tracking. Thin maroon lines connecting dots indicate nights of normal (most common) patterns of activity, which were concentrated in areas of moderate-use (90% UD - red delineated area) and high-use (70% UD - blue delineated area) within the home range. Shortest distances traveled by the owl between triangulation fixes, indicated by shortest lines between dots, were typically located within the areas of high-use. In that, saw-whets are a sit-and-wait predator, areas of closest dots are likely to be areas where the owl concentrated its hunting activity. The thin green line indicates a night of an extended foray, which took the owl away from areas used normally for foraging and roosting. The owl moved quickly during the foray (indicated by greater distances between fixes than those of normal activity), suggesting the owl was engaged in an activity other than hunting. Activity during extended forays might be that of conspecific communication or exploration.

On nights when forays were taken, owls spent a portion of the observed time foraging normally, then moved away from their typical areas of activity for brief but highly mobile interludes. Locations of day roosts which were found the day following nights of observed extended forays indicated that these longer excursions were terminated by the owl the same night to return back to areas used normally for roosting. Patterns of roosting between early- (March – April) and mid- (May – July) breeding season periods, when these forays typically occurred, did not appear to change, thus providing further evidence to the temporary nature of the forays. These forays appeared to be more closely associated with exploratory movements or intraspecies interactions, rather than with normal foraging, and produced the greatest effect on home range size of any discernable nightly activity.

Three of the four largest home ranges in the study were those of owls which had been observed on extended forays (owls 114, 185, 725). The data sets of all tagged owls do not include such observations of extended forays. Therefore, these observations at least partially explain the variability in home range size among owls. Extended forays continued into mid-breeding season for one owl, but this behavior appears to occur less frequently after the early season. Forbes and Warner (1974) also observed a single saw-whet owl take extended nightly "trips" away from normal areas of activity on two of 20 nights it was radio-tracked during fall months.

Patterns of Movement with Respect to Season

Patterns of roosting for the period from March to August (associated with the biological periods of mating, nesting, and post-fledging) indicate that roost MCPs of all 8 owls analyzed were generally contained within the night activity MCPs of those owls for the same period (Figs. 11 A-H). During this period, owls returned from each night's foraging to roost in roughly the middle third of their home range (see "Home Range Placement" and "Home Range Size" in this section). Roosting activity after August (the predicted end of the breeding season and beginning of movements to overwintering sites) was recorded for 5 of the 8 owls (067, 114, 725, 747 and 859; Figs. 11 A, B, E, F and H, respectively). Post-breeding season roosting activity indicated a shift from breeding season roost locations to locations peripheral to or well away from both the breeding season roost MCP and the larger night activity MCP for each owl.

Post-breeding season roosts were geographically orientated down slope from each owl's breeding season roost locations. No specific compass direction of change from breeding to post-breeding season was indicated among owls. Changes in roost activity generally indicated a shift from more exposed, high elevation locations of the breeding season to sheltered forest coves and stream corridors of the late season.

Of the five owls with post-breeding season roost data, four (owls 067, 725, 747, 895) moved down slope to roost at elevations below their breeding season roost elevations (Table 2 - indicated by differences in elevation for harmonic mean centers of roosting of each seasonal period, Fig. 15 - shown as a graph of roost elevations over

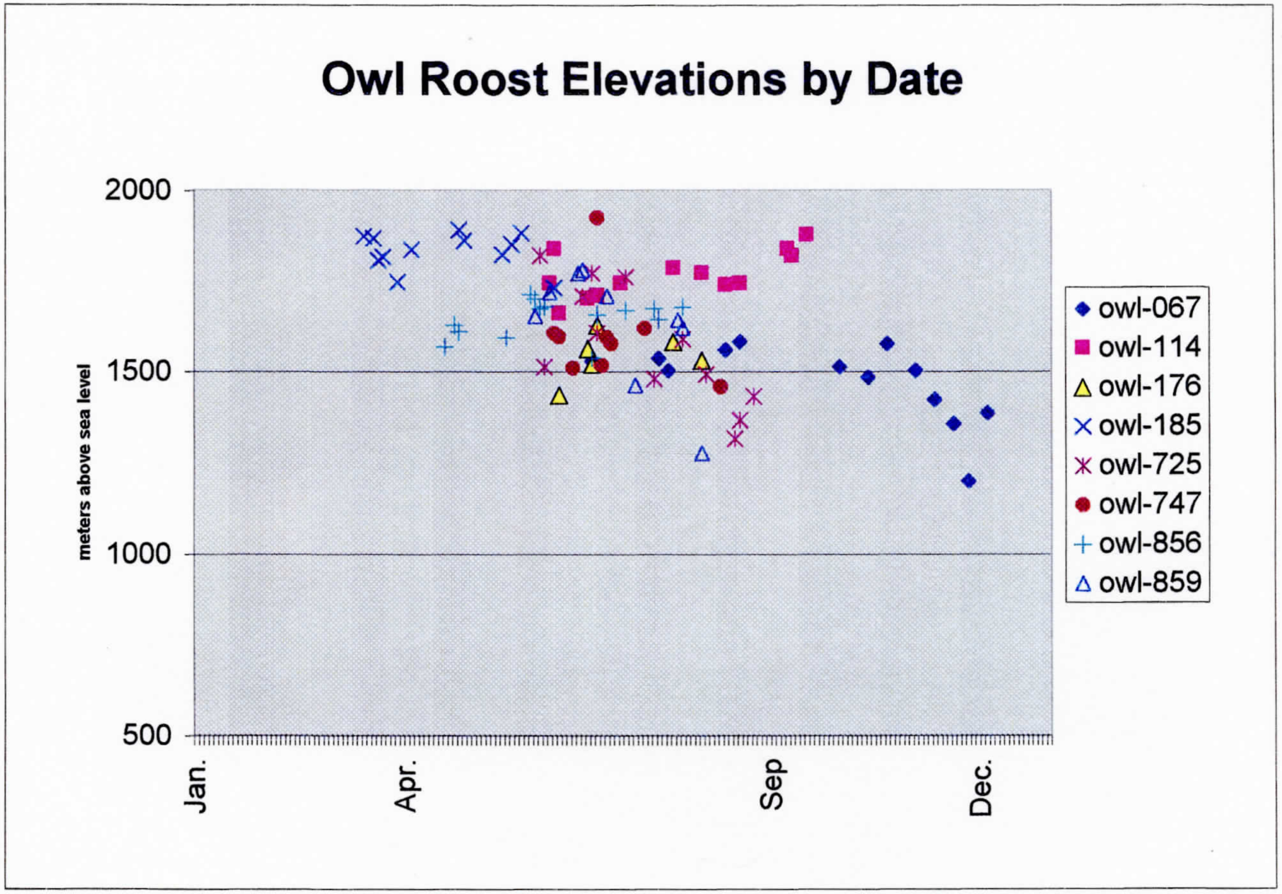

Figure 15. Elevations of roosts of each owl by date. Roosting elevations decreased after August, signaling a change in biological season from spring/summer breeding to fall elevational migration.

