HABITAT SELECTION BY THE RED-BACKED VOLE (*MYODES GAPPERI*) IN THE BOREAL FOREST OF NORTHERN ONTARIO

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ABSTRACT

HABITAT SELECTION BY THE RED-BACKED VOLE (*CLETHRIONOMYS GAPPERI*) IN THE BOREAL FOREST OF NORTHERN ONTARIO

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Habitat selection studies provide insight into what species require for survival and successful reproduction. I examined habitat selection by red-backed voles (*Clethrionomys gapperi*) in two boreal forests in Northern Ontario. Previous studies identified a number of habitat features selected by red-backed voles. This variation may be an artefact of resource availability or spatial extent and resolution at which studies have been conducted. To test the influence of spatial resolution on habitat features a generalized mixed-effects model was used to assess habitat selection, while accounting for spatial resolution.

Trapping was conducted biannually (spring and autumn) for two years in two study areas (Kapuskasing and Ear Falls, Ontario), in different landscapes (logged and unlogged) and in a variety of forest stand types. My results show that spatial resolution affected the perception of which habitat features were selected voles, explaining 45% of the variation in the data. Horizontal vegetation density, volume of fine woody debris (<10 cm diameter), soil moisture, lichen, and fern cover, and season also influenced habitat selection, explaining an additional 10% of the variation in the data, suggesting that these habitat features are preferred by red-backed voles.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Wildlife species, in general, do not distribute themselves randomly in space and time (Boyce and McDonald 1999). Habitat selection studies help to identify potential causal factors for the presence of a species. Not only is habitat useful in ecological studies, it is essential for evaluating and conserving vital resources used by species in their environments (Morris 1987, Boyce and McDonald 1999, Manly et al. 2002). Knowledge of a species' resource use provides insight into its needs for survival (Manly et al. 2002). By combining knowledge of resource use, habitat selection, and life history requirements of a given wildlife species, it may be possible to gain insight into the needs of a species or population. However, despite the general acknowledgement of its importance and its frequent occurrence in the literature, habitat selection remains one of the most poorly understood ecological processes (Krebs 2001).

Individuals are considered to select habitat when they are more closely associated with particular habitat features than would be expected by chance (Boyce and McDonald 1999, Manly et al. 2002). Habitat selection studies assume that species select resources (consumable) or conditions (non-consumable) that enhance their fitness, and therefore high quality habitats will be selected over low quality ones (Begon et al. 1996, Kingston and Morris 1999, Manly et al. 2002). Of course, the validity of this assumption is dependent on resource and condition availability. As the availability of high quality resources decreases, lower quality habitat patches may be used with increased frequency.

Some researchers suggest that small mammals are potential indicators of ecosystem function owing to their role in distributing seeds and fungal spores, physically mixing soil and decomposed matter, and providing food to predators (Allen 1983, Carey and Harrington 2001). Red-backed voles (*Myodes gapperi*, formerly *Clethrionomys gapperi*) are one of the most abundant small mammals in the boreal forest ecosystem and are an important food of several carnivores, such as boreal owls (*Aegolius funereus*) and and American marten (*Martes americana* ; Allen 1983, Coffin et al. 1997, Keinath and Hayward 2003, Cheveau et al. 2005). Changes in abundance of martens have been positively correlated with changes in abundance of small mammals (Thompson and Colgan 1987, Fryxell et al. 1999). Orrock et al. (2000) have linked the presence of red-backed voles to other small mammal species, including water shrew (*Sorex palustris*), rock vole (*Microtus chrotorrhinus*), and northern flying squirrel (*Glaucomys sabrinus*), owing to their similar habitat requirements.

Despite the many studies that examined habitat selection by red-backed voles (e.g., Martell 1981, Allen 1983, Keinath and Hayward 2003), there is little general agreement about the habitat features that they select or avoid. Among the contradictions are information regarding cover, nesting, and diet-related variables. A review of studies suggests that red-backed vole diet varies with location. In eastern North America, red-backed voles are thought to mostly consume herbaceous vegetation and insects, whereas in western North America they are thought to consume mostly hypogeous fungi (Allen 1983, Terwillinger and Pastor1999). Other studies have suggested that food choices were varied, depending on the successional stage of the forests (Schloyer 1977). In Ontario, Martell (1981) found that, although red-backed voles were opportunistic in their food choice, lichen and epigeous fungi (mushrooms and puffballs) accounted for 95-100% of the diet of red-backed voles, depending on the month. Other important seasonal food items included new green vegetation, seeds, and berries (Schloyer 1977, Martell 1981).

The habitat variables that are most strongly associated with the presence of red-backed voles often concern cover. Keinath and Hayward (2003) suggest that a closed overstory canopy is the most influential factor in habitat selection by red-backed voles, whereas other studies suggest that abundant shrubs and forbs are essential (Allen 1983, Wywiaslowski and Smith 1988). Downed woody debris, including coarse (diameter ≥ 10 cm) and fine woody debris (diameter <10 cm) are thought to enhance the ability of voles to avoid predators, by providing travel runways, and cover (Allen 1983, Bowman et al. 2000, Andruskiw 2004). Additionally, downed woody debris is thought to promote fungal growth (Allen 1983, Higgelke and MacLeod 2000). Although most studies agree that red-backed voles select for coarse woody debris, the size, type, decay class, and amount selected is still debated. Additionally, most studies have not examined the effects of fine woody debris on the presence of red-backed voles. Moisture is generally accepted as a limiting factor in the distribution of red-backed voles (Getz 1968). They are thought to be able to potentially occupy almost any habitat, because of the availability of water found in foods such as succulent plants, and moisture in soils. Studies report that red-backed voles have a preference for mesic sites, especially moist conifer or mixed-wood stands with fine soil (Allen 1983, Kingston and Morris 1996, Boos and Watts 1997).

