The Journal of Wildlife Management; DOI: 10.1002/jwmg.471

Research Article

Do Trappers Understand Marten Habitat?

PHILIP A. WIEBE,[1] *Canadian Forest Service, 1219 Queen Street E., Sault Ste. Marie, ON, Canada P6A 2E5*
JOHN M. FRYXELL, *Department of Integrative Biology, University of Guelph, Guelph, ON, Canada N1G 2W1*
IAN D. THOMPSON, *Canadian Forest Service, 1219 Queen Street E., Sault Ste. Marie, ON, Canada P6A 2E5*
LUCA BÖRGER, *Department of Integrative Biology, University of Guelph, Guelph, ON, Canada N1G 2W1, Centre d'Etudes Biologiques de Chizé, CNRS (U.P.R. 1934) & INRA (USC 1339), 79360 Villiers-en-Bois, France*
JAMES A. BAKER, *Ontario Ministry of Natural Resources, 1 Stone Road, Guelph, ON, Canada N1G 4Y2*

ABSTRACT Previous studies of the effects of fur trapping on marten populations have not considered habitat variation and how trappers use available habitat. We investigated the behavior of fur trappers with respect to roads, waterways, and the forest habitats on trap lines, using registered trap lines in northern Ontario as a study system. The objectives of this study were to 1) develop models for predicting trap location based on access and habitat features, 2) determine whether trappers target the same habitat preferred by American marten, and 3) investigate effects of spatial resolution on predictive models, using a geographic information system (GIS) for coarse resolution variables and direct forest mensuration for fine resolution variables. Distance to roads and water were by far the most influential factors in logistic models for predicting trap presence, accounting for 51.2–61.7% of the observed deviance. At a coarse spatial resolution, trappers selected sites that were close to vehicular access, and in older mixed wood forest stands. Similarly, at a coarse resolution, marten selected old stands, but dominated by coniferous trees. At a finer spatial resolution, trappers selected sites with high basal area of trees, pronounced proportion of black spruce, high canopy cover, and high density of coarse woody debris, consistent with previous studies on marten habitat selection at a fine resolution. Although coarse resolution models are easily applicable because of the wide availability of GIS land cover data, fine resolution models had greater predictive power when considering habitat variables. By quantifying trapper behaviors, these results suggest that the effectiveness of marten sanctuaries used in forest management depend not only on the age and species composition of forest stands left unlogged, but also on the degree to which they are accessible to trappers. © 2012 The Wildlife Society.

KEY WORDS American marten, boreal forest, fur trapper, habitat selection, marten, Ontario, reservoir strategy, resource selection, road access.

American marten (*Martes americana*) are thought to be useful indicators of ecosystem function in the boreal forest because they prefer mature and old forest habitats (Snyder and Bissonette 1987, Thompson and Colgan 1994, Payer and Harrison 2003). Forest management guidelines in the boreal forests of northern Ontario have been developed around marten habitat requirements, based on the assumption that if marten populations are adequately maintained, then other boreal wildlife species that require similar habitats will also be sustained (Watt et al. 1996). As with any population, marten population dynamics are determined largely by recruitment rates and death rates. Marten juvenile recruitment rates are affected by availability of prey and population densities (Thompson and Colgan 1987, Fryxell et al. 1999). Death rates are affected by predation by natural predators and fur trapping by humans, prey availability, and weather conditions (Strickland and Douglas 1987). Many past studies on marten have focused on habitat use (Chapin et al. 1997, Potvin et al. 2000, Smith and Schaefer 2002, Poole et al. 2004, Gosse et al. 2005) and on prey availability (Hargis and McCullough 1984, Thompson and Colgan 1990). Although marten recruitment rates may be tightly linked to prey availability and habitat suitability, mortality from predation is also an influential factor in determining marten population dynamics. Marten are preyed on by fisher, red fox, raptors, and humans (Yeager 1950; Marshall 1951; Strickland and Douglas 1987; Hodgman et al. 1994, 1997). Marten mortality may be particularly high in areas where they are heavily harvested for their fur and trapping is the leading cause of death (Thompson and Colgan 1987, Hodgman et al. 1994).

Resource selection studies often show that marten preferentially use certain habitat types (Bowman and Robitaille 1997, Chapin et al. 1997, Gosse et al. 2005), but little is known about how trappers use different habitats. The system of registered fur-trapping lines in northern Ontario offers an excellent opportunity to study trapper behavior because each trapper has a designated area to trap. These areas can be considered analogous to a predator's territory. Under this scenario, trappers can increase profitability either

Received: 10 January 2011; Accepted: 10 July 2012

[1] *E-mail: pwiebe@nrcan.gc.ca*

by increasing capture rates, or by decreasing trapping effort. Capture success should be improved by setting traps where marten are most likely to occur. Effort, on the other hand, would be reduced by setting traps in places that are easy to set and check. If maximizing captures is the goal of trap placement, then traps should be located in habitat types preferred by marten. If minimizing effort is more important, then traps should be placed close to logging roads or waterways. These hypotheses need not be mutually exclusive, in which case trappers will select habitat that most closely resembles preferred marten habitat, but do so only in areas that are easy to access. If these hypotheses are true, then forest management practices that include marten core areas need to consider that accessibility to trappers via roads or easily navigable waterways reduces the effectiveness of sanctuaries.

Studies on habitat or food selection by marten across North America are numerous (Chapin et al. 1997, Potvin et al. 2000, Smith and Schaefer 2002, Poole et al. 2004, Gosse et al. 2005). Although most of these studies support the notion that marten prefer old, coniferous or mixed-wood forest, marten have been found to persist in forests with greater proportions of young deciduous stands (Poole et al. 2004). Some studies have found that marten use younger stands, noting that marten preferred structural characteristics in younger stands that were more commonly found in older forests (Bowman and Robitaille 1997, Payer and Harrison 2003, Poole et al. 2004, Porter et al. 2005, Hearn et al. 2010). Martens may not prefer the older stands but the structural characteristics that are commonly associated with them, such as coarse woody debris and canopy cover.