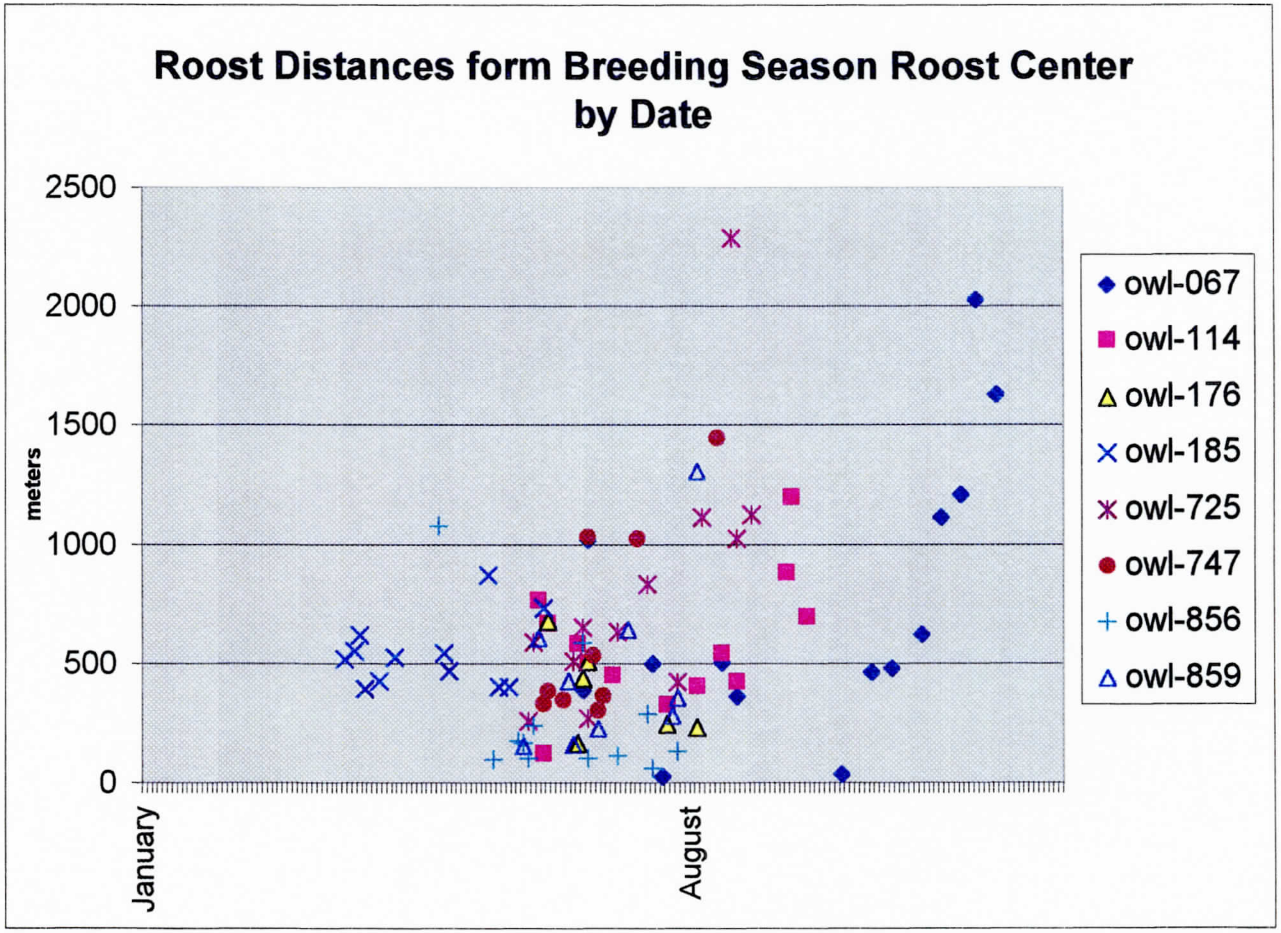

Figure 16. Distances of roosts from the breeding season center of roosting of each owl. Distance increased dramatically after August, thus apparently signaling a change in biological season from spring/summer breeding to fall elevational migration.

time). One other (owl 114) roosted in locations that were roughly at the same elevations as its breeding season roosts. The change in elevation between breeding and post-breeding centers of roosting averaged 223 m among owls (range 23 to 452 m). Only one owl (owl 067) was tracked beyond September. This owl showed the second greatest drop in roosting elevation between the two seasonal periods (339 m) and the lowest recorded roost elevation for any of the five owls (1,200 m - occurring on November 26).

Horizontal distances between breeding and post-breeding season roosting centers (harmonic mean of each owl's roosts for each seasonal period) averaged 1,153.6 m among the 5 owls (Table 2). Distances of all roosts to the breeding season roost center are graphed by date in Figure 16. The average maximum distance of post-breeding roosts to the breeding season center of roosting for the 5 owls was 1652.6 m (range 1199 to 2286 m), which occurred 23 to 47 days after the beginning of seasonal shifts in roosting activity for each owl. A return, following these post-breeding season maximum distances to roost distances closer to the breeding season center of roosting, was observed in three of the five owls, suggesting that wintering home ranges may have been reached.

Elevations of all roosts for each owl and distances of roosts from the breeding season center of each owl's roosting activity were measured to determine if a significant change in patterns of roosting activity was occurring over time. Roost elevations and roost distances from breeding centers of roosting were pooled among owls. I ran Mann-Whitney U-Tests (Bruning and Kintz 1977) to compare elevation and distance parameters of roosts encountered before the seasonal shifts (the period corresponding to mating and nesting activity) to those encountered after seasonal shifts (the period corresponding to post-breeding activity and migratory movement).

Mann-Whitney U-tests revealed that both roost elevations and roost distances from breeding season centers of roosting were significantly different between the two seasons ($z = -4.97$ and 3.96, respectively, $p<0.001$ for both), indicating that a seasonal change in the locations of roosting activity had occurred among owls. Thus, results indicate a shift in locations of roost activity between breeding and post-breeding periods. Seasonal changes in roost activity appear to occur independently among owls, and direction of change appears to be orientated down slope, typically in the same watershed as the breeding season home range of each owl.

Activity Patterns as indicators of Nesting

No nests were found for any of the radio-tagged owls in this study. Therefore, the direct relationship between movements of tagged owls to nesting activity is not known. However, the examination of movement patterns of tagged owls during the most likely nesting period, predicted from the seasonal change in male vocal activity (Milling et al. 1997) and from concurrent nesting records (Barb 1995), may provide clues as to possible nesting activity. If a tagged owl nested, this parental male's frequent return on most nights to the site of its nest tree, to feed its mate or nestlings, should be detected by the overlap of nightly activity polygons (nightly MCP polygons) at a single area of the home range (Sonerud et al. 1986).

The predicted peak hatching dates of clutches from nesting owls of the regional population (indicated by a reduction in vocal activity of calling males) were May 26-27 in 1993 and May 11-14 in 1994. In 1993, no owls were trapped before the dates of decline in vocal activity, though three had vocalized from home ranges where owls were eventually tagged at least two weeks prior to trapping. In 1994, four owls were tagged by the predicted hatching date. Two of these (owls 185 and 260) were tagged early in 1994 and had been lost, either because they left the area or their transmitters failed, well before dates of declining vocal activity. However, within two weeks after the predicted peak hatching dates for nesting owls of the regional population, all owls of both years had been tagged. Therefore, 8 owls were tracked for an extended period beginning shortly after the predicted hatching date, the period corresponding to the care and feeding of hatchlings in the nest and the fledging of young.

Seven of the 8 owls with data sets that covered much of the breeding season used multiple sites for foraging and night activity. Nightly activity polygons (convex polygons of each owl's activity per night) of four of the 8 owls overlapped or were tangential to a common area on most nights (owls 176, 185, 747, 856; Figs. 11 C, D, F, G), suggesting the potential for those areas to be locations of active nests. One of these, owl 747, produced a pattern of overlapping nightly polygons until early July, then shifted roosting and night activity away from this earlier activity center (owl 747; Fig. 11 F). This was interpreted as a possible nesting, with the fledging of nestlings or nest failure occuring shortly before the first date the shift was observed. Owl 856 exhibited the most concentrated pattern of activity at and around a single area, with all its nightly polygons overlapping and bounding a 5 ha area (owl 856; Fig. 11 G). Additionally, roosting patterns of this owl were highly restricted compared to those of other owls and were limited almost exclusively to a single multiple-use area in the proximity of the area of overlap of nightly polygons. The possibility that owl 856 nested is further supported by the fact that a young-of-the-year (the only one encountered during this study) was trapped in the home range of owl 856 during the fall of the year while attempting to retrap and retag owl 856.

Other evidence for nesting is inferred from home range size. Cannings (1987) determined home range sizes of two saw-whet owls during the time of nesting to be 142 and 159 ha Though prey availability has also been linked to differences in the home range size of other owl species (Carey et al. 1992), home ranges of saw-whet owls in Cannings' (1987) study were considerably less than the average for owls in this study (193.7 ha). One of Cannings' nesting owls remained in a single 27 ha core area 85% of the time tracked, behaving much as owl (856) did in this study (Table 2, "cumulative roost area"). Three other owls in this study (owls 067, 176, 859) each had comparatively small home ranges (range 91.4 to 158.3 ha), but of these, only owl 176 exhibited the predominant pattern of overlapping nightly polygons suggestive of nesting.

The similarities between owl 856 and actively nesting saw-whet owls in Cannings' (1987) study in their use of single core areas and in their comparatively small home ranges provides the strongest evidence that, of any owl in this study, owl 856 likely nested. However, based on nightly activity patterns, owls 176, 185, and 747 showed noticeable indicators of concentrated activity in a single area, suggestive of parental behavior at a likely nest site. Thus, using activity patterns as potential indicators for nesting activity, only 4 (owls 176, 185, 747, 856) of the 8 owls tracked through some or all of the breeding season showed noticeable signs suggestive of nesting.

Habitat Use

General Observations of Habitat Use

Data of habitat use were minimal for a few owls (n=4), only suggestive of usage patterns for some (n=4), but suitable for statistical analysis of usage versus availability for others (n=7; see "Criteria for Analysis of Positional Data Sets" in this section). However, some comparisons can be made among all owls (n = 15). Data of owl positions, including the location for which each was trapped, indicates that movements of all 15 owls included locations within the high-elevation spruce-fir zone. Most of the owls (n=13) remained in or near these high-elevation boreal forests during the periods of the breeding season in which each was tracked. Movements of only two owls (767 and 926) took them away from the spruce-fir zone for any appreciable period of time. Not surprisingly, these owls had the lowest recorded roost elevations for owls during the mating and nesting periods (Fig. 6, Table 2). Activity patterns of these two owls, and possible reasons for them, are discussed in a later section (see "Cases of atypical habitat use" in Discussion). Data sets of these owls were insufficient for analysis of habitat use.

As previously stated, owls typically utilized 2 to 4 areas on a heavy or frequent basis during nocturnal activity periods. High-use areas of each owl were generally situated on or to either side of a high ridge, topped by stands of spruce-fir, which bordered or straddled the home range (Figs. 3, 4, 5). Day roosts were quite often located at the edge of core areas (Figs. 12 A-G), suggesting a relationship between the use of certain core areas during the night and the location of the roost site the next day.

Measurements and Observations at Roosts

From descriptions and measurements of vegetative and topographic conditions recorded at roost sites during owl roost checks, owls roosted in forest types that ranged in composition from total (100%) hardwood to near total (95%) conifer tree species. Roost perches were located in the shrub and understory vegetation for 83% and in canopy vegetation for 17% of roosts found. Owls consistently located their perches in densely foliated micro-habitat conditions within forest stands. Virtually all roosts were overtopped, often enveloped on all sides, by dense woody vegetation, which was often densest within 0.5 m of the owl's perch. These perching conditions were consistent with Swengel and Swengel's (1992b) findings for saw-whet owls in Wisconsin. Within forest stands, roost sites were typically located in dense patches of vegetation (thickets), which ranged in size from small "clumps" of a few closely clustered trees, to extensive "thickets" covering one to many hectares. Owl roosts were located in clumps or thickets of spruce and/or fir for 62%, of heath shrub (predominantly rhododendron, but occasionally mountain laurel) for 23% and of hardwood for 15% of the roosts found.