Inconsistent habitat selection patterns by red-backed voles may result from variation in the availability of resources and/or the different scales of analysis among studies. Individuals may respond to their environment at different spatial scales (Holland et al. 2004). This is an important consideration when collecting data, since the scale at which habitat variables are collected can influence the outcome of habitat models (Boyce and McDonald 1999). Habitat selection is thought to occur in a hierarchical manner, starting at the geographic range of a species, then sequentially narrowing to the home range, to habitat features in a home range, and finally to particular features or resources within habitats (Johnson 1980, Manly 2002).

Many studies of resource selection by red-backed voles have lacked replication, been representative of few forest stands types, or were conducted only at a single spatial scale (Orrock et al. 2000, Jorgensen 2004). Of those studies that examined the effects of spatial scale, processes occurring at a regional scale have been suggested to play a stronger role in habitat selection than those at a local scale (Bowman et al. 2001, Holland et al. 2004, Jorgensen 2004). Examples of regional processes that may affect habitat use include inter- and intraspecific competition or the risk of predation, whereas examples of local processes include the availability of mates or food, shelter and cover (Morris 1987, Bowman et al. 2001). Predators and prey may overlap in requirements in habitat selection, suggesting that predators may occupy areas that are perceived optimum habitat for their prey. Conversely, prey may occupy habitats that offer escape routes or cover from predators. Due to their position in the food chain, it has been suggested that red-backed voles select habitats at a regional scale (Morris 1987, Orrock et al. 2000).

I studied habitat use by red-backed voles at two sites in northern Ontario, each of which contained both logged and unlogged landscapes. Two study sites were choosen in order to compare habitat selection by red-backed voles in different areas of boreal forests in Ontario that are undergoing similar pressures. By sampling multiple forest stand types available to red-backed voles, I assessed the degree of preference for habitat features in proportion to their availability (Boyce and McDonald 1999). If red-backed voles select solely for specific habitats (i.e. local level), then the inclusion of relevant habitat covariates should improve the predictability by resource selection models. However, if red-backed voles select habitat due to influences at the regional level, then scale covariates (as measured by the sampling resolution) will improve the predictability of resource selection models. The objective of this study was to evaluate effects of scale on habitat selection by red-backed voles and to determine small scale, site level predictors of habitat use

METHODS

Study Area

This study was conducted from May 1 – October 30 in each of 2005 and 2006, in two regions of boreal forest in Ontario: Ear Falls (northwestern Ontario; 50º38’N, 93º13’W) and Kapuskasing (northeastern Ontario; 48˚48’N, 82˚33’W) respectively (Figure 1). Each site comprised both logged (approximately 50 years old) and unlogged landscapes. Logged landscapes were comprised mostly of young mixed stands, whereas unlogged landscapes were comprised mostly of old-conifer and mixed stands (Table 1). Forest stands in Ear Falls were dominated by jack pine (*Pinus banksiana*), black spruce (*Picea mariana*), trembling aspen (*Populus tremuloides*), with some white birch (*Betula papyrifera*), and balsam fir (*Abies balsamea*). Forest stands in Kapuskasing were only somewhat similar to those at Ear Falls in species composition, with more mixedwoods, more balsam fir, and sparse jack pine. Details regarding each of these study areas are in Thompson et al. (2007).

Red-backed Vole Data Collection

Sampling was conducted to assess red-backed vole habitat selection across forest stands, with equal replication in logged versus unlogged areas, and in two different ecological zones of Ontario. As part of a larger collaborative study design, I arbitrarily chose to place traplines in areas occupied by marten (hereby referred to as sampling area). Each sampling area was much larger, however, than the expected lifetime home range of an individual red-backed vole. The average dispersal distance of transient red-backed voles is 60 m (Perrin 1979). Hence, my study measures resource selection across the spectrum of resource types than any single animal might reasonably be expected to experience during its lifetime. Forest stand types were based on custom forest stand classifications formed from Forest Resource Inventory maps obtained from the Ontario Ministry of Natural Resources and analysed using Geographic Information System (GIS).

Paired traplines were placed in each forest stand type, composed of two 50 m parallel traplines separated by 100 m. The assumption of independence between traplines was satisfied by ensuring that traplines were placed at distances greater than the average dispersal distance of red-backed voles (Perrin 1979, Allen 1983, Higgelke and MacLeod 2000). Two 3 x 3 x 10" Sherman traps (H.B. Sherman Traps, Tallahassee, Florida, USA) were placed approximately 1 m apart at 10 m increments along each trapline (Figure 2).

The actual location of each paired trapline was chosen by placing one of the two traplines on marten travel trajectories, found by snow tracking during the winter of 2005 and 2006 (see McKague 2007 for details). If possible, a segment of the trajectory showing signs of predation was chosen over a segment showing a straight-line pattern indicative of travel. If a forest stand type in a sampling area did not have a known travel trajectory, then a paired trapline were placed at random locations in each stand type to maximize the sampling of the vegetation types across the sampling area.

Small mammal trapping sessions were conducted in spring (May-June) and autumn (August-October). Traps were baited with oats and peanut butter, supplied with cotton to act as bedding and thermal insulation, and covered with moss or leaf litter, to provide shelter. When possible, the traps were placed adjacent to downed woody debris, otherwise they were placed at the base of a tree or stump. The placement of traps next to coarse woody debris has been found to increase capture rate (Bowman et al. 2001, Keinath and Hayward 2003). Traps were set for 3 consecutive nights and checked daily. Traps were recorded as open, closed, inactive, or a capture, noting the species of capture. In the case of a captured red-backed vole, each animal received a No. 1 monel ear tag (National Band and Tag Company, Lexington, Kentucky, USA), for individual recognition. Upon subsequent captures in a trapping session, the ear tag number was recorded and the animal was released.