Several studies have investigated the impact of trapping on marten populations and noted the potential influence of availability of roads to trapper behavior. Quick (1956) speculated that marten populations in northern British Columbia might get depleted close to roads as a result of trapping, but he did not measure marten densities or habitat characteristics of trapping areas. Soukkala (1983) calculated the effects of trapping on the viability of a marten population in Maine, demonstrating a positive correlation between road access and mortality rates for marten. However, their results were based on untested assumptions about trapping effort and trap coverage, since they had no spatial data on trap placement. Thompson (1994) found that marten mortality due to commercial trapping was 2.4 times greater in logged versus unlogged habitats, with close to 100% of collared marten in logged areas killed each year, and suggested that the increased risk was due to greater access in logged areas. In Maine, Hodgman et al. (1994) found that 54% of collared marten died annually as a result of fur trapping in a logged landscape. Although each of these authors noted a possible connection between roads and marten mortality rates, neither directly investigated trap placement in relation to roads or other habitat features.

We investigated the behavior of fur trappers with respect to roads, waterways, and forest habitats in 2 widely separated regions in northern Ontario. Our objectives were to 1) develop resource selection models for predicting trap presence based on access and habitat features, 2) test whether marten select specific habitat features disproportionally to their abundance, 3) determine to what extent trappers target habitats selected by marten, and 4) investigate effects of spatial resolution on patterns of resource selection by trappers and marten.

STUDY AREA

Our 2 study areas were located in the boreal region of northern Ontario. One was located close to Kapuskasing, in northeastern Ontario (48°48′N, 82°33′W) and the other was close to Ear Falls in northwestern Ontario (50°38′N, 93°13′W; Fig. 1). The Ear Falls study area was dominated by jack pine (*Pinus banksiana*) and black spruce (*Picea mariana*), with substantial stands of trembling aspen (*Populus tremuloides*) in regenerating areas and other boreal tree species in much smaller proportions (Thompson et al. 2007). Logging has taken place in the region since the 1940s, consisting mainly of clear-cut machine logging. At Kapuskasing, a greater proportion of species favor moist soils than at Ear Falls including black spruce, tamarack (*Larix laricina*), eastern white cedar (*Thuja occidentalis*), and balsam poplar (*Populus balsamifera*). Logging has occurred in Kapuskasing since the 1920s, beginning with horse logging up to the early 1960s, followed by machine clear-cutting. Compared to Ear Falls, the landscape in the Kapuskasing area has considerably flatter topography, is swampier, has fewer lakes, and contains more large rivers and creeks.

METHODS

We arbitrarily chose trappers who were a part of the local trappers' council, and whose trap line areas were within the boundaries of the marten radio-telemetry study areas, and asked them to participate in our trap site selection study for a small reward. We believe that the trappers who agreed to participate represented a good cross-sectional background of experience and education similar to other trappers in the area. We used 8 trappers as study subjects: 4 trappers in Ear Falls, each managing 1 trap line, and 4 trappers in Kapuskasing, each managing 1 or 2 trap lines. All trap lines were either adjacent to the marten radio-telemetry study area, or were within the marten radio-telemetry study area, but in years following completion of radio-tracking field work. Trappers agreed to keep track of the locations of all of their fur traps set with the intent to catch marten during trapping seasons between 2004 and 2008. Each marten trapping season occurred from 25 October to the end of February of the following year, but the majority of trapping of marten occurred between 25 October and the end of December. Each trap line consisted of an area in which the trapper managed all fur harvests not covered by a regular hunting license. The trappers exclusively trapped in the areas they were licensed to trap. Moving to another area is complicated for a trapper and usually involves buying and selling cabins and equipment contained on the trap lines involved. As a result, trappers seldom move to another trap line. Trap lines covered a mean area of 373.6 km^2 (167.8–688.9 km^2) at Ear Falls, and a mean area of 216.4 km^2 (102.3–269.4 km^2) at Kapuskasing. The boundaries were mostly delineated