Owls commonly used one to two locations as recurrent roosting areas (multiple-use areas). In contrast to forest conditions associated with all roosts, these "multiple-use" areas were located in spruce-fir or spruce-fir ecotone 90% of the time. These sites were generally situated varying distances down slope of a main ridge, in locations that would apparently provide some shelter from high winds, and were regularly associated with forest stands composed of multiple layers of evergreen or mixed evergreen/hardwood vegetation. Within the home range of each owl multiple-use areas appeared to be located where thickets of sapling to pole-aged spruce-fir and/or heath shrub (i.e., conifers and/or rhododendron/mountain laurel) were most extensive, though not necessarily contiguous. These areas were partially to totally covered by a canopy of pure conifer (spruce-fir) or mixed conifer/hardwood.

Though other less-used sites within each owl's home range were composed of similar vegetative conditions as multiple-use areas, the difference appears to be associated with the topographic position and physical surroundings of areas used multiple-times versus those that are not. More exposed areas along or near ridgelines were little-used, whereas locations that provided a higher degree of shelter from wind (i.e., areas of suitable forest condition within the upper reaches of mountain stream watersheds or at the base of rock outcrops) appeared more preferential. In fact, the only multiple-use roost area of any owl found in non-boreal forest was that of owl 859 (Fig 12 G), in mature northern hardwood forest at the base of a large rock outcrop.

Analysis of Habitat Use

Habitat use was statistically analyzed for the seven owls with data sets which satisfy the (5/50) criteria for night-time activity data. Data sets for each of the 7 owls included 7 to 14 day roosts and five to nine nights of activity (ranging from 14.75 to 36.5 total hours of night tracking per owl; Table 1). Among owls in this group, the nightly tracking period averaged 4 hours, with fixes of owl locations spanning all hours of the night.

Measured areas of moderate (90% UD) and high use (70% UD) contours varied considerably among owls (Table 2). The total area used by owls at the moderate usage level (90% UD contour) ranged from 42.5 to 177.06 ha (avg. 84.15 ha per owl). The total area used by owls at the high usage level (70% UD contour) ranged from 9.27 to 62.95 ha (avg. 29.44 ha per owl). The average proportions of available area (100% home range MCP) utilized by owls at high usage and moderate usage levels were 18.81% (range 2.48 to 62.98%) and 47.25% (range 12.81 to 106.63%), respectively. The area of the kerneled 90% utilization distribution contour for one owl (856) was actually larger than the MCP of its home range (Table 2, Fig. 13 G). This was the only monomodal distribution pattern created by any owl's night activity, which indicates the intensive use of a single core area that essentially covered the area of the home range MCP. The larger area of this owl's 90% UD compared to its home range MCP is due to the smoothing factor of the kerneling algorithm. Areas of UD contours and home range MCP's are graphically compared among owls on figure 17.

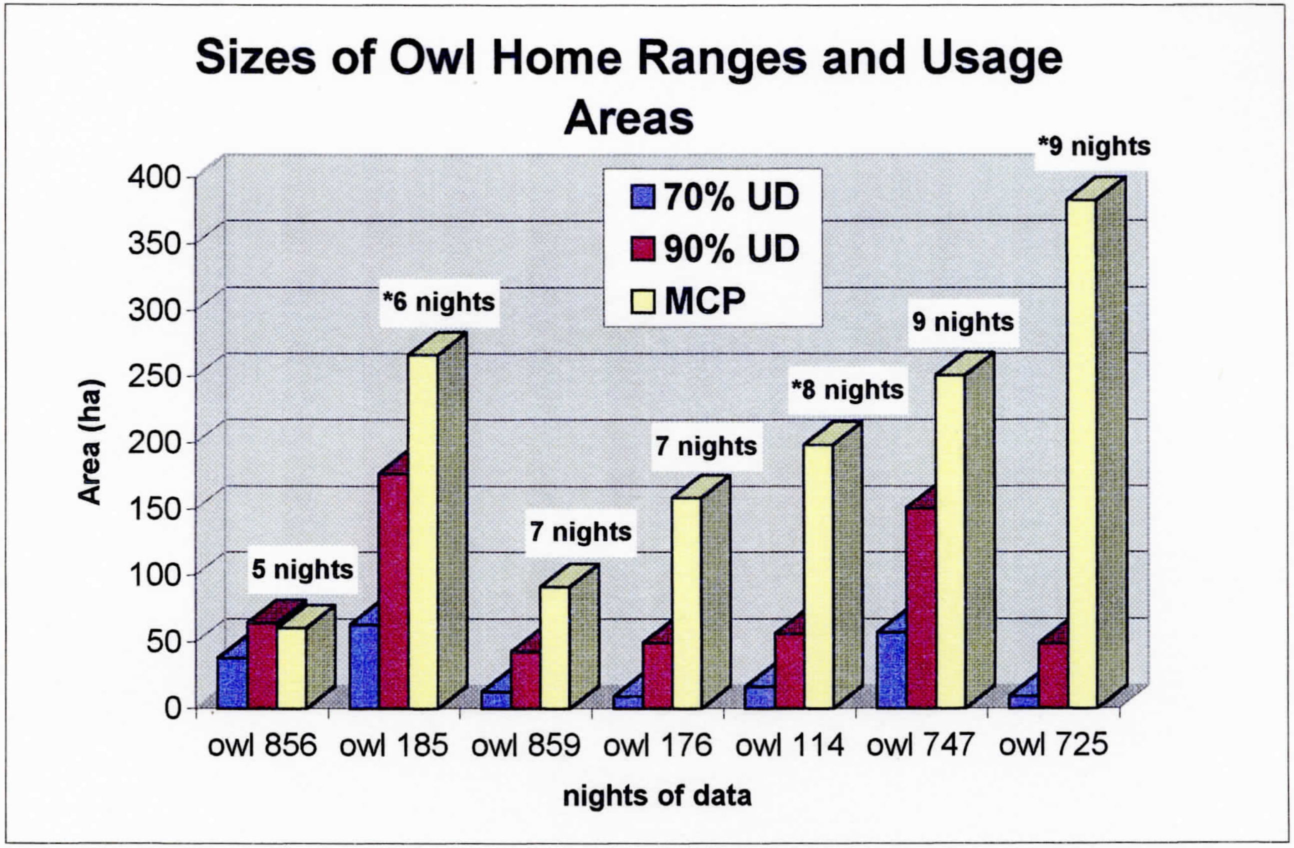

Figure 17. Comparative areas of owl home ranges, and areas of high and moderate use. A correlation between nights of tracking and size of usage areas is not strongly indicated. A star before the nights of tracking identifies owls that were observed on extended forays away from normal areas of activity. These forays contributed greatly to the size of home ranges but little to the size of high and moderate usage areas.

Differences among owls in total area utilized at moderate and high-use levels were apparently not the result of differences in sample size. This is illustrated by the fact that two owls with widely differing sample sizes of night data for owls in this group (owl 176 with 66 points from 7 nights, versus owl 725 with 129 points from 9 nights) had virtually identical sizes for areas of high use (owl 176 with 9.27 ha, versus owl 725 with 9.47 ha) and moderate use (owl 176 with 49.41 ha, versus owl 725 with 48.92 ha). However, home range area for these two owls differed greatly (owl 176 with 156.91 ha, versus owl 725 with 381.78 ha). As previously mentioned, differences in home range size were apparently most affected by the presence or absence of an extended foray event recorded in each owl's data set, which, when present, added only minimally to the area of moderate use and not at all to the area of high use.

Use of habitat types

Home ranges of all 7 owls contained components of spruce-fir, spruce-fir ecotone, open, and hardwood habitat types (Fig. 18). Proportions of spruce-fir forest within 100% home range MCPs ranged from 4.2 to 48.0%. Proportions of spruce-fir ecotones ranged from 18.0 to 74.0%. The combined proportion of spruce-fir and its ecotones in home range MCPs of owls ranged from 57.7 to 78.2%, averaging 63.7% for the group. Proportions of high- and mid-elevation hardwood forest types in owl MCPs ranged from 4.0 to 39.3%, averaging 20.0%. Home ranges of all except one owl (owl 859) also contained small proportions of other conifer forest types (primarily hemlock cove, but also pine ridge). Proportions of these ranged from 0.0 to 23.1% in MCPs, averaging