Habitat Variables

Five spatial extents were analysed, study site, landscape, sampling area, trapline, and trap site (Table 2). I measured 16 habitat variables for predicting the presence of red-backed voles (Table 2), based on findings from previous studies of red-backed vole habitat selection (Table 3). Data from six vertical vegetation strata at the trap site extent were collected: overstory, understory, shrub, herbaceous, canopy and soil/litter level. These variables were collected at sites where red-backed voles were present (i.e., used) and where they were absent (i.e., available).

Species Captures Per Unit Effort

Captures per unit effort (CPUE) were calculated for each species in this study in order to compare abundance between different seasons and study areas. Calculations of CPUE were converted to catches per 100 trap nights (C/100 trap nights):

$$\text{CPUE} = \frac{\text{\# Individuals of Species of Interest}}{\begin{array}{c}\text{(\# Open traps + \# Individuals of Species of Interest + (0.5* \#Closed traps) +} \\ \text{(0.5* \# Bi-catch (i.e. all individuals not of the species of interest)}\end{array}}$$

where species represented the number of captures for each species, open trap represented a functional trap that was open, closed trap represents a functional trap that did not yield a capture but was triggered, and bi-catch represents capture of any other species. Since only red-backed voles were tagged for individual recognition, each red-backed vole capture was treated as a unique event.

Statistical Analyses

To eliminate multico-linearity, a Spearman's rank correlation matrix was used to examine all predictor variables. In cases of highly correlated variables, only one variable was retained ($r > 0.5$; Burnham and Anderson 2002; Table 2). Using the predictor variables, four subset models were created, based on habitat features selected in recent studies based on understanding of the biology of red-backed voles. The categories were as follows with the model name in parentheses: food source (food), habitat structure (travel), cover from predators or for nesting (cover), and the most cited variables from previous published studies (literature; Table 3). In addition to these four sub-set models, a maximal model that used all variables was tested. A two-fold approach was used, comparing binary logistic regression with generalized linear mixed models. Each method analyzed the same four multivariate models and the 13 univariate habitat selection models for each study site and season, in order to assess any seasonal or regional differences in selection

Pseudoreplication has been found to be a particular problem with small mammal trapping (Hurlbert 1983). Temporal pseudoreplication was a concern in this study, since trapping occurred at the same sites but at different times (i.e., spring and autumn) and over different years. Spatial autocorrelation was also a concern from the close proximity of trap sites along the traplines. I was able to control for autocorrelation and pseudoreplication by using generalized linear mixed models, using the lme4 package in R 2.5.0. This procedure also allowed me to identify which spatial resolution accounted for most of the variation in vole presence is accounted for. Recent research has identified resolution as an important aspect to consider (Orrock et al. 2000, Jorgensen 2004). Specifically, all different resolutions of the sampling design (i.e., study site, landscape, sampling area, trapline, and position) were included as random effects in the model (Table 4). These 6 levels of resolution are as follows with the average distance between traps within each level in parenthesis: trap sites within a trapline (represented by 10-50 m), trap sites between trap lines (100 m), within a sampling area ($\bar{x}$ = 938 m), within a landscape ($\bar{x}$ = 25 km), within study area ($\bar{x}$ =2349 m) and between study areas (approximately 1090 km). After accounting for the grouped data structure, I evaluated the effect of the habitat covariates on red-backed vole presence/absence by fitting them as fixed effects. Random effects influence the variation of the presence/absence of red-backed voles, whereas fixed effects influence the mean (Crawley 2002). Thus, by including random variables in the model, potential sources of variation other than the fixed variables are reduced. For further details on mixed effects models see Pinheiro and Bates (2000).

Due to the large number of potential combinations of variables, which would have precluded analysis with interaction terms, a backwards elimination process was performed. Akaike's information criterion (AIC) values were calculated with adjustments for small sample size (AIC_c) to compare the univariate and multivariate models in the binary logistic model. *AIC* was calculated for each model. Model parsimony was scored using the following equation:

$$\Delta_i \, AIC = AIC_i - \min AIC$$

where *i* represents the candidate model for comparison and min *AIC* represents the candidate model with the lowest *AIC* score (i.e., the best of the candidate models, Burnham and Anderson 2002). Similarly *AIC* values (without adjustments for large sample size) between models were determined for model comparison in the mixed effects models. Backwards simplification of the maximal model into the most parsimonious model that adequately explained the data, was achieved using AIC values with a P value < 0.01 . Part of the process of determining the most parsimonious model was the removal of all non-significant two-way interactions between the remaining variables (Crawley 2005).

Since these models had a number of similar variables, two-way interactions were then examined to increase parsimony, again using a backwards elimination (Crawley 2005). During preliminary model fitting, variables were arc sin transformed to normalize the data and reduce any potential problems with normality of distributions. Using Markov chain Monte Carlo methods, a 95 percent confidence interval for each parameter estimate was obtained (Crawley 2005). SPSS 9.0 software (SPSS Inc 1998) was used to perform all statistical analysis, except the generalized mixed effects model, for which R 2.5.0.was used (R Development Core Team 2006).

RESULTS

Small Mammal Trapping

A total of 698 individual red-backed voles were trapped on 11,787 trap nights during the 2-year study. Red-backed voles accounted for the majority of small mammal captures (64%) among 12 species captured (Appendix 3). The captures per unit effort for red-backed voles was higher in Ear Falls (12.128/100 trap nights) than at Kapuskasing (7.21/100 trap nights).