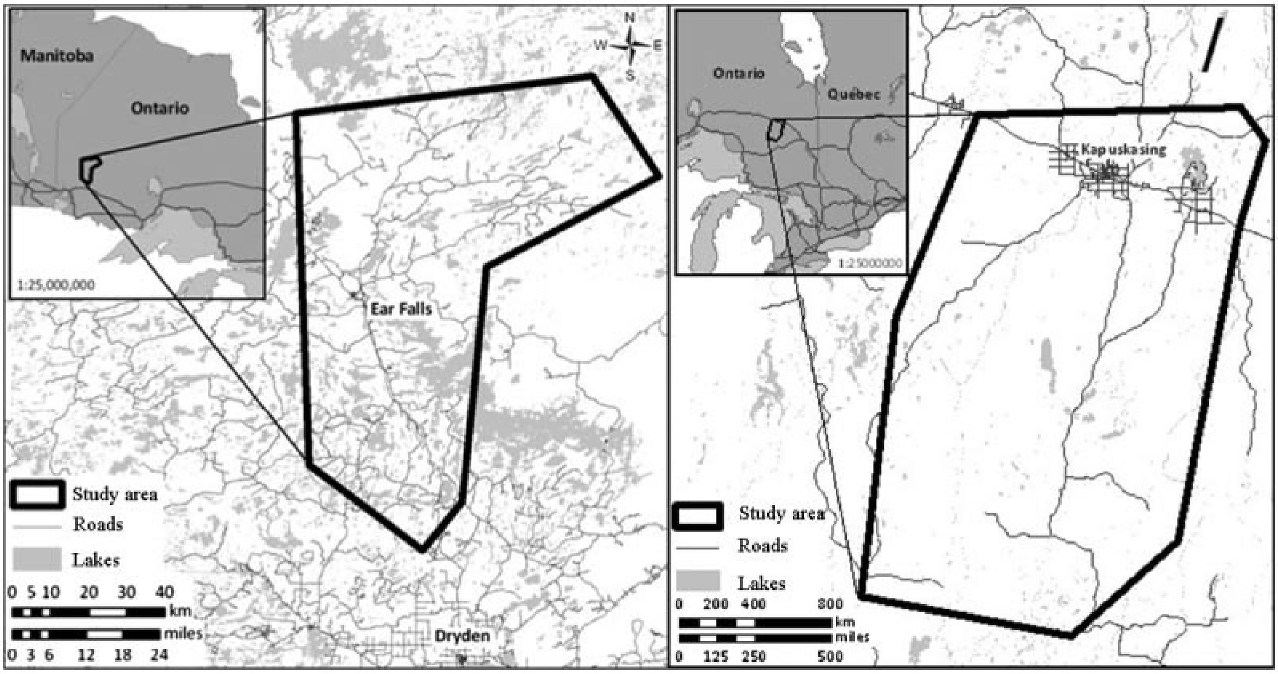

Figure 1. Study areas used for trapper data collection as well as marten radio-telemetry data collection near Ear Falls, and Kapuskasing, Ontario, Canada from 2001 to 2007.

according to watersheds in the area and were enforced by the Ontario Ministry of Natural Resources (OMNR).

To study habitat selection by trappers, we used geographic information system (GIS) land cover data in the form of forest resource inventory (FRI) data. The FRI data are useful for wildlife habitat studies because they are readily available, spatial, and include data on forest age, density, height, and species composition. Unfortunately, data from FRI are not perfect and have been shown to include considerable error when compared to ground-truth measurements that varied with the resolution of the data (Thompson et al. 2007). We also measured fine resolution habitat variables at trap sites and randomly selected points in a 60-m band along travel routes that allowed passage of motorized vehicles.

Coarse Resolution of Trapper Data

We recorded trap site locations using a global positioning system (GPS) for all traps on 10 trap lines, providing location accuracy to within 10 m. To estimate habitat availability, we generated 2,000 random points per trap line and compared the composition with trap location points using Arc View (version 3.2, Environmental Systems Research Institute, Redlands, CA) and the Animal Movement extension (Version 2.0, http://alaska.usgs.gov/science/biology/spatial/gistools/index.php/animal_mvmt.htm, accessed 22 Aug 2012). We removed points overlapping water or other non-forested habitats. We used 16,613 random points (range = 1,239–1,851 per trap line), and 734 trap sites (range = 22–123 per trap line) in the analysis. We created access variables by calculating distance in meters to the nearest road, trail, lake, or creek. We obtained road layers from Tembec Inc. and Weyerhaeuser Inc. and added several segments that we mapped from the ground while working on the trap lines. These segments included older logging roads, mining roads, and trails that had been cut for access from all terrain vehicles (ATVs) and snowmobiles. We completed analyses separately for the Kapuskasing and Ear Falls study areas because there were substantial differences in the available habitat in each study area.

Marten have been shown to be mostly associated with mature forest stands in several previous studies (Marshall 1951, Soutiere 1979, Thompson and Colgan 1994), suggesting that FRI age and height indices are potentially influential predictor variables. Stand age and height were highly correlated ($r > 0.9$), so only 1 of these variables could be included in the statistical models of trapper selection to avoid multicollinearity. We used an information theoretic approach to determine which would better describe the data for each analysis.

Marten are often associated with high proportions of coniferous forest (Soutiere 1979, Spencer et al. 1983, Bissonette et al. 1989, Thompson 1994, Thompson and Curran 1995). In northeastern Ontario, McKague (2007) found a positive association between marten use and the percent of white cedar in the stand. Trap placement may be affected by the forest species composition, whether for selecting marten habitat, or for reasons relating to access. For example, even though marten may favor cedar-rich stands, these are difficult to walk through, and trappers may avoid them because they decrease ease of access to traps. Percent cedar was not included in models for trap site selection in the Ear Falls study area because cedar comprised only 0.2% of trees in the area, compared to 2.7% in the Kapuskasing study area. We further classified conifer stands according to whether they were upland or lowland. Marten are thought to prefer upland stands because they have greater prey densities than lowland stands (Boos and Watt 1997). Lowland stands were composed of 100% black spruce on sites with organic soils. Trappers may prefer upland stands because they have less standing water, providing easy access. To investigate the effect of tree species composition on trap site selection, we included the proportions of conifer, black spruce, and cedar in stands, and whether stands were denoted as lowland or upland on the FRI in the species composition set of candidate models.

Fine Resolution of Trapper Data

We conducted vegetation sampling at trap site locations and at randomly selected points along all travel routes accessible to the trappers. For each trap line, we sampled at least 23 trap sites (we randomly selected sites if >23 were available), and randomly chose ≥30 points along all paths or creeks deemed accessible to the trapper at intervals of 10 m, 20 m, or 30 m from the access route. We later eliminated points that did not contain >1 tree in the plot from the analysis. We used 327 (range = 24–49 per trap line) random points, and 293 (range = 23–45 per trap line) trap sites in the analysis. At each sample point, we took 7 vegetation measurements on a variable radius plot determined by a 2-factor wedge prism to describe forest maturity, species composition, and physical structure. Using this method, each tree determined by the prism to be within the plot represented 2 m^2/ha basal area. Because traps were almost always nailed to live tree trunks at each trap site, we measured vegetation 5 m from each trap, in a random direction. We chose this distance to avoid being directly under the branches of the trap tree but close enough to be representative of the local area.