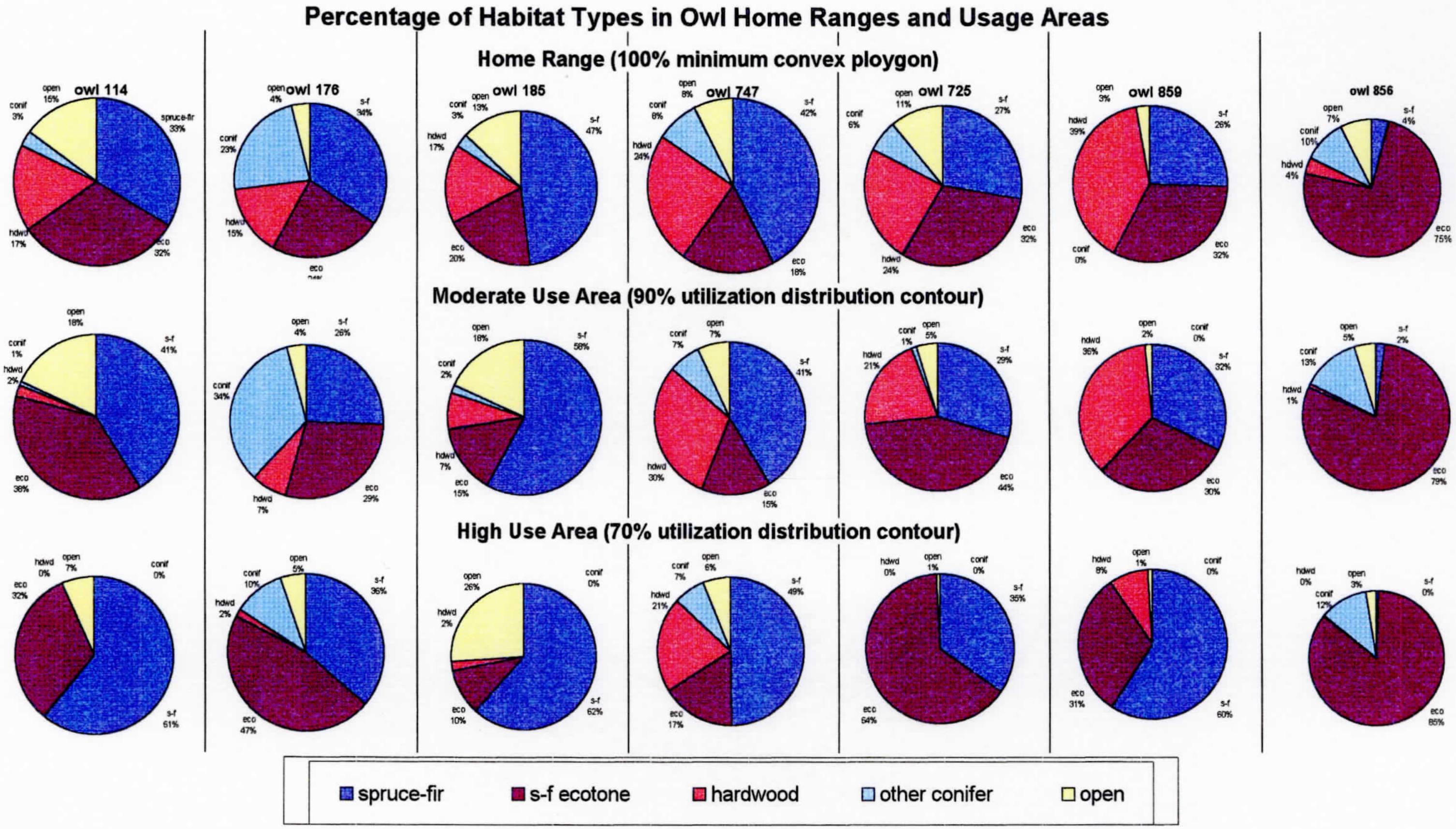

Figure 18. Proportion of habitat types in the home range and in contours of both usage levels are presented in a column for each owl. The graphs show that either spruce-fir or spruce-fir ecotone increased in proportion within moderate and high-use contours in relation to their availability within home ranges for 5 of the 7 owls at the moderate-use level, and for all owls at the high-use level. Proportions of other habitat types in high and moderate-use contours compared to their availability were mixed. However, of these others, open habitats (categorized as either grass/forb meadows or disturbed soil areas which are paved or barren) were consistently present in each owl's high and moderate-use contours, whereas categories of hardwood and other conifer were not.

7.6%. And, home ranges of all owls contained small to moderate proportions of open habitats, which consisted of areas of paved or exposed soil condition (e.g., roadways and disturbed areas) and/or habitats dominated by an herbacious ground cover (e.g., mountain meadows and balds). Total proportions of these open habitats in home ranges ranged from 2.9 to 15.1% in MCPs, averaging 8.7%.

Proportions of spruce-fir and/or its' ecotones within 5 of 7 owl moderate-use areas (90% UD) and high use (70% UD) were higher when compared to their proportions in the home ranges of each owl (Fig. 18). In contrast, hardwood forest types decreased in 6 owls' 90% UDs, and all 7 owls' 70% UDs, when compared to availability. Pure hardwood stands were not found in 3 owls' core areas. Proportions of conifer forest types other than spruce-fir were lower in 4 owls' 90% UDs, and 5 owls' 70% UDs, compared to availability, with the core areas of 4 owls devoid of these forest types. Usage of open habitats was mixed, with proportions of all open habitats increasing for 2 owls, decreasing slightly for 4 owls and remaining constant for 1 owl when 90% UDs were compared to availability. Proportions decreased in 6 of the 7 owl 70% UDs compared to availability. However, core areas for each owl were never devoid of open habitats.

Compositional analyses of habitat use during nocturnal activity periods illustrates a disproportionate use of forest types at high (70% UD) levels of use. The chi-square approximation for the Wilks' Λ multivariate statistic revealed significant differences from random at high ($\chi^2 = 13.043$, 4 df, $p<0.025$) use levels when data were pooled among the 7 owls (Table 3 A). The use of habitats neared a significant difference from random use at the moderate-use level ($\chi^2 = 8.274$, 4df, $p<0.10$). Rank order of forest type use during night activity periods, when pooling across owls, was the same for the top 3 ranks (spruce-fir ecotone, spruce-fir and open) at both UD levels, with the order of habitats (hardwood and other conifer) switched for the two usage levels at the bottom two ranks.

Rank order of habitat use at the moderate-use (90% UD) level:

spruce- fir ecotone > spruce-fir > open > hardwood > other conifer

Rank order of habitat use at the high-use (70% UD) level:

spruce-fir ecotone > spruce-fir > open > other conifer > hardwood

Pairwise comparisons of forest type usage from the among owl matrix showed significant differences between spruce-fir ecotone and hardwood forest types at the 90% UD level and between all forest types compared with "other conifer" at the 70% UD level.

Rankings of habitat use by individuals generally followed the same order as ranks pooled across owls. However, when owls were analyzed individually, spruce-fir was ranked highest in use for most owls and spruce-fir ecotone was second (Table 3 B). Spruce-fir or its ecotones were used more than expected for all pairwise comparisons at both levels of use, except at the 90% UD level for one owl (owl 176). Spruce-fir was used more than expected when compared to all other forest types by 4 of the 7 owls at both 90% UD and 70% UD levels. Spruce-fir ecotone was top ranked for 2 of the 7 at the 90% UD level, and 3 of the 7 owls at the 70% UD level. Conifer other was top ranked for one of the 7 owls at the 90% UD level, but ranked least in use at the 70% UD level for the same owl. The alternation of spruce-fir and spruce-fir ecotone in the rankings of use

Table 3A. Wilks' lambda values for night data pooled among owls. The values in each matrix show comparative use of the habitat to the left (in the same row as the value) when compared to the habitat above (in the same column as the value). Positive values indicate greater than expected use of the habitat in the row compared to use of the habitat in the column. The number of positive values in the row determines the habitat's rank order in use when compared to all other habitats. Highest numbered rank indicates most preferred habitat. The top table shows the moderate-use level (habitat use within the 90% UD contour), the chi-square approximation of Lambda was not significantly different from random. The bottom table shows comparative usage at the high-use level (habitat use within the 70% UD contour). The chi-square approximation of lambda for habitat use within high-use areas did indicate a significant difference from random at the 97.5 confidence level.

Pairwise Difference Values and Ranks of Habitat Use for All Owls Combined

($x^2 = 8.274$, $0.05<p<0.10$, df=4)

All Owls - 90 UD

	spruce-fir	ecotone	hardwood	conifer	open	**rank**
spruce-fir		-0.48336	2.218821	1.344624	0.689231	**3**
ecotone	0.483362		2.237463	1.648689	1.007515	**4**
hardwood	-2.21882	-2.23746		0.438129	-1.29284	**1**
conifer	-1.34462	-1.64869	-0.43813		-1.44363	**0**
open	-0.68923	-1.00751	1.292838	1.443632		**2**

spruce-fir ecotone > spruce-fir > open > hardwood > other conifer

($x^2=13.043$, $p<0.025$, df=4)

All Owls - 70 UD

	spruce-fir	ecotone	hardwood	conifer	open	**rank**
spruce-fir		-0.16262	**3.455929**	2.707323	0.822887	**3**
ecotone	0.157156		**3.778041**	**2.880184**	0.9939	**4**
hardwood	-3.58138	-3.85142		-0.62609	-2.95804	**0**
conifer	-2.88559	-3.26219	0.752715		-2.30639	**1**
open	-0.79027	-1.03279	**2.916172**	1.824855		**2**

spruce-fir ecotone > spruce-fir > open >>> other conifer > hardwood

Table 3B. Wilks' lambda values for night data of individual owls. The values in each matrix show comparative use of the habitat to the left (in the same row as the value) when compared to the habitat above (in the same column as the value). Positive values indicate greater than expected use of the habitat in the row compared to use of the habitat in the column. The number of positive values in the row determines the habitat's rank order in use when compared to all other habitats. Highest numbered rank indicates most preferred habitat. The left tables show the moderate-use level (habitat use within the 90% UD contour). The right tables show the high-use level (habitat use within the 90% UD contour).