Habitat Selection by Red-backed Voles

The cover model was ranked among the top models for autumn in both study sites (Table 5). Spring yielded different results between the two study sites, with the literature model ranked as the top model in Ear Falls and horizontal density ranked as the top model in Kapuskasing. Multivariate models clearly outperformed the univariate models, with one exception for spring at Kapuskasing. However, no clear overall pattern emerged from the model comparison using this method (Table 5). Additionally, top ranked models contained several non-significant variables and poorly fit the data ($r^2 < 0.15$ in all cases).

A generalized mixed effects model was a better fit to the data than the simple binary logistic regression. This latter model showed marked spatial resolution effects at the sampling area, trapline, and position along the trapline scale that accounted for a large part of the deviance ($r^2 = 0.45$). Both study site and landscape were not significant variables, as either a fixed or random effects, as was the case for between paired lines. After accounting for the different spatial resolutions, the maximal model generally outperformed all other models ($\Delta AIC > 10$). The one exception was the cover model, which received similar support ($\Delta AIC \sim 2$). Nevertheless the models were complex, with several non-significant variables retained. Additionally, the effect of interactions between the variables had not been considered. Thus, a post-hoc analysis was conducted, to firstly simplify the maximal model, and secondly, to investigate all the two-way interaction terms that may be obscuring the impact of variables (Crawley 2005).

The post-hoc analysis produced the most parsimonious model, with substantially improved fit over that of the simple binary logistic regression model (Table 6). The resultant model explained 55% of the variation in the data ($r^2 = 0.55$). Parameter estimates, represented as fixed effects, explained 10% of the variation and were highly significant ($p < 0.01$). Lichen had a slightly negative association with the presence of red-backed voles, whereas soil moisture, horizontal density, fern, fine woody debris, and season were positively associated with red-backed voles. Two-way interactions in the model received substantial support and were found to be highly significant ($p < 0.01$). The model indicated a positive interaction between lichen and soil moisture, suggesting a positive relationship between the presence of red-backed voles and soil moisture as lichen increased. Conversely, the interaction between fine woody debris and lichen, as well as fine woody debris and fern, was negative. Thus, the strength of the positive relationship between the presence of red-backed voles and fine woody debris decreased as lichen or fern increased (Table 6).

DISCUSSION

Considerable discussion in the habitat selection literature has been about the most appropriate scale for measuring a species' interaction with its environment (Morris 1987, Holland et al. 2004, Jorgensen 2004). The results from this study suggested that study site and landscape type did not have a significant effect on the presence of red-backed voles. Thus, primary determinates for habitat selection may have been at the regional, rather than the local level. Although random effects of sample resolution explained most of the variation, vegetation variables at the finest resolution were significant. This finding was consistent with Bowman et al. (2001), who found that the strength of relationship between vegetation and small mammals depended on resolution. Other studies have suggested that red-backed voles primarily select habitat at coarse spatial scales rather than fine spatial scale, because of adaptive mechanisms that microhabitat variation does not explain (Morris 1987, Orrock et al. 2004). These results suggested that both micro and macro scales of resolution are necessary to explain habitat selection by red-backed voles in the boreal forests.

Comparison of the performance of simple binary logistic models and the generalized linear mixed effects models suggested that the mixed effects models better resolve some of the variability in the data. Generalized linear mixed effects models are powerful tools for analyzing grouped data, because they are flexible and identify within-group correlation often present in these types of data (Pinheiro and Bates 2000).

The favoured variables in the most parsimonious model contributed to either cover (fern, fine woody debris, horizontal density), and/or food (lichen, fine woody debris, and fern). Red-backed voles are believed to be physiologically limited by water

(Getz 1968; Orrock et al. 2000). Water can be obtained from saturated soil, free-standing water, or through consumption of succulent plants and fungi. The availability of moisture-rich foods may allow red-backed voles to use drier, upland areas (Getz 1968, Allen 1983). This could also explain why soil moisture was positively associated with red-backed voles in my study. The decrease in vole presence predicted by lichen is likely a covariate influence whereby areas that are lichen rich have little ground cover and vice versa (McCarthy et al. 1994).

Carey and Harrington (2001) suggest that habitat complexity may increase the total useable space and thereby increase habitat suitability. More complex habitats are also believed to increase the abundance of seeds, fungi, fruiting plants and invertebrates that are important components of the diet of red-backed voles. It could be that habitat complexity could be a surrogate for food and shelter availability. My results compliment other studies that have also found that red-backed voles prefer areas with high structural complexity (Coffin et al. 1997, Carey and Harrington 2001).

Several studies have identified coarse woody debris as an important predictor of habitat use for small mammals, because of its diverse ecological function as cover, nesting habitat, and association with food sources, such as fungi (Allen 1983, Carey and Johnson 1995, Higgelke and MacLeod 2000). Downed woody debris is thought to trap water, thereby promoting fungal growth (Allen 1983, Higgelke and MacLeod 2000). Fungi are an important source of food for red-backed voles (Martell 1981, Terwilliger and Pastor 1999), thus fine woody debris may act as a surrogate predictor of food availability. Martell (1981) found that both lichen and fungi were a mainstay of red-backed vole diets in Ontario (Martell 1981). My results show that red-backed voles tended to avoid locations with lichen, which appear to contradict the findings of Martell (1981). However, there may be a threshold of lichen abundance above which other ground cover is much reduced and therefore such areas are avoided by red-backed voles. In my study, lichen was only measured at the ground level or on downed woody debris. In addition, red-backed voles can climb trees in search of lichen (Martell 1981), so the amount of available lichen may have been underestimated.