We indexed forest maturity by the basal area of trees and snags (standing dead trees) and diameter at breast height. We determined basal area of live and dead trees at each plot by counting the number of trees included in the plot using the prism, multiplied by 2 m^2/ha. We counted all live trees on the plot, identified them to species, and measured diameter at breast height. For snags, we estimated height and classified decomposition based on a standardized scale from 1 to 5, where we assigned values of 5 to the most decomposed snags. We calculated basal area of snags for all stems >10 cm diameter at breast height and for all deciduous stems >10 cm diameter at breast height. We calculated species composition from the trees included on the prism plots for live tree basal area. We included the percentage of total stems that were conifer, spruce, and cedar as variables in candidate models for all trees included in the prism plot and for trees >10 cm diameter at breast height.

Variables describing forest structure included canopy cover, coarse woody debris, and shrub density. We measured canopy cover with a spherical densiometer by averaging readings from the 4 cardinal directions at each point (Lemmon 1956). Since we measured vegetation in the summer when leaves were present, but trapping seasons occurred in the autumn, after leaves had fallen, we applied a correction factor to summer readings to represent winter coverage. To correct for seasonal differences in canopy cover, we conducted a regression analysis of canopy cover before leaf emergence versus canopy cover after leaf emergence at a sample of trap site locations and included percent conifer at those locations as a cofactor. We applied the intercept and slope that resulted from the regression to all summer canopy cover measurements to estimate coverage. We measured coarse woody debris along 30-m sides of equilateral triangles centered on the point. We measured logs with a diameter >10 cm at the point of intersection and classified them by decomposition state. We calculated volume of coarse woody debris using the formula:

$$V = \frac{\left(\pi^2 \times \sum d^2\right)}{8L}$$

where V is the volume of coarse woody debris in m^3/ha, d is the diameter of each log segment where it crossed the transect line, and L is the length of the transect line in meters (van Wagner 1968). We measured shrubs from the random point to the closest stem and then between stems for the next 2 closest shrubs. We used mean distance between shrubs as an index to shrub stem density (Cottam and Curtis 1956).

Coarse Resolution of Marten Data

We estimated marten resource selection using logistic regression, where the response variable consisted of radio-telemetry locations for marten versus randomly selected points considered to be available to them. We based the locations on radio-telemetry data from radio-collared animals collected in 2004, near Ear Falls, Ontario and from 2003 to 2007 near Kapuskasing, Ontario, as well as visual locations from walk-ins (approx. 10% of data). Detailed methods on marten capturing, collaring, and radio-telemetry techniques are discussed in Andruskiw et al. (2008). Experiments involving marten were in accordance with the guidelines of the Canadian Council on Animal Care and were approved by the Animal Care Committee at the University of Guelph. We described habitat use according to FRI attributes overlaid on radio-telemetry locations of marten in a GIS. We compared attributes of radio-locations to 12,000 available points that were randomly sampled in a GIS from a buffer zone of 2.5 km surrounding roads. We chose 2.5 km because this was the maximum distance at which radio-collars could be accurately located. At Ear Falls, we used 867 telemetry locations from 46 different marten during 1 season. At Kapuskasing, we used 1,925 telemetry locations from 216 marten-season combinations (138 individual marten). We calculated distance from each point to the nearest road, trail, or waterway using the Nearest Features extension (Jenness Enterprises, version 3.8, www.jennessent.com/arcview/nearest_features.htm, accessed 22 Aug 2012) in Arc View. We divided variables into categories according to whether or not they related to vehicular access, forest maturity, or species composition using the same methods employed for the trapper resource selection functions.

Models included stand age as a continuous variable, and age as a categorical variable where we classified stand ages from 1–10 years as recently disturbed; 11–40 years as young machine logged; 41–70 years as older machine logged, horse logged, or burn origin; 71–100 years as mature, and >100 as over-mature. We also classified conifer stands as upland or lowland. We included percent conifer and lowland conifer classification in the species composition component of candidate models. At Kapuskasing, we included percent cedar as a variable in model selection, but as with the trapper selection, we did not include cedar in models for Ear Falls selection because it represented less than 1% of trees in the study area. We also included a model that categorized species composition into conifer (>70% conifer), mixed (30–70% conifer), and deciduous stands (<30% conifer). The conifer category was further divided into upland and lowland, where lowland was defined as 100% black spruce with a site class of 3 or 4, which indicated a slow rate of growth resulting from poor soil conditions. Roads included OMNR classifications of: primary, secondary, tertiary, and winter. We grouped the primary, secondary, and tertiary roads into one category because they indicated that the roads had been made with gravel, and grouped winter roads with quad trails because they had no ground preparation associated with them and were generally only accessible with all terrain vehicles.

We eliminated all points where no stand age data were available on the FRI layer, including all water points. We retained 90% of random points and 93% of marten locations.

Statistical Analyses

We used Program R (version 2.14.0, http://cran.r-project.org/bin/windows/base/, accessed 22 Aug 2012) for all analyses. During preliminary analyses for all coarse resolution analyses, we used generalized additive models (GAMs; binomial family) to identify nonlinear relationships between the response and explanatory variables. Generalized additive models are an extension of generalized linear models (GLMs) and allow estimation of nonlinear response curves using non-parametric smoothing functions (Wood 2006). We fitted smooth terms using penalized thin plate regression splines and cubic regression splines in the mgcv library (version 1.7-11, http://cran.r-project.org/web/packages/mgcv/index.html, accessed 22 Aug 2012) following the recommendations in Wood (2006). The degrees of freedom for a GAM model vary smoothly between zero and infinity. The smoothing parameters and the degrees of freedom for a certain model term are reduced by the application of the corresponding model fitting penalties (Wood 2006:170–171). Hence, the degrees of freedom for a GAM may assume non-integer values. Having found the best combination of linear and smooth terms, we conducted goodness-of-fit tests on the global models to evaluate model performance. We evaluated goodness of fit with 10-fold cross validation, using the true skill statistics (TSS; Allouche et al. 2006) and the area under the curve (AUC) statistics, following the recommendations in Liu et al. (2011).