Pairwise Difference Values and Ranks of Forest Type Use for Individual Owls

owl 114 - 90 UD

	spruce-fir	ecotone	hardwood	conifer	open	rank
spruce-fir		0.028451421	2.17684004	1.416907751	0.025929422	4
ecotone	-0.028451421		2.148388618	1.38845633	-0.002522	2
hardwood	-2.17684004	-2.148388618		-0.759932289	-2.150910618	0
conifer	-1.416907751	-1.38845633	0.759932289		-1.390978329	1
open	-0.025929422	0.002522	2.150910618	1.390978329		3

owl 176 - 90 UD

	spruce-fir	ecotone	hardwood	conifer	open	
spruce-fir		-0.476225338	0.41370275	-0.669830287	-0.406897648	1
ecotone	0.476225338		0.889928088	-0.193604949	0.06932769	3
hardwood	-0.41370275	-0.889928088		-1.083533037	-0.820600398	0
conifer	0.669830287	0.193604949	1.083533037		0.262932639	4
open	0.406897648	-0.06932769	0.820600398	-0.262932639		2

owl 185 - 90 UD

	spruce-fir	ecotone	hardwood	conifer	open	
spruce-fir		0.490206337	1.013501723	0.604445948	-0.147880329	3
ecotone	-0.490206337		0.523295387	0.114239611	-0.638086666	2
hardwood	-1.013501723	-0.523295387		-0.409055775	-1.161382053	0
conifer	-0.604445948	-0.114239611	0.409055775		-0.752326277	1
open	0.147880329	0.638086666	1.161382053	0.752326277		4

owl 747 - 90 UD

	spruce-fir	ecotone	hardwood	conifer	open	
spruce-fir		0.186775907	-0.225688399	0.131115466	0.092375144	3
ecotone	-0.186775907		-0.412464306	-0.055660441	-0.094400763	0
hardwood	0.225688399	0.412464306		0.356803866	0.318063543	4
conifer	-0.131115466	0.055660441	-0.356803866		-0.038740323	1
open	-0.092375144	0.094400763	-0.318063543	0.038740323		2

owl 725 - 90 UD

	spruce-fir	ecotone	hardwood	conifer	open	
spruce-fir		-0.276993853	0.207937371	1.665910323	0.942938859	3
ecotone	0.276993853		0.484931223	1.942904175	1.219932712	4
hardwood	-0.207937371	-0.484931223		1.457972952	0.735001488	2
conifer	-1.665910323	-1.942904175	-1.457972952		-0.722971464	0
open	-0.942938859	-1.219932712	-0.735001488	0.722971464		1

owl 859 - 90 UD

	spruce-fir	ecotone	hardwood	conifer	open	
spruce-fir		0.300104592	0.318355969	4.835956288	0.774479246	4
ecotone	-0.300104592		0.018251377	4.535851696	0.474374654	2
hardwood	-0.318355969	-0.018251377		4.517600319	0.456123277	1
conifer	-4.835956288	-4.535851696	-4.517600319		-4.061477042	3
open	-0.774479246	-0.474374654	-0.456123277	4.061477042		0

owl 856 - 90 UD

	spruce-fir	ecotone	hardwood	conifer	open	
spruce-fir		-0.860572899	0.637272325	-1.009006504	-0.32230534	1
ecotone	0.860572899		1.497845223	-0.148433606	0.538267558	3
hardwood	-0.637272325	-1.497845223		-1.646278829	-0.959577665	0
conifer	1.009006504	0.148433606	1.646278829		0.686701164	4
open	0.32230534	-0.538267558	0.959577665	-0.686701164		2

owl 114 - 70 UD

	spruce-fir	ecotone	hardwood	conifer	open	rank
spruce-fir		0.570002202	5.708567208	3.993230979	1.386713569	4
ecotone	-0.570002202		5.138565007	3.423228777	0.816711367	3
hardwood	-5.708567208	-5.138565007		-1.715336229	-4.32185364	0
conifer	-3.993230979	-3.423228777	1.715336229		-2.60651741	1
open	-1.386713569	-0.816711367	4.32185364	2.60651741		2

owl 176 - 70 UD

	spruce-fir	ecotone	hardwood	conifer	open	
spruce-fir		-0.602530762	2.237829544	0.856754782	-0.288090282	2
ecotone	0.602530762		2.840360306	1.459285544	0.31444048	4
hardwood	-2.237829544	-2.840360306		-1.381074762	-2.525919825	0
conifer	-0.856754782	-1.459285544	1.381074762		-1.144845063	1
open	0.288090282	-0.31444048	2.525919825	1.144845063		3

owl 185 - 70 UD

	spruce-fir	ecotone	hardwood	conifer	open	
spruce-fir		0.895671445	2.410832174	3.534323657	-0.439559355	3
ecotone	-0.895671445		1.51516073	2.638652212	-1.3352308	2
hardwood	-2.410832174	-1.51516073		1.123491483	-2.85039153	1
conifer	-3.534323657	-2.638652212	-1.123491483		-3.973883012	0
open	0.439559355	1.3352308	2.85039153	3.973883012		4

owl 747 - 70 UD

	spruce-fir	ecotone	hardwood	conifer	open	
spruce-fir		0.251314428	0.320328621	0.301199042	0.37710383	4
ecotone	-0.251314428		0.069014193	0.049884613	0.125789402	3
hardwood	-0.320328621	-0.069014193		-0.019129579	0.056775209	1
conifer	-0.301199042	-0.049884613	0.019129579		0.075904788	2
open	-0.37710383	-0.125789402	-0.056775209	-0.075904788		0

owl 725 - 70 UD

	spruce-fir	ecotone	hardwood	conifer	open	
spruce-fir		-0.490227894	5.719690054	4.398210242	2.717031237	3
ecotone	0.490227894		6.209917949	4.888438136	3.207259132	4
hardwood	-5.719690054	-6.209917949		-1.321479812	-3.002658817	0
conifer	-4.398210242	-4.888438136	1.321479812		-1.681179005	1
open	-2.717031237	-3.207259132	3.002658817	1.681179005		2

owl 859 - 70 UD

	spruce-fir	ecotone	hardwood	conifer	open	
spruce-fir		0.854415328	2.364471035	5.437681238	1.833801062	4
ecotone	-0.854415328		1.510055707	4.58326591	0.979385734	3
hardwood	-2.364471035	-1.510055707		3.073210203	-0.530669972	1
conifer	-5.437681238	-4.58326591	-3.073210203		-3.603880176	0
open	-1.833801062	-0.979385734	0.530669972	3.603880176		2

owl 856 - 70 UD

	spruce-fir	ecotone	hardwood	conifer	open	
spruce-fir		-2.371812079	1.479706597	-2.358436132	-1.185034316	1
ecotone	2.371812079		3.851518676	0.013375947	1.186777763	4
hardwood	-1.479706597	-3.851518676		-3.838142729	-2.664740913	0
conifer	2.358436132	-0.013375947	3.838142729		1.173401816	3
open	1.185034316	-1.186777763	2.664740913	-1.173401816		2

Table 4. Multiple chi-square tests of the roosting data show habitat is used differently for different observed patterns of roosting. Owls when roosting at multiple-use area showed a preference for of spruce-fir and its ecotones, whereas isolated roosts were randomly distributed in habitats of owl home ranges.

Habitat Use during Diurnal Roosting

[roosts pooled among owls]			spruce-fir	s-f ecotone	hardwood	other conif	open	x2=	
	%	n=	30	32	9	3	2		
All Roosts	expect		23.391	42.255	21.115389	3.5867452	9.652359	**9.216**	p<0.10
(breeding & post-breeding)	observ		39.473684	42.105263	11.842105	3.9473684	2.6315789		
		n=	27	28	6	1	2		
Breeding Season Roosts	expect		23.391	42.255	21.115389	3.5867452	9.652359	**12.137**	p<0.025
(all of breeding season)	observ		42.1875	43.75	9.375	1.5625	3.125		
		n=	17	19	1	0	1		
Breeding Season Roosts	expect		23.391	42.255	21.115389	3.5867452	9.652359	**26.293**	p<0.001
(multiple-use sites)	observ		44.736842	50	2.6315789	0	2.6315789		
		n=	10	8	6	1	2		
Breeding Season Roosts	expect		23.391	42.255	21.115389	3.5867452	9.652359	**4.3563**	p<0.25
(single-use sites)	observ		37.037037	29.62963	22.222222	3.7037037	7.4074074		

from the Wilks' Λ statistic during nocturnal periods and the lack of statistically significant differences in use between these forest types suggest that these two boreal associated forest types are virtually interchangeable in rank and in importance to the owl during nocturnal activity periods.

The chi-square test for usage versus availability of forest types during day-time roosting revealed differences in both within breeding season and between seasonal period roosting patterns (Table 4). Data pooled among owls showed significant differences in habitat use during the breeding season ($\chi^2 = 12.137$, 4 df, $p<0.05$). Differences in usage from random were not significant when post-breeding season roosts were added ($\chi^2 = 9.216$, 4 df, $p< 0.10$). For breeding season roosts alone, spruce-fir and its ecotones were the only forest types in which roosts were located at greater than expected levels. Conversely, roosting activity over the entire data taking period indicated the use of spruce-fir and "other conifer" at greater than expected levels, while spruce-fir ecotone was used at equivalent to expected levels and all other forest types were used at less than expected levels.