Previous studies of red-backed voles report that areas with 25% coarse woody debris cover yielded more than three times as many red-backed voles as areas with less debris (Allen 1983), whereas my study indicated that coarse woody debris was a poor predictor of habitat selection. One explanation might be that all of the habitats meet or exceeded the minimum requirements for coarse woody debris that are necessary to sustain voles. Additionally the trapping design of placing a trap close to downed woody debris could have conceivably biased the results. I consider this unlikely, however, because the methods used in this study mirror other studies that have found coarse woody debris to be an important variable (Boos and Watts 1997, Bowman et al. 2000, 2001). Another consideration is inconsistent definitions of coarse woody debris and fine woody debris in the literature. Like several previous studies, I defined coarse woody debris as any downed woody material with a diameter of ≥10 cm (e.g., Wywialowski and Smith 1988, Orrock et al. 2000). Some other studies, however, have used a diameter < 10 cm (e.g., Allen (1983) and Coffin et al. (1997) used ≥ 7.6 cm (3”), Bowman et al. (2000) used ≥ 8 cm), or even a diameter of > 10 cm. For example, Keinath and Hayward (2003) used ≥ 15 cm. Inconsistent definitions of coarse woody debris makes it difficult to offer a clear interpretation of the apparent discrepancy among studies. My results suggest that fine woody debris was a stronger indictor of red-backed vole presence than coarse woody debris, consistent with Orrock et al. (2000). He suggested that this was due to a more heterogeneous cover provided by twigs and branches. Many previous studies have not considered fine debris at all.

Two universal shortcomings are inherent in experiments that study microhabitat of animals by trapping. First, when traps are baited, one cannot say with certainty that the animals were "using" a particular site and were not attracted to the site from adjoining areas. Second, when assessing microhabitat use, there is a chance that a key variable is not measured. Habitat selection studies must strive to correctly identify, measure, and classify features in order to reveal type preference or avoidance (Morrison et al. 1992, Coady 2005). This type of study assumes that researchers can gather information relevant to the species' perspective, anticipating their decision-making processes. It is possible there were mechanisms at the trapline and sampling area level that were not identified in this study such as ambient temperature, elevation, and aspect. These three variables have been found to have an influence on habitat selection by red-backed voles in logged forests (Orrock et al. 2000).

This study offered new insights into red-backed vole habitat selection. The scale of resolution in combination with finer resolution of habitat variables can improve predictive capacity of habitat selection models. In summary, red-backed voles selected some fine-scale habitat features, but most of the explained variance resulted from coarser scale differences in sampling area and trap line. The results of this study suggest that fine woody debris and horizontal density are variables that may have been under-appreciated in previous red-backed vole habitat selection studies. The use of a generalized mixed effects statistical design detected patterns that could have been masked otherwise. Future studies should further examine the effects of regional and local processes on habitat selection by red-backed voles. Furthermore, future researchers should consider using the generalized linear mixed effects model as a statistical analysis tool to assess the effect that various spatial levels may have on habitat selection.

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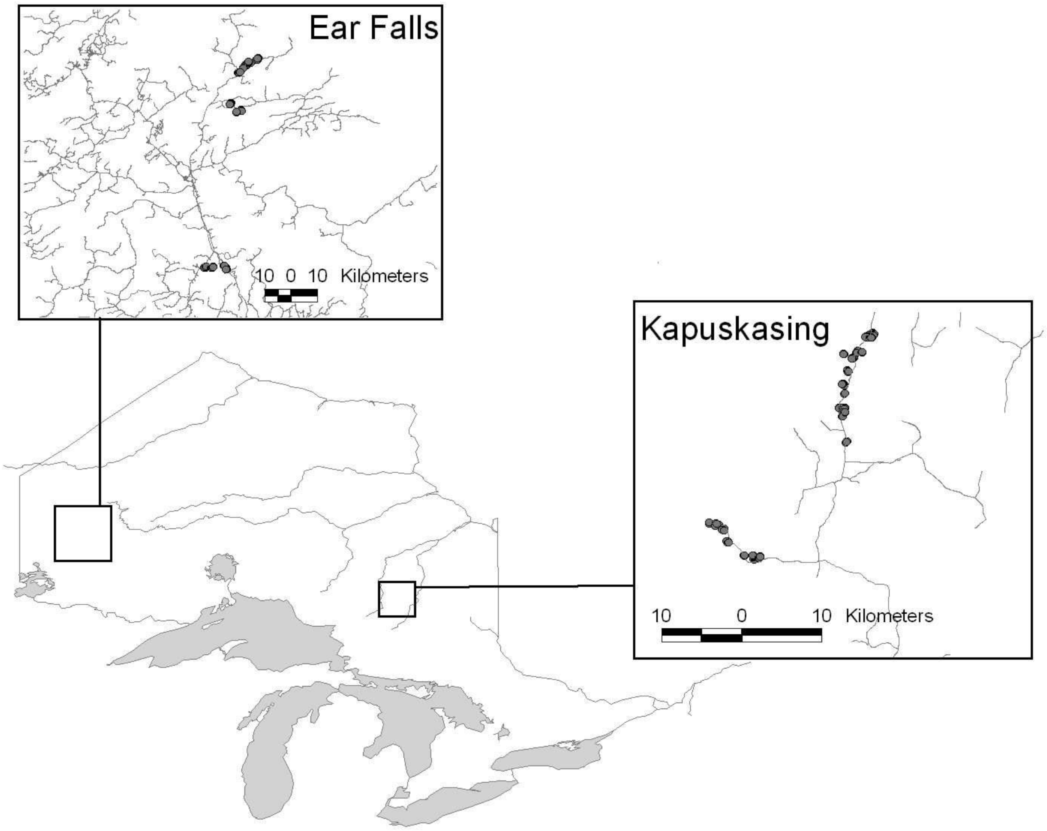

Figure 1. Location of red-backed vole (*Myodes gapperi*) habitat selection study areas near Ear Falls and Kapuskasing, Ontario