To evaluate habitat selection by trappers at a coarse resolution, we used an information theoretic model selection approach. We constructed a series of candidate models using 3 categories of variables: vehicular access, forest maturity, and tree species composition. To avoid problems from multicollinearity, we selected only 1 covariate for each category. We used a model selection procedure based on Akaike's information criterion (Akaike 1973) with a correction for small sample sizes (AIC_c; Sugiura 1978) to determine which covariate in each category was the strongest predictor of trap presence (i.e., we chose the model with the lowest AIC_c value). We then used these covariates to construct a global model and meaningful subsets. The best overall model for predicting trap presence was then assessed using the AIC_c score and Akaike weights (w_i; Manly et al. 2002). Results were reported for models with w_i values ≥ 0.01 as well as a few others of interest. We carried out the process separately for Kapuskasing and Ear Falls and drew comparisons.

To control for variance among trappers within each study area and reduce pseudo-replication, we included trap line as a random effect in all models. We used the lme4 package (version 0.999375-42, http://cran.r-project.org/web/packages/lme4/index.html, accessed 22 Aug 2012) in Program R to fit generalized linear mixed effects models; for GAM models a random effect was included via a ridge penalty (see documentation in the mgcv package).

For the vehicular access term, we used the distance from each point to the nearest road or navigable water. We included distance to nearest water to account for trapping via motorized boats, and distance to nearest creeks for the Kapuskasing area to account for navigable creeks that were not present as water in the FRI layer. Distance to nearest access was the shortest distance from the point of interest to road, water, or creek. Access route densities were greater in Kapuskasing than in Ear Falls, and the mean distances to nearest access were 190.0 m and 450.2 m, respectively.

For the stand maturity term, we considered age and height in 2 candidate models, and chose the model with the smallest AIC_c value. For the species composition term, we tested 8 models using 5 variables and 3 combinations of variables that were not highly correlated ($r < 0.5$). All 8 models included access as a fixed effect and trap line as a random effect. We selected the most parsimonious model using AIC_c for the species composition component during final model selection.

To select the best predictive model, we chose candidate models using the access, stand maturity, and species composition variable sets and sensible interaction terms. We evaluated model fit using AIC_c (Burnham and Anderson 2002). We completed further analysis of trap-site selection relative to tree species composition using only points that were within 10 m of access routes for Kapuskasing and 40 m of access routes for Ear Falls. These values approximated the mean distance traps were set from access routes at the 2 study areas. We used this analysis to determine if patterns of use in relation to tree species composition resulted from different availability near travel routes relative to randomly distributed points across the entire trap line.

Analysis of fine resolution data was similar to that of the coarse resolution data. We included trap lines as a random effect. We controlled for access by using random locations within a 60 m band along the travel routes available to the trappers, which were spaced from vehicular access in a way that simulated trap setting. We included physical structure as a component of candidate models in the fine resolution analysis. Once we determined the variable or combination of variables that best predicted trap presence for each category, we constructed a set of candidate models for predictive model selection. During predictive model selection, many of the models produced AIC_c values that were close to one another. We used statistical package MuMIn (version 1.6.1, http://mumin.r-forge.r-project.org/, accessed 22 Aug 2012) in Program R to generate AIC_c values for subsets of the global model and to calculate parameter estimates by model averaging using all models with ΔAIC_c values ≤ 5. We used generalized linear mixed models (GLMM) for selection in the fine resolution analysis.

The analysis of resource selection by marten echoed that of the coarse resolution selection by trappers with a few exceptions. In the categories of forest maturity and species composition, we retained both the most parsimonious categorical components and the most parsimonious continuous components for predictive modeling.

We tested whether the TSS and AUC values were affected by the large disparity in sample sizes of random versus observed data points by re-analyzing the data using the same models but with a smaller sample of random points. We re-ran the TSS and AUC tests on the top 3 models from the Ear Falls coarse resolution trapper analysis using all 334 trap locations compared to 500 random points. We also conducted the same tests on the top 3 models from the Ear Falls marten habitat selection analysis using all 857 of the marten locations with 1,000 random points. We analyzed differences among means using analysis of variance while controlling for differences among models.

RESULTS

Coarse Resolution Trap Location Selection at Kapuskasing

Trappers selected trap sites based on shortest distance to road or water access in older stands that had a low proportion of black spruce (Fig. 2). The most parsimonious overall model included access (i.e., distance from roads, trails, or waterways), stand age, and black spruce proportion as main effects, in addition to a random factor controlling for variation among trap lines (Table 1). Few traps were found >60 m from roads or water (Fig. 2).

Trappers also appeared to avoid stands with greater proportions of black spruce based on data analyzed using only