Roosts observed during the breeding season were classified either as components (Table 4) of single-use ($n = 28$) or multiple-use sites ($n = 38$). When χ^2 tests were computed for each of these roosting patterns separately, the difference from random for forest type use at multiple-use areas was found to be highly significant ($\chi^2 = 26.293$, df = 4, $p< 0.001$), whereas forest type use at single-use sites was not significantly different from random ($\chi^2 = 4.356$, df = 4, $p>0.25$). Both spruce-fir and spruce-fir ecotone were used more than expected at multiple-use areas. Conversely, though not significant, roosts at single-use sites were found in spruce-fir, hardwood, and other conifer forest types at slightly greater than expected levels, suggesting a lack of preference for any forest type while roosting at single-use sites vs. a strong preference while roosting at multiple-use sites.

Discussion

Home Range Analysis

Estimating seasonal home-range size is complicated by short-term (within season) and long-term (among season) biological periods of activity. Short-term activity periods can be attributed to different reproductive stages of the breeding season (Harris et al. 1990). Biological demands during mating, nesting and post-fledging stages may cause owls to alter their movements and patterns of activity during each stage of reproduction. Owls may use only a portion of their seasonal home ranges during each breeding stage (Jacobsen and Sonerud 1987). Alternately, long-term shifts in locations of activity have been found to correspond with seasonal changes, which may result in relocations of the home range from season to season (Hayward et al. 1987). Arbitrary time periods used to determine home range size can span more than one reproductive stage or biological season, thus causing exaggerated estimates of home range size for the presumed stage or season (Harris et al. 1990). Estimates of seasonal home range size or of area used during reproductive stages must be linked to data which confirms the biological period of observation (Harris et al. 1990).

The yearly observation periods of this study (May 17 to December 5, 1993 and March 12 to September 9, 1994) were assumed to cover much of the mating, nesting and post-fledging stages of owls in the regional population for each of the two study years. Only after determinations to confirm breeding periodicity were made from calling data (Milling et al. 1997) and from nesting data (Barb 1995) were the yearly periods of observation for all but three owls (owls 185, 260, 856) reassessed as corresponding with nesting, post-fledging periods and early post-breeding stages. Data of these three owls likely only included records from early and mid-periods of the breeding season.

Although not all tagged owl's in this study are believed to have nested, data pooled among owls show differences in activity patterns and in use of seasonal home ranges among progressive stages of the breeding season (Figs. 9 and 10). During the early breeding season (March to April), activity tended to be unsettled for some owls, at which time extended night forays and home range translocations occurred. During the mid-breeding season (May to early July), the nightly travels of owls tended to remain closest to the center of breeding season roost activity. And, during the late breeding season (late July to August), areas used nightly (nightly MCPs) were smallest, while distances varied the most among owls from these areas of nightly activity to centers of breeding season roosting. At this late stage of the breeding season, relatively permanent shifts in locations of activity began to occur, (Figs. 11F) suggesting a seasonal change in centers of activity during this time. It is uncertain whether these changing patterns resulted from actual breeding and nesting activity of tagged owls or from activity patterns that are not necessarily indicative of nesting. Nonetheless, home ranges continued to increase in area for some owls through the yearly observation period (indicated by non-asymptoting cumulative home range sizes; Figs 7 and 8), likely due in part to changing activity patterns of the late breeding season.

In that observation periods for most owls reflect patterns of activity and areas of use corresponding to more than one breeding stage or biological season, observed home range sizes would tend to over-estimate the area used by owls during the predicted nesting period alone (the mid-breeding season period of May to early July). In support, the average home range size in this study (193.7 ha) was larger than home ranges of nesting owls in British Columbia (142 and 159 ha; Cannings 1987). Though factors other than breeding periodicity can affect home range size (i.e., regional differences in habitat or prey availability), the observed changes in areas of use through yearly tracking periods suggest that areas of activity are most limited, thus causing home ranges to be smallest, during the time of nesting. Therefore, despite non-asymptoting home range sizes, the estimated average home range size from this study is believed to adequately represent the area used by most owls during the entire breeding season.

Seasonal Movements

Analyses of post-breeding season roosting activity are based on comparatively few records (5 owls with one to five roost records each). Therefore, interpretations of observed patterns of roosting from late summer to early winter are preliminary and should be treated cautiously.

Roosting patterns of tagged owls tracked into the fall indicated seasonal movements from their high elevation home ranges of the breeding season to locations lower in elevation but likely adjacent to breeding season home ranges during the autumn and winter. Roosting activity during the breeding season was generally confined to an area within or adjacent to each owl's larger area of night activity, (Figs. 11 A-H). During late summer (July and August) and into the fall months, owls took up roosts in new areas not previously used. These new sites were often located lower in elevation than breeding season roosts, and for 2 of the 5 owls (114 and 747) were located closer to the centers of neighboring owl territories (identified from census; Milling et al. 1997) than to the centers of their own breeding season roost activity, suggesting that aggressively defended territory boundaries of the breeding season are dropped during this fall period. Shifts were gradual and incremental in nature, making identification of changing roosting patterns difficult. However, at some point during the late summer or early fall, shifts in locations appeared to become relatively permanent, suggesting a complete shift in locations of roosting activity by season.

Short term relationships between locations of day roosting and night foraging suggest that night activity during the fall would also shift in the direction of fall roosts. When, during the breeding season, roost searches were conducted for owls the day after their night activity had been recorded, these next-day roosts were often found closer in proximity to the previous night's area of activity than were other roosts of the same seasonal period (Figs. 11B, D, E, F, H). This indicates the tendency of owls to roost near recently used foraging areas. These short-term relationships in the proximity of roosting and foraging locations have been observed in boreal owls (*Aegolius funereus*), a close relative of the saw-whet with a similar breeding ecology (Hayward et al. 1987). The tendency of owls to roost near recently used foraging areas suggests that the shift of roosts down slope of breeding season roosting areas during the late summer and fall months would be accompanied by the shift of night foraging activity to the vicinity of those post-breeding season roost locations. Such shifts would result in the complete relocation of each owl's centers of roosting and foraging activity during the fall months and in the repositioning of each owl's home range by season. The beginnings of this seasonal shift are suggested in late breeding season (July and August) patterns of foraging and roosting for owl 747 (Figs. 11 F).

Seasonal shifts occurred asynchronously among tagged owls (Figs. 11A, B, E, F, H), beginning as early as mid-July (747; Fig. 11F) and continuing into September (114; Fig. 11B) and October/November (067; Fig. 11A). The asynchronous nature of these post-breeding season movements may be suggestive of different activity patterns for owls that successfully nested versus those that did not. Owls that fledged young the year they were radio-tagged may remain in breeding season home ranges into the fall to feed and care for fledglings until the fledglings disperse. Whereas, owls than did not successfully nest, have no demands compelling them to stay in their breeding season home ranges, thus may move more independently of breeding season boundaries during this fall time period. A concerted effort was not made to find nests, so this assumption remains unverified.

Post-breeding shifts suggest only short, elevational migrations to overwintering locations. Given that owls were heard in the spruce-fir zone during early March and February of 1993 and 1994, respectively (Milling et al. 1997), and that telemetry data of late season roosting activity located an owl (067) down slope but near its breeding season home range during November and December of 1993 (Fig. 11A), only one to two months of the year are not accounted for relative to the location of at least some males of the southern Appalachian breeding population. Migratory records of saw-whet owl populations in the northern United States and Canada (Cannings 1993) indicate that latitudinal migration regularly occurs for members of those populations in the spring (March to May), after earliest dates of observed territorial activity (i.e., breeding season vocal behavior) for the southern Appalachian population; and in the fall (September to October), before latest seasonal observations of saw-whets in the study areas. This suggests that long-distance migrations do not occur among territorial males of the southern Appalachian population. It appears, rather, that only short-distance shifts in elevation, from breeding season home ranges to overwintering sites, are made by adult males which held territories the previous breeding season. Such shifts may extend greater distances from breeding season home ranges in years of heavy snow cover, but, from these data, territorial male saw-whets apparently linger in areas adjacent to their summer home ranges for much of the fall and winter.

Observations of Potential Nesting Activity

In the absence of direct evidence for nesting by tagged owls, the association of activity patterns to nesting and parental care is only suggestive. However, several sources of evidence point to the possibility that few owls in this study successfully nested.

Roosting activity of owl 856 was markedly different than other owls in this study. Roosting activity for this owl was almost completely confined to a single multiple-use area. Other owls in the study regularly used one or two multiple-use roost areas interchanged with frequent use of single-use sites. Researchers have found parental saw-whet males during the time of nesting to roost in the vicinity of the nest site on a consistent or frequent basis (Webb 1982, Cannings 1987). Therefore, of any owls in the this study, owl 856 exhibited the most comparable roosting pattern to those of nesting saw-whets.

Other evidence comes from patterns of night activity. Sonerud et al. (1986) suggest a potential, though unverified in this study, for detecting nesting activity from nocturnal movements of radio-tagged owls. Nests are potentially detectable from the movement patterns of transmittered parental males, which frequently return to the nest site to bring food and care for nestlings. Given known periods of nesting within the population, observed activity patterns of radio-tagged owls might be used to locate nest sites or, at least, to determine if movements are suggestive of nesting behavior. Overlapping patterns of night activity were indicated for most nights observed by 4 of the 8 owls (maps C - 176, 185, 747, 856), suggesting that these owls showed, through their activity patterns, the greatest potential of having nested. If these patterns do indeed point to actual nesting activity, the implication is that few (approximately 50%) tagged owls nested during the time period each was tracked (the time period, for 6 of the 8 owls, predicted to be the peak for nesting activity in the population).