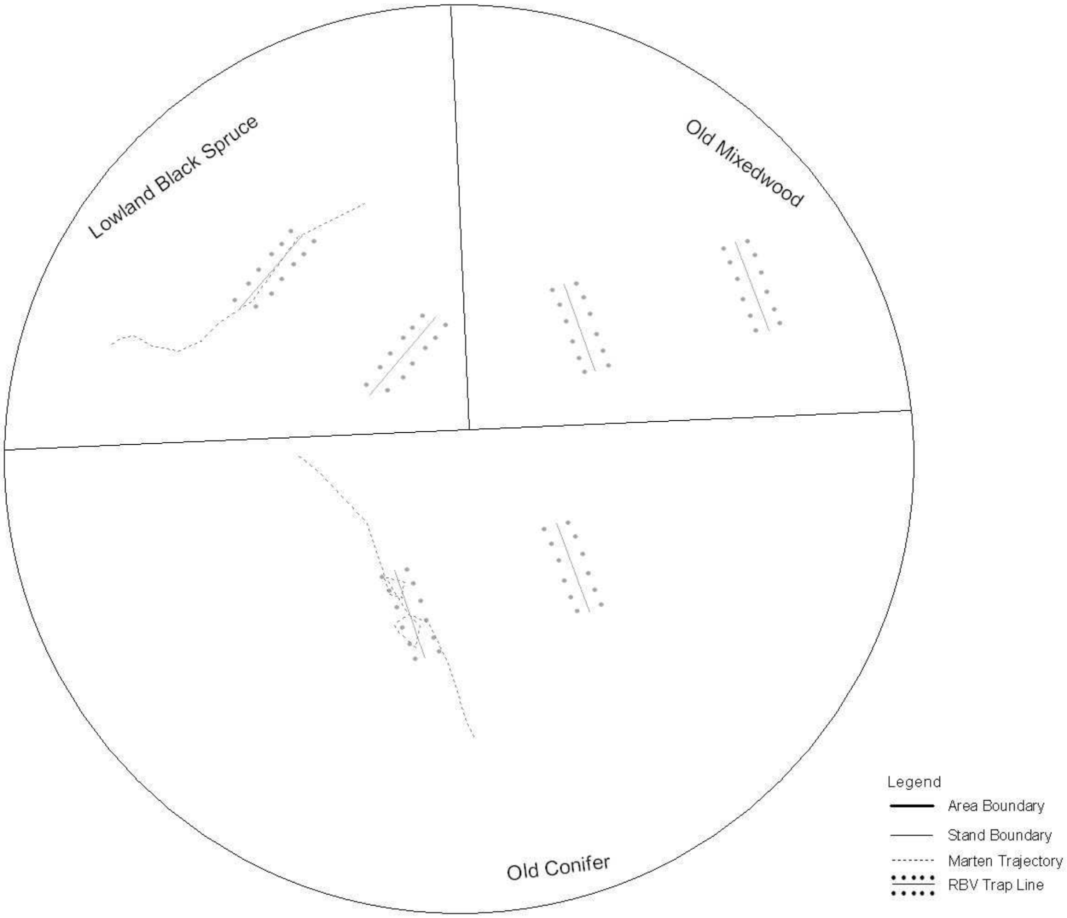

Figure 2: Schematic of trapping protocols used in assessing habitat selection by red-backed voles (*Myodes gapperi*) in Ear Falls and Kapuskasing, Ontario

Table 1: Definitions of forest-stand terms used in determining locations of red-backed vole (*Myodes gapperi*) trapping.

Forest-stand Term	Definition	Number of Old Stands Sampled	Number of Young Stands Sampled
Old	Age ≥ 80 years	37	--
Young	20 years ≤ Age ≤ 79 years	--	38
Recently Disturbed	Age < 20 years	--	6
Conifer	Stand composition ≥ 80% conifer tree species	20	22
Mixed	20% < composition < 80% Conifer tree species Conifer tree species	16	12
Deciduous	Composition ≤ 20% Conifer tree species	1	4
Wetland	Open muskeg Treed muskeg Marsh and Fen*	--	--
Black Spruce Lowland	100% Black Spruce Lowland site type*	6	--
Unproductive	Brush and Alder Unclassified land Rock Developed agricultural land Grass and meadow Miscellaneous and not identified for classification*	--	1
Water	Lake Reservoir River Waterbody – update Stream buffer Falls*	--	--

* identifies code from the Ontario Ministry of Natural Resources forest resource inventory data layers.

Table 2: Red-backed vole (*Myodes gapperi*) habitat selection predictor variables and descriptions.