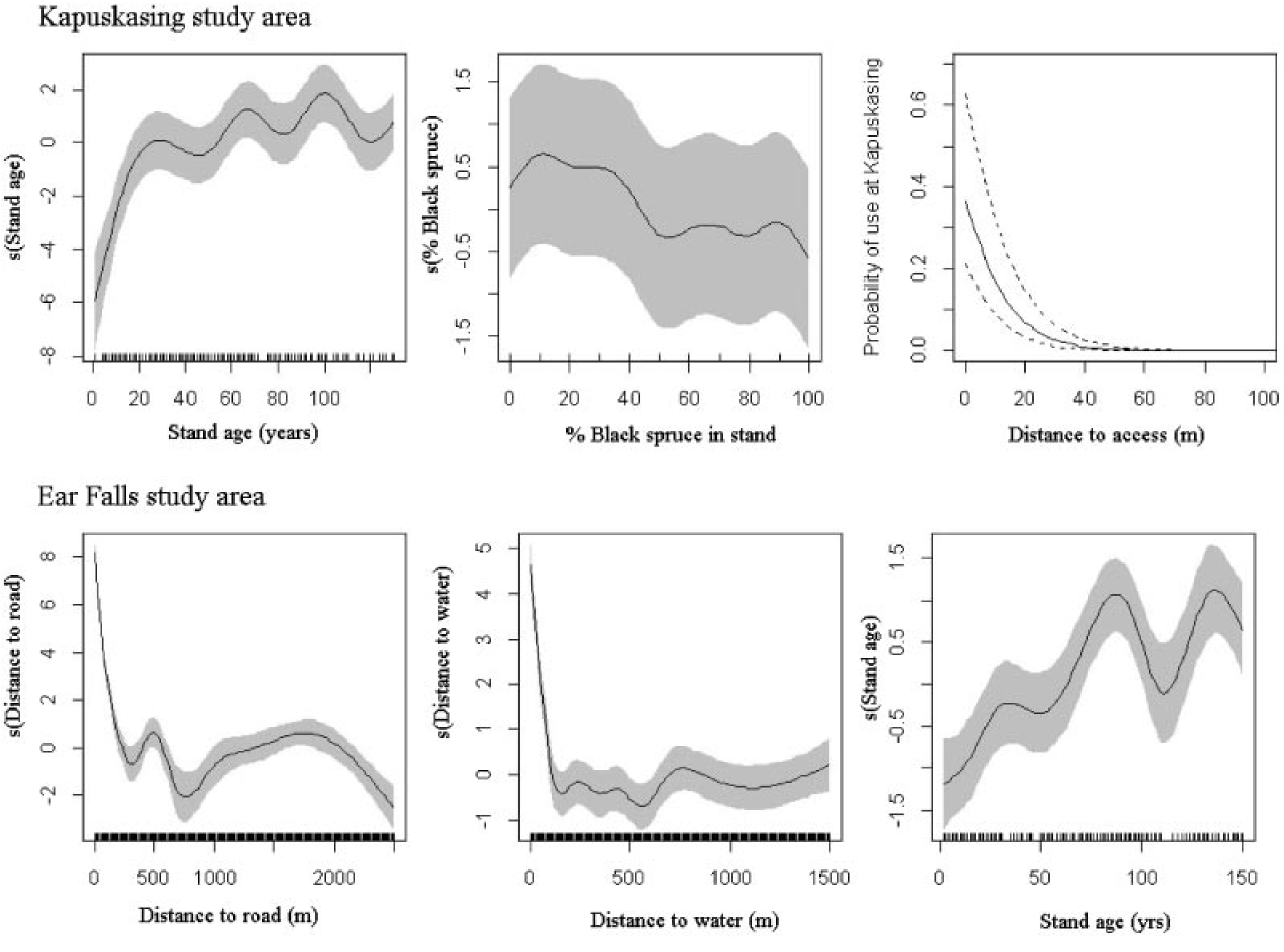

Figure 2. Graphical model outputs from resource selection models of marten trappers from Kapuskasing, Ontario, Canada (top) and Ear Falls, Ontario, Canada (bottom), 2004–2007, based on the most parsimonious coarse resolution logistic regression models. Additive terms of models are presented as a continuous line (s: smoothing component of the generalized additive model for each variable) with 95% confidence intervals (gray shading). The parametric term shows mean predicted response (solid line) with 95% confidence intervals (dashed lines).

Table 1. Model selection results for analyses of habitat selection by marten trappers at the coarse resolution scale at Kapuskasing and Ear Falls, Ontario, Canada, 2004–2007. For parameters that were not smooth, superscript signs beside each variable indicate a negative relationship (−), or non-selection (ns; 95% CI for estimate bounds zero). Every model contained trap line as a random effect with 4 or 6 levels, and an intercept. An s preceding a variable indicates that smoothing parameters were used to estimate the effect of that variable. Estimation of smoothing parameters allowed for non-integer values for degrees of freedom (K). We present the difference in corrected Akaike's information criterion (AIC_c) values between the minimum value in the set and model i (ΔAIC_c) as well as AIC_c weights (w_i). We calculated true skills statistics (TSS), and area under the curve (AUC) values by 10-fold cross-validation.

Model[a]	K	AIC_c	ΔAIC_c	w_i	% Deviance explained	TSS	AUC
Kapuskasing study area							
$D^- + s(G) + s(M)$	21.83	1466.58	0.00	1.00	58.5	0.834	0.973
$s(G) + s(M)$	18.59	3169.72	1703.14	0.00	8.6	0.344	0.728
Ear Falls study area							
$s(A) + s(B) + s(G)$	28.12	988.43	0.00	0.52	64.5	0.894	0.974
$s(A) + s(B) + s(G) + s(M) + L^{ns}$	30.10	989.71	1.28	0.28	64.6	0.899	0.977
$s(A) + s(B) + s(G) + s(M)$	29.10	990.35	1.92	0.20	64.5	0.893	0.980
$s(G) + s(M) + L^{ns}$	13.82	2,525.27	1536.85	0.00	5.0	0.308	0.668

[a] A, distance to nearest road; B, distance to nearest water; D, distance to nearest road, water, or creek; G, stand age; L, lowland spruce stand; M, percent black spruce in stand.

points that were close to access routes; therefore, avoidance of black spruce was not a consequence of differential availability of black spruce close to roads that were most often used for access. The second most parsimonious model of habitat selection near access had a ΔAIC_c value 25.3 units greater than the black spruce model and was therefore not considered competitive.