In the absence of direct evidence for nesting, other possible reasons for the observed patterns of activity should be considered. One possibility is that overlapping polygons of the area used nightly by each owl are not a good indicator of nesting, and that nesting activity was simply undetected or under-estimated. Nonetheless, given that feeding rates of a nesting male saw-whet averaged one prey delivery to the nest each hour over a six hour period (Santee and Granfield 1939), intervals between triangulations (typically 15 min.) in this study and the time span of nightly tracking (averaging 3.75 hrs. per night) should have been sufficient to place a nesting owl within the vicinity of its nest on most nights tracked. However, intervals between nightly tracking events for some owls were at times as much as or greater than two weeks apart. So, it is possible that fledging could have occurred at the nests of one or two tagged owls before enough nights of tracking were conducted to show an overlapping pattern of nightly activity at the nest site.

If, however, nesting activity was consistently detected through the overlapping of nightly activity polygons, some possible reasons for the apparent low nesting rate should be considered. One possibility is that trapping and tagging owls could disrupt nesting. In such a case, only the nesting activity of the sample animals would be effected. Contrary to this possibility, a female saw-whet owl, trapped during a different study, was tagged on the east slope of Grandfather Mountain (located within the breeding range of the southern Appalachian meta-population; Fig. 2) and later nested successfully at a different site on the western side of the mountain (Cooper, Rowe pers. comm.).

Alternatively, if the perceived low nesting activity of tagged owls is actually indicative of the nesting rate for the population as a whole, then two possibilities are likely. Either prey abundance, which fluctuates from year to year causing a positively correlated, cyclic effect on nesting rates of owls (Swengel and Swengel 1995), was at low levels during the two years of the study, or more permanent changes to the owl's breeding environment are occurring, which could adversely effect breeding activity and severely impact the regional saw-whet owl population on a long-term basis. Within the past decade, summer-time temperatures (symptomatic of global warming) have risen to all-time highs. Saw-whet owls exhibit heat stress at 33 degrees C, with mortality occurring when owls are exposed to temperatures above 42 degrees C for even short periods of time (Ligon 1969). High summer temperatures are implicated as a limiting factor in the owl's placement of home ranges to only the coolest habitats (high-elevation spruce-fir and riparian cove forests) within the mid and southern Appalachian regions (Dodge et al. 1999). If these recent summer temperature increases are causing new or additional stresses to owls of the regional population, decreased natality and/or increased mortality rates could result. If indeed these owls are not nesting or mortality has increased in the population due to environmental stresses, population declines may be presently occurring or will occur in the near future. Though merely suggestive, these data point to an immediate need for long-term monitoring and yearly nesting surveys to assess southern Appalachian saw-whet owl population trends.

Habitat Use

On a 2nd order scale of habitat use (where within the region do saw-whets place their home ranges), positional data indicates 87% of the radio-tagged saw-whet owls tracked during the breeding season used the boreal spruce-fir ecosystem intensively. Seasonal activity for 13 of the 15 tagged owls was located in areas where boreal forests dominated or co-dominated the high elevation landscape. Activity of all tagged owls was limited to the upper half to third of valley-to-peak elevations available within the region.

At the population level, these findings support results from previous censuses (Simpson 1972, Milling et al. 1997) which reported population centers to be largely restricted to the region's spruce-fir forests.

Within the southern Appalachian region, isolated encounters of saw-whet owls in various non-boreal forest types during the breeding season suggest that saw-whets might successfully use other forest types for breeding. Accounts from experienced observers, accumulated over the past decade, have identified locations of calling male saw-whets in hemlock cove, pine ridge, northern hardwood and northern red oak forests down to an elevation of 3200 ft during the breeding season (Murdock, Rowe, Hughes pres. comm. and unpubl. data). However, accounts of the owl's use of forest types other than spruce-fir are relatively rare. Moreover, numbers encountered in these atypical (non-boreal) habitats have been very low. Usually only one or two individuals are heard calling from these isolated pockets of activity. Furthermore, though based on very little data, territories in atypical habitats do not appear to be used consistently from year to year (Milling et al. 1997 and unpubl. data), suggesting that these locations are of minimal quality as breeding habitat, and perhaps only used in years with high numbers of breeding-aged owls and ample prey abundances to support breeding activity in marginal habitat. Results from this study and from regional censuses of forest types at high and mid-elevations (Simpson 1972, Milling et al. 1997) confirm the owl's consistent use of only the region's high-elevation boreal forests during the breeding season. Additionally, nesting activity of saw-whets has only been confirmed in forests associated with the boreal spruce-fir (Mayfield and Alsop 1992, Barb 1995 and Boynton, Cooper pers.

comm.), indicating that, within the southern Appalachian region, the boreal spruce-fir is the owl's primary breeding habitat.

Habitat quality has been found to affect territory occupancy in populations of Tengmalm's owl. Korpimaki (1988) demonstrated a relationship between territory quality (based on vegetative cover types) and occupancy, where fewer poor-quality territories were occupied during years of low prey availability, but high-quality territories were filled most years regardless of prey availability. Korpimaki observed that while prey base may ultimately determine population density, needs of owls for roosting, nesting and shelter from predators must also be met by the habitat. Thus, habitat quality is affected by conditions which support adequately large prey bases, as well as habitat features that meet the owl's requirements for roosting and nesting.

Differences in observed densities of saw-whet owl territories across high elevation boreal landscapes may be attributable to differences in habitat quality. Within the boreal spruce-fir zone, differences in owl territory densities were noticed between local landscapes containing spruce-fir stands of greater than 40 hectares with minimal fragmentation between stands, and landscapes containing smaller stand sizes of spruce-fir with greater distances between stands (Milling et al. 1997 and unpubl. data). Highest densities of owls (> 1 per km^2) were found in areas with large, contiguous stands of spruce-fir. Additionally, territories in landscapes composed predominantly of boreal associated forest types were the most consistently occupied during the two-year study. Of all locations of territories found during the census, 45% of those in landscapes dominated by spruce-fir (multiple stands, each of 40 ha or greater) were occupied during both years of census, whereas only 28% of territories in landscapes with spruce-fir as a minor landscape component were occupied during both years.

Poor habitat quality may have been a factor in the translocation part-way through the breeding season of one owl (856) from the location it was trapped and radio-tagged. The site where this owl was trapped contained only small, scattered stands of spruce that were devoid of well-developed evergreen thickets in the lower vegetative layers. This owl translocated to a new home range 3 km from the trap site in late April, 1994, three weeks after it was trapped and tagged.

These observations suggest that preferred sites for home ranges (corresponding with Korpimaki's territories of high quality) are located where spruce-fir forest dominates the high elevation landscape. Landscape conditions for saw-whets which correspond to Korpimaki's habitats of high, medium and low quality might be inferred from these data. Highest quality landscapes would be those of contiguous spruce-fir or of multiple, minimally fragmented stands, each of 40 ha or greater. Medium quality landscapes would contain smaller, scattered stands of spruce-fir, which are isolated by greater than 1 km from more contiguous boreal forest. And low quality would be those habitats other than spruce-fir which are sporadically used by saw-whets.

Analyses of habitat use on a 3rd order scale (do saw-whets use certain habitat types within their home ranges preferentially) reinforce observed patterns of 2nd order habitat selection for high-elevation boreal forests. Though the data obtained of owl movements and habitat use varied widely among owls, results show that 13 of 15 saw-whets limited their movements and activity patterns to locations where spruce-fir or spruce-fir ecotone was present. Of the 13 owls residing in boreal forests, locations of day roosts appeared to be more confined to stands composed predominantly of boreal components than did areas used for night activity and foraging (Fig. 6). However, during their nightly travels, these 13 owls rarely ventured more than a few hundred meters from stands of spruce-fir or spruce-fir ecotone.

Compositional analysis of habitat use during nocturnal activity periods for 7 owls with the largest data sets indicates that most night activity (moderate use areas) of saw-whets occurs largely within spruce-fir associated forest types and that saw-whets select boreal associated forests, primarily the spruce-fir ecotone with hardwood forests, as core areas (high use areas) for foraging (Table 3A, Figs. 13 A-G).

Compositional analysis of night activity determined open habitats to be used more than expected when compared to hardwood or "other conifer" forest types. Though a selection for open habitats for foraging might be interpreted from these results, accounts of saw-whet foraging ecology should first be examined more closely. Cannings (1993) states that saw-whets will utilize open habitats during foraging. Contrarily, a study of habitat partitioning among five owl species in Idaho found that saw-whets forage in denser forest conditions than do western screech (*Otus kennicottii*) or boreal (*Aegolius funereus*) owls (Hayward and Garton 1988). And, two studies of saw-whet prey preferences, (1) - a multi-year study in Wisconsin (Swengel and Swengel 1992a) and (2) - a winter study in Ohio (Randle and Austing 1952) determined that saw-whets predominantly took forest dwelling small mammal species. In fact, analysis of prey remains in regurgitated pellets from radio-tagged owls in this study (Cockerel 1997) indicates a diet consisting primarily of small mammals from woodland habitats. Of the four small mammal species found at highest frequencies in saw-whet pellets (together comprising 82.2% of all prey items found), two species - the deer mouse (*Peromyscus maniculatus*) and the masked shrew (*Sorex cinereus*) are habitat generalists, while, two others - the red-backed vole (*Clethrionomys gapperi*) and the smoky shrew (*Sorex fumeus*) are forest dwellers (Burt and Grossenheider 1980, Allen 1979).