Variable	**Description**	**Mean ± SE (min- max)**
Study site	Kapuskasing or Ear Falls, Ontario	--
Landscape	Previously logged or Unlogged	--
Sampling area	Sampling area that RBV trapping lines were placed in	--
Trapline	50 metre RBV trapline	--
Position	Position on the trapline (in 10 m increments)	(1-6)
Season	Spring (May-June) or Autumn (August-October)	--
Vole Canopy	Percent canopy taken at a height of 5 cm using a densiometer averaged from four measurements in each of the cardinal directions	83.45 ± 0.56 % (4.25-100)
Large Coarse Woody Debris	Volume of fallen logs ≥20 cm along two 10m lines intersecting at the trapsite	78.86 ± 5.77 m^3/ha (0-675.31)
Coarse Woody Debris	Volume of fallen logs ≥10 cm along two 10m lines intersecting at the trapsite	129.03 ± 4.32 m^3/ha (0-881.01)
Fine Woody Debris	Volume of fallen logs between 2 and 9 cm along two 10m lines intersecting at the trapsite	17.076 ± 0.59 m^3/ha (0-123.709)
Grass	Percentage of grass cover in a 2x2 m quadrat	2.303 ± 0.20 % (0-78.00)
Moss	Percentage of moss cover in a 2x2 m quadrat	26.00 ± 0.95 % (0-94.00)
Lichen	Percentage of lichen in a 2x2 m quadrat	0.94 ± 0.08 % (0-47.00)
Fern	Percentage of fern in a 2x2 m quadrat	0.71 ± 0.06 % (0-22.00)
Horizontal Density	A measure of forest complexity (Nudds 1977). Number of 30 cm increments covered by Vegetation	5.12 ± 0.05 (1.00-7.00)
Soil moisture	Ratio of leaf litter/moss layer to organic layer	0.41 ± 0.01 cm (0-4.00)
Surface Material	Sum of leaf litter/moss layer and organic layer	23.25 ± 0.53 cm (1.25-67.00)
Ground Stem Count	Number of woody and herbaceous stems less than 10 cm in a 1x1 m quadrat	99.19 ± 3.00 (0-593.00)
Shrub Stem Count	Number of woody and herbaceous stems less between 10 and100 cm in a 1x1 m plot	14.51 ± 0.53 (0-97.00)
Stump Distance	Distance to the closest stump or tip-up	198.00 ± 3.96 cm (0-970.00)
Conifer Basal Area*	Tree density of conifer tree species using a 2m cruise master prism	21.47 ± 0.70 (2 – 74)
Deciduous Basal* Area	Tree density of deciduous tree species using a 2m cruise master prism	14.57 ± 0.61 (2 – 86)

* Variable not used in analysis due to high correlation with another variable

Table 3. Univariate and multivariate models assessing habitat selection by red-backed voles (*Myodes gapperi*) divided by study area and season.

Number of Variables	**Model**	**Variables**	**Reference***
1	Canopy	Vole Canopy	1, 2, 10
1	Coarse woody debris	Coarse woody debris	1, 3, 10
1	Fine woody debris	Fine Woody Debris	5
1	Grass	Grass	6
1	Lichen	Lichen	1, 3, 6a
1	Moss	Moss	3, 5, 12
1	Fern	Fern	6b, 11
1	Soil moisture	Soil moisture	3, 5, 7
1	Ground	Ground stem count	2, 8, 9
1	Shrub	Shrub stem count	3, 5, 10
1	Stump	Distance to closest stump or tip-up	4
1	Surface Material	Surface material (duff layer)	5
1	Horizontal density	Horizontal density	12
6	Cover	Canopy + Coarse woody debris + Fine woody debris + HD + Shrub + Stump	
6	Food	Grass + Fern + Soil moisture + Ground + Moss + Lichen	
4	Travel	Stump + Moss + Fine woody debris + Coarse woody debris	
5	Literature	Canopy + Coarse woody debris + Fine woody debris + Moss + Soil	
13	Maximal	All variables	

* 1. Allen 1983
2. Wywialowski and Smith 1988
3. Carey and Johnson 1995
4. Bowman et al. 2000
5. Orrock et al. 2000
6a. Martell 1981
6b. Martell 1983
7. Getz 1968
8. Nordyke and Buskirk 1988
9. Yahner and Smith 1991
10. Keinath and Hayward 2003

11. Schloyer 1977
12. Rosenzweig and Winakur 1969

Table 4: Variables considered in the generalized linear mixed model to assess habitat selection by red-backed voles (*Myodes gapperi*).

Effect	*Variable*
Random	Sampling area
	Trap Line
	Position
Fixed	Landscape *
	Study site *
	Season
	Vole Canopy
	Coarse Woody Debris
	Fine Woody Debris
	Grass
	Moss
	Lichen
	Fern
	Horizontal Density
	Soil Moisture
	Surface Material
	Ground Stem Count
	Shrub Stem Count
	Stump

* also checked as a random effect

Table 5: Model selection results of binary logistic regression models, explaining habitat selection by red-backed voles (*Myodes gapperi*) by study site and season.

Area – Season	*Top Model*	*# Variables*	*r^2 value*	*ΔAICc*	*Model Rank*
Ear Falls – Spring	**Literature Model**	5	0.138	0	1
	Cover Model	6	0.132	3.36	2
Kapuskasing – Spring	**Horizontal Density**	1	0.064	0	1
	Cover Model	6	0.103	4.45	2
Ear Falls – Autumn	**Cover Model**	6	0.130	0	1
	FWD	1	0.079	3.13	2
	Literature Model	5	0.108	3.66	3
	Travel Model	4	0.096	4.71	4
Kapuskasing – Autumn	**Maximal Model**	12	0.149	0	1
	Cover Model	6	0.091	1.02	2
	Ground Stem Count	1	0.037	3.07	3
	Horizontal Density	1	0.029	4.88	4

* Bold text represents top candidate models (i.e., models with a $\Delta AIC_c < 2.0$)

Table 6: Most parsimonious model for explaining habitat selection by red-backed voles (*Myodes gapperi*).