A comparison of the explanatory power of models was also instructive. A model containing only stand age and another containing only black spruce proportion was 1,544.5 and 1,588.9 AIC_c units greater than a model containing only distance to access. The proportion of deviance explained by models (51.2% for access vs. 6.5% and 5.1%, respectively, for stand age and black spruce proportion) suggested that access accounted for >7 times more of the underlying deviance than either of the other 2 habitat variables.

Coarse Resolution Trap Location Selection at Ear Falls

Trappers at Ear Falls also selected trap-site locations based on proximity to access, older aged stands, and low proportions of black spruce (Table 1). The most parsimonious overall model included distance to roads, distance to water, stand age, and a random factor controlling for trap line. Few traps in Ear Falls were located >150 m from vehicular access (Fig. 2).

For the species composition component of analysis, the top 2 models, containing black spruce proportion, and conifer proportion both received support, with w_i values of 0.59 and 0.41, respectively. Although the difference between these variables was small, we chose black spruce proportion as the species composition component because it performed better than the other components and made the global models comparable with those for Kapuskasing. Considering the 3 models that were competitive after predictive model selection (Table 1), the relative variable importance of distance to roads, distance to water, and stand age was 1.00. The relative variable importance values for black spruce proportion and lowland class were 0.48 and 0.28, respectively.

As was the case at Kapuskasing, trap location was best predicted by proximity to vehicular access. A model containing only access terms performed 1,478.15 AIC_c units better than the best model without access terms. The deviance explained by a model containing only access terms was 61.7%, whereas the best model without access explained 5.0% of deviance.

Fine Resolution Trap Location Selection at Kapuskasing

At the finest resolution, trappers at Kapuskasing selected specific locations for traps within older stands based on basal area of trees, high percentage of black spruce trees, high cedar proportion, and areas with substantial canopy cover. The most parsimonious model for predicting trap presence based on forest maturity included basal area of trees (>10 cm dbh). For predicting trap presence based on species composition, the best model included percent black spruce and percent cedar. All other models for these two categories were substantially less likely with $\Delta AIC_c \geq 10$. For forest structure, the best model included percent canopy cover. Two other competing models had ΔAIC_c values ≤ 2, both of which included canopy cover. Many of the models compared in predictive model selection were competitive ($<5\ \Delta AIC_c$; Table 2), so we employed model averaging techniques to estimate parameters and relative variable importance (Table 3).

Fine Resolution Trap Location Selection at Ear Falls

At fine resolution at Ear Falls, trappers selected trap sites with greater tree density, greater black spruce proportion, substantial canopy cover, and greater levels of coarse woody debris (Table 2). As with the Kapuskasing analysis, many of the competing models were similarly supported by the data ($<6\ \Delta AIC_c$; Table 2), hence we employed model averaging techniques to estimate parameters and relative variable importance (Table 3). Trap selection was positively associated with all of the main effect variables, but only percentage of black spruce and coarse woody debris produced model-averaged parameter estimates that were significantly >0.

The best descriptive variable for forest maturity at Ear Falls was basal area of trees. For forest structure, 2 models were competing, but canopy cover plus coarse woody debris had the lowest AIC_c value. In the category of species composition,

Table 2. Model selection results for analyses of habitat selection by marten trappers at the fine resolution at Kapuskasing and Ear Falls, Ontario, Canada, 2004–2007. Superscript signs beside each variable indicate positive selection (+), avoidance (−), or non-selection (ns; 95% CI for estimate bounds zero) based on model-averaged parameter estimates. Every model contains trap line as a random effect, an intercept, and a variance component. We present the number of parameters for each model (*K*), the difference in corrected Akaike's information criterion (AIC_c) values between the minimum value in the set and model *i* (ΔAIC_c), and AIC_c weights (w_i). We calculated true skills statistics (TSS), and area under the curve (AUC) values by 10-fold cross-validation.

Model[a]	*K*	AIC_c	ΔAIC_c	w_i	TSS	AUC
Kapuskasing study area						
$b^{+} + h^{+} + f^{ns} + b \times h^{-} + h \times f^{ns}$	8	377.08	0	0.19	0.529	0.770
$b^{+} + h^{+} + f^{ns} + b \times h^{-}$	7	377.42	0.34	0.16	0.510	0.777
$b^{+} + h^{+} + g^{ns} + f^{ns} + b \times h^{-}$	8	377.51	0.43	0.15	0.520	0.781
$b^{+} + h^{+} + g^{ns} + f^{ns} + b \times h^{-} + h \times f^{ns}$	9	378.40	1.32	0.1	0.521	0.780
$b^{+} + h^{+} + f^{ns} + b \times h^{-} + b \times f^{ns} + h \times f^{ns}$	9	379.15	2.07	0.07	0.518	0.766
$b^{+} + h^{+} + f^{ns}$	6	379.18	2.1	0.07	0.503	0.773
$b^{+} + h^{+} + f^{ns} + b \times h^{-} + b \times f^{ns}$	8	379.32	2.24	0.06	0.513	0.771
$b^{+} + h^{+} + g^{ns} + f^{ns} + b \times h^{-} + b \times f^{ns}$	9	379.61	2.53	0.05	0.512	0.772
$b^{+} + h^{+} + g^{ns} + f^{ns}$	7	380.18	3.1	0.04	0.520	0.776
$b^{+} + h^{+} + g^{ns} + f^{ns} + b \times h^{-} + b \times f^{ns} + h \times f^{ns}$	10	380.43	3.35	0.04	0.517	0.780
$b^{+} + h^{+} + f^{ns} + h \times f^{ns}$	7	380.47	3.39	0.03	0.507	0.767
$b^{+} + h^{+} + f^{ns} + b \times f^{ns}$	7	380.98	3.9	0.03	0.502	0.770
$b^{+} + h^{+} + g^{ns} + f^{ns} + h \times f^{ns}$	8	381.99	4.91	0.02	0.536	0.777
Ear Falls study area						
$b^{ns} + j^{+} + f^{+} + b \times f^{ns}$	7	364.55	0	0.24	0.400	0.675
$b^{ns} + j^{+} + f^{+}$	6	365.32	0.77	0.16	0.395	0.674
$b^{ns} + h^{ns} + j^{+} + f^{+} + b \times h^{ns} + b \times f^{ns}$	9	365.61	1.06	0.14	0.383	0.664
$b^{ns} + h^{ns} + j^{+} + f^{+} + b \times h^{ns}$	8	365.69	1.15	0.13	0.351	0.665
$b^{ns} + h^{ns} + j^{+} + f^{+} + b \times f^{ns}$	8	365.83	1.29	0.13	0.368	0.664
$b^{ns} + h^{ns} + j^{+} + f^{+}$	7	366.75	2.21	0.08	0.372	0.661
$b^{ns} + f^{+} + b \times f^{ns}$	6	368.39	3.84	0.03	0.374	0.668
$b^{ns} + h^{ns} + f^{+} + b \times h^{ns} + b \times f^{ns}$	8	369.08	4.53	0.02	0.395	0.662
$b^{ns} + h^{ns} + f^{+} + b \times h^{ns}$	7	369.19	4.65	0.02	0.361	0.667
$b^{ns} + f^{+}$	5	369.42	4.88	0.02	0.371	0.661
$b^{ns} + j^{+}$	5	369.83	5.29	0.02	0.370	0.661