One possible interpretation of results from compositional analysis might be that open areas were not actually used to the extent indicated. Open habitats, primarily roads, within owl home ranges are located within and between stands of spruce-fir (Figs. 13 A - G), therefore 90 and 70 % UD contours would likely include the borders with open habitats in their areas of usage, even if owls generally foraged within spruce-fir stands. Alternatively, saw-whets may use open habitats to some extent. Two types of open habitats were pooled in this category, those covered by herbaceous vegetation (meadows and mountain balds) and those of disturbed or exposed soil conditions (barren or paved areas). Core areas of 5 of 6 owls with roadways in their home ranges were located at or along the roadways (Figs. 13 A - E). Conversely, larger open areas in some owl home ranges were not utilized or were used only at moderate-use levels (Figs. 13 D - F). Roadways create narrow openings in the surrounding forest cover (typically no wider than 20 to 30 m). If saw-whets are using roads for foraging, the owls might actually be selecting suitable conditions within forest stands, such as treefall gaps or road openings, rather than stand-level conditions, such as the edges of large non-forested area, for foraging sites.

Owl roost sites of the breeding season were found in spruce-fir more frequently than expected (Table 8). Roosting patterns of individual owls indicated the frequent use of one or two (multiple-use) areas interchanged with one-time use of other, scattered (single-use) sites within the home range. When χ^2 analysis was conducted on each of these roosting patterns individually, habitat use at single-use sites was not different from random, whereas the use of habitat types at multiple-use areas was found to be highly significant, with spruce-fir selected preferentially to other habitats within owl home ranges.

Habitat preference differences between single and multiple-use roost sites suggest that owls use these two types of roost sites for different purposes. Statistical analysis shows a selection for specific forest types (spruce-fir and spruce-fir ecotone) only when roosting at multiple-use sites. Little or no preference was indicated for a selection of forest types when owls roosted at single-use sites, suggesting that these locations may be used opportunistically, based on movements of each owl the night before, and are of little importance to activity patterns of the owl within its home ranges. The high level of significance in the selection of forest types at multi-use areas and the close proximity of these areas to core areas of night activity suggests that these areas are of central importance to each owl's activity patterns. Because of this, suitable forest conditions necessary for establishment of multiple-use roosting areas may be critical to the placement of owl home ranges within the spruce-fir zone.

Cases of atypical habitat use

The movements of only two owls indicated patterns of activity away from the spruce-fir zone for extended periods of time. One of these two owls (767, in the Great Balsam Mountains) roosted predominantly in an extensive rhododendron thicket within a hardwood cove and foraged in the hardwood forests surrounding the cove. The other owl (926 on Roan Mountain) was found roosting in hardwood forests where a dense shrub layer of rhododendron and hardwood saplings was available, and appeared to make heavy use of mid-elevation hardwood forests for foraging with occasional returns to the spruce-fir zone. Both of these owls were trapped at locations where the dominant forest type was spruce-fir or spruce-fir ecotone and where vocal activity (presumably that of these owls) was heard for weeks prior to trapping.

Factors pertaining to human activity in the home range of owl 767 and to sex or breeding status or competition of owl 926 may have caused these owls to alter their activity patterns. Owl 767 was trapped from a 57 hectare stand of spruce mixed with northern hardwood, which is isolated from other boreal forest stands by >8 km and [as part of a mountaintop resort] is subject to intensive human activity during the tourist season. The owl's departure from this site coincided with the opening of the resort and the increase of human activity in the spring. Owl 926 was trapped at a location of intensive spring-time vocal activity, where at least two (occasionally three) saw-whet owls were heard calling. Using the wing-mass discriminate function (Brinker unpubl. manusc.), wing-cord and mass of this owl indicates that it was a male. The response of this owl, by its departure from the area 3 weeks after the trapping date, may suggest it was a subordinate male who surrendered his territory in the spruce-fir due to competitive pressure.

Only one other owl (owl 223 from the Black Mts.), for which very little data were obtained, exhibited a similar elevational translocation before the post-breeding season. The wing-cord and body mass of this owl suggests it was likely a female. Ergo, owl 926 was a subordinate male displaced downslope by competition and owl 223 was an unpaired female, an elevational separation may exist in the home ranges of breeding owl pairs and non-breeding owls (adolescent males and unpaired females). However, the lack of responses from auditory census at elevations below 1500 m (Milling et al. 1997) indicates one of two possible scenarios. Either owls, if present at these lower elevations, do not respond vocally to conspecific male territorial calls (as do breeding males) and are not likely to be of breeding status, or, very few owls occupied mid-elevation home ranges in the years of this study, indicating that saw-whet owl populations at each mountain range were largely contained within the elevational range and spatial distribution of spruce-fir forests.

Habitat Carrying Capacity for the Regional Saw-whet Population

The size of the regional population, originally determined from densities of owl territories along auditory census transects in high and mid-elevation forests (Milling et al. 1997), was estimated to be within the rather broad range of 150 to 400 breeding pairs due to different densities of owls heard from each of the three study areas and different estimates of total spruce-fir in the region. This range includes a twenty percent addition to population totals estimated for the spruce-fir alone to account for owls nesting in atypical habitat, thus should be considered a generous estimate. To revisit the question of population size, this time to estimate regional carrying capacity of saw-whet breeding territories (the projected maximum number of territories the habitat can hold according to the amount of spruce-fir utilized by each owl), a suitable estimate of total regional spruce-fir was needed. Maps of spruce-fir forests from Dull et al. (1988) closely mirror spruce-fir stands (> 70% spruce-fir) delineated within each owls home range in this study, thus Dull et al.'s region-wide spruce-fir estimate was used to extrapolate carrying capacity.

The total area of spruce-fir region-wide is estimated to be 26610 ha (Dull et al. 1988, SAMAB 1996). I divided the amounts of spruce-fir in owl home ranges (ranging from 51 to 86 ha) by the regional estimate of spruce-fir. Based on these values, the regional carrying capacity is estimated to be 309 to 521 territorial males. The population size estimates from auditory census indicate that only 34.4% to 69.5% of available spruce-fir was occupied during the years of this study. Indeed, during census, gaps were observed between occupied territories where apparently suitable spruce-fir habitat existed (Milling et al. 1997 and unpubl. data).

This suggests that factors other than habitat alone are limiting the population size of saw-whets in the southern Appalachians. Korpimaki's (1988) examination of habitat quality may apply here; where a low prey base or less-than-adequate conditions may limit territory occupancy in some years to only territories of highest quality. However, more insidious and long-lasting problems may be confronting the owl population if global warming or boreal forest decline is compromising suitability of regional habitat.

Conclusion

During the breeding season saw-whet owls consistently selected forests of spruce-fir or spruce-fir/hardwood ecotones at frequencies greater than expected for diurnal roosting (table 4) and nocturnal foraging (table 3B). Such strong preferences for a particular forest type are apparently unique among saw-whet owl breeding populations in North America (Cannings 1993). For example, breeding populations in the northeastern United States and eastern Canada have been found in various deciduous and coniferous forest types of both upland and lowland ecosystems (Cannings 1993, Forbes and Warner 1974). Populations in western North America and Mexico are essentially restricted to montane or riparian ecosystems, but are known to occupy a variety of coniferous and coniferous/deciduous mixed forest types within those ecosystems (Webb 1982, Hayward and Garton 1988, Binford 1989). In contrast, results from this study and from censuses of the regional population (Milling et al. 1997, Simpson 1972), indicate that saw-whet owls of the southern Appalachian meta-population (specifically, mature males which establish breeding season territories) choose forests of spruce-fir as their primary breeding habitat, though saw-whets apparently occur at lower densities (perhaps largely as the non-breeding demographic) in other high and mid-elevation forests of the region.

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VITA

Timothy Charles Milling was born in Asheville, North Carolina, on October 6, 1960. He attended elementary schools in that city and was graduated from T.C. Roberson High School in June 1980. The following August he entered Brevard College, and then completed requirements for his B.A. degree in 1985 at Warren Wilson College.

Tim entered the work force following graduation. From June 1987 to December 1987, he served as a Forestry Technician for the U.S. Forest Service, where he worked on "Oak Decline" and gypsy moth projects. From January 1998 to April 1988, he worked as a Survey Technician with Hampton, Hintz and Associates in Fletcher, N.C. In April 1988, he moved to Charleston S.C., to accept the position of Biological Technician with the U.S. Forest Service. Tim served as supervisory technician for research of the endangered Red-cockaded Woodpecker (*Picoides borealis*) in the Francis Marion National Forest. Work consisted of trapping with mist nests and color banding birds to gathering data on nesting success, clan composition, home range, habitat preferences, roost cavity competition and population status. After Hurricane Hugo devastated colony sites, work shifted to habitat restoration. Tim received a Congressional Award for his successful work on habitat restoration.

Tim left his job with the Forest Service in 1992 to pursue a Master's degree in Biology at Appalachian State University. During the period of his graduate work, he held several contract positions with the U.S. Forest Service and other agencies. He married Marla Hardee on April 22, 1995, and celebrated the birth of a son, Benjamin, on October 29, 1997, and the birth of a daughter, Hannah, on December 28, 1999.