Variables

Season (-ve)
Lichen (-ve)
Fine Woody Debris (+ve)
Horizontal Density (+ve)
Fern (+ve)
Soil Moisture (-ve)
Fine Woody Debris: Lichen (-ve)
Fine Woody Debris: Fern (-ve)
Lichen: Soil Moisture (+ve)

Notes:

1. Random effects represented as Sampling area, Trapline, and Position along the trapline
2. Bold text represents those variables with a p<0.01

For more information refer to Appendix 2

Appendix 1: Description of all habitat variables collected

Variable	Description and Sampling Method
Ground Cover	percent of graminiod, ferns, shrubs, herbs, moss (feather and *Sphagnum*), lycopodium, lichen, fungi, coniferous litter, evergreen litter, cones, logs, slash, and bare soil or rock within 4.0 m^2 plot at three separate layers: >10 cm, 10-50 cm, 50-100 cm
Stem Density	Density of woody and herbaceous stems at various heights within a 1.00 m^2. Dominant species was noted
Tree Composition	Tree species and diameter at breast height (dbf) of trees that fell on plot using a 2m factor Cruise Master prism
Species Dispersion	Average distance, species and decay class of closest large tree (≥ 20 cm dbh), tree (between <20 and ≥10 cm dbh), small tree (<10 cm dbh and ≥ 3 m in height), shrub (< 3 m in height), snag, and stump or tip up to the trapsite
Species Size	Average diameter and species of closest large tree, tree, small tree, snag, and stump or tip up to the trapsite
Species Density	Density of live or dead standing trees within a trapsite. Obtained using a 2m factor prism
Downed Woody Debris	Number of fallen logs along two 10 m lines intersecting the trapsite
Downed Woody Debris Decay Class	Structure of downed woody debris along two 10 m lines intersecting at the trapsite
Canopy Cover	Average percent canopy at both waist height and a height of 5 cmusing a densiometer and taken in each of the four cardinal directions.
Soil Moisture	Average depth of both the leaf litter-moss layer and the organic layer 1m from the trapsite in each of the four cardinal directions
Horizontal density	A measure of forest complexity (Nudds 1977). Number of 30 cm increments covered by vegetation 5 m from trapsite in each of the four cardinal directions
FEC V-type*	Vegetation type under the Forest ecological classification system

* Different keys and vegetation types exist between northeast and northwest Ontario.

Appendix 2: Sampling area estimates used in the present study to trap small mammal in

Study site	Treatment	Age/Sex	Marten	Home Range Area (km2)
Ear Falls	Logged	Adult male	150.070	1.45
		Adult male	150.463	1.52
		Adult male	150.384	4.35
		Adult male	150.553	4.39
		Adult female	150.367	6.37
		Adult female	150.800	14.80
	Unlogged	Adult female	151.951	1.58
		Adult female	150.942	7.85
		Adult female	151.833	24.70
		Adult male	151.873	2.53
		Adult male	150.297	4.57
Kapuskasing	Logged	Juvenile female	150.719	20.05
		Adult male	150.137	22.32
		Adult female	151.600	25.05
	Unlogged	Adult male	150.247	7.07
		Adult female	150.008	19.02

Appendix 3: Small mammal number of individuals caught per 100 trap nights among seasons and study sites

Species	Ear Falls, Spring 2005	Ear Falls, Autumn 2005	Kapuskasing, Spring 2006	Kapuskasing, Autumn 2006
Red Backed Vole	5.292	18.963	3.578	10.843
Deer Mouse	1.680	4.336	3.405	5.179
Eastern Chipmunk	0.141	0.000	0.215	0.433
Least Chipmunk	0.141	0.000	0.000	0.000
Jumping Mouse	0.035	0.000	0.000	0.108
Meadow Vole	0.071	0.000	0.107	0.072
Red Squirrel	0.212	0.287	0.247	0.757
Flying Squirrel	0.000	0.000	0.000	0.108
Rock Vole	0.000	0.000	0.036	0.000
Bog Lemming	0.000	0.000	0.000	0.036
Shrew spp.	0.106	0.459	0.000	0.217
Weasel spp.	0.000	0.058	0.000	0.577

Appendix 4: Model selection results explaining habitat selection by red-backed voles for consolidated data of both study site and season.

Random Effects	*Fixed Effects*	*# Fixed Variables*	*ΔAICc*	*Candidate*
Sampling area Position Trapline	Season, Fine woody debris, Moss, HD Soil moisture, Grass	6	0	1
Sampling area Position Trapline	Season, Fine woody debris, Moss, HD, Soil moisture	5	0.17	2
Sampling area Position Trapline	Season, Fine woody debris, Moss, HD, Soil moisture, Grass, Lichen	7	0.25	3
Sampling area Position Trapline	Season, Fine woody debris, Moss, HD, Soil moisture, Grass, Lichen, Fern	8*	1.12	4
Sampling area Position Trapline	Season, Fine woody debris, HD, Soil moisture	4	1.81	5

*represents the model used for post-hoc analysis of two-way interaction term

Appendix 5: Model output of most parsimonious model

Random effects:

Group Name	Variance
TrapLine ┼	4.56251
Position #	0.27382
Sampling area ¶	1.65635

--------------- No over dispersion -----------

┼ Number of groups = 173
Number of observations = 1011
¶ Number of groups = 16

Fixed effects:

	Estimate	Standard Error	Z value	P	MCMC Interval Lower*	MCMC Interval Upper*
Intercept	2.267264	0.640412	-3.540	<0.0001	-2.361682	-1.172383
Season	-1.182030	0.193129	-6.120	<0.0001	-1.335562	-0.940701
FWD	0.043625	0.009656	4.518	<0.0001	0.032721	0.053994
Lichen	-0.337831	0.158399	-2.133	0.0329	-0.470441	-0.137153
Fern	0.301892	0.105438	2.863	0.0042	0.101158	0.491346
HD	0.443377	0.090054	4.923	<0.0001	0.275673	0.511192
Soil Moisture	-1.634827	0.437251	-3.739	0.0002	-2.165183	-1.335600
FWD:Lichen	-0.019244	0.005904	-3.259	0.0011	-0.023898	-0.013577
FWD:Fern	-0.021464	0.007007	-3.063	0.0022	-0.035998	-0.008882
Lichen: Soil moisture	1.117522	0.347269	3.218	0.0013	0.528899	1.4822262

Notes: FWD = fine woody debris
HD = horizontal density
* MCMC = Markov chain monte carlo with 95% confidence intervals at a repetition of 50,000