[a] b, basal area of trees >10 cm diameter at breast height; f, % black spruce; g, % cedar; h, canopy cover; j, coarse woody debris.

6 models were competing with $\Delta AIC_c \leq 2$. Although percent of conifer trees was included in the most parsimonious model, it was highly correlated with canopy cover ($r = 0.69$). Since canopy cover was selected as a variable in the forest structure component, we chose percent of black spruce trees because it had the next lowest AIC_c value and was not correlated with canopy cover ($r = 0.18$).

Pronounced differences existed in the predictive power of habitat components from coarse resolution models versus fine resolution models. For example, the best coarse resolution model at Kapuskasing that contained only habitat variables had TSS and AUC values of 0.34 and 0.73, respectively. The best fine resolution model at Kapuskasing had TSS and AUC values of 0.53 and 0.78, respectively.

Table 3. Model-averaged parameter estimates with standard errors for Kapuskasing and Ear Falls, Ontario, Canada, 2004–2007 fine resolution habitat selection by marten trappers. Positive estimates indicate positive selection and negative estimates indicate avoidance, provided that confidence intervals do not include zero.

Parameter	β estimate	SE	Lower 95% CI	Upper 95% CI	Variable importance
Kapuskasing study area					
Intercept	−6.658	2.154	−10.880	−2.436	
Basal area of trees	0.158	0.077	0.007	0.310	1.00
% Black spruce in plot	3.800	2.356	−0.818	8.419	1.00
Canopy cover	6.649	3.128	0.518	12.779	1.00
% Cedar in plot	0.740	0.620	−0.476	1.956	0.39
Basal area: canopy cover	−0.186	0.089	−0.360	−0.012	0.82
Canopy cover: % spruce	−4.756	3.736	−12.080	2.567	0.44
Basal area: % spruce	−0.003	0.038	−0.078	0.072	0.24
Ear Falls study area					
Intercept	−2.858	1.183	−5.178	−0.539	
Basal area of trees	0.086	0.053	−0.017	0.190	1.00
% Black spruce in plot	1.504	0.758	0.019	2.990	0.98
Coarse woody debris volume	0.006	0.002	0.001	0.011	0.90
Canopy cover	2.498	2.116	−1.648	6.644	0.53
Basal area: canopy cover	−0.145	0.090	−0.322	0.031	0.32
Basal area: % spruce	−0.049	0.030	−0.107	0.009	0.56

Although overall predictive models at the coarse resolution had greater predictive power (TSS = 0.83 and 0.89, for Kapuskasing and Ear Falls, respectively) than those at the fine resolution (TSS = 0.53 and 0.40, for Kapuskasing and Ear Falls, respectively), vehicular access accounted for the greatest effect in coarse resolution models. Considering only forest-related variables, fine resolution models had more predictive power than coarse resolution models at Kapuskasing and Ear Falls. The best coarse resolution models for Kapuskasing and Ear Falls that did not include access had TSS values of 0.34 and 0.31, respectively.

Marten Habitat Selection

At Kapuskasing, the most parsimonious model for describing marten habitat selection indicated that marten showed positive selection for locations that were <1 km from gravel roads, <2.5 km from water, >5 km from creeks, and <400 m from winter roads and quad trails, in stands with 10–40% cedar and that their response to stand age depended on the species composition category of stands (Fig. 3). The next most parsimonious model was much less likely, with a ΔAIC_c value of 121.2. The best model that did not include distance to linear features had the same habitat components as the most parsimonious model but had much less predictive power (Table 4). Although the response of marten to stand age varied with species composition, they showed negative selection for stands <35 years old in all categories, and selection peaked between about 50 and 70 years. Marten selection for lowland conifer stands was significantly less than that for upland conifer stands (β 95% CI: -1.025 to -0.462, $Z = -5.28$, $P < 0.001$). Selection for mixed and deciduous stands was not significantly different ($P > 0.1$) from upland conifer.

At Ear Falls, marten locations also tended to be close to roads and to water. The most parsimonious model indicated that marten showed positive selection for locations <1 km from water, and <1 km from roads (Fig. 4). The response of marten to stand age varied depending on the stand species composition category. In upland conifer and deciduous stands, marten showed positive selection for stands >50 years old. In lowland conifer stands, selection peaked at 40 years of age, and in mixed stands, marten showed positive selection for stands that were either <10 or >30 years old. The most parsimonious model was 155.5 ΔAIC_c units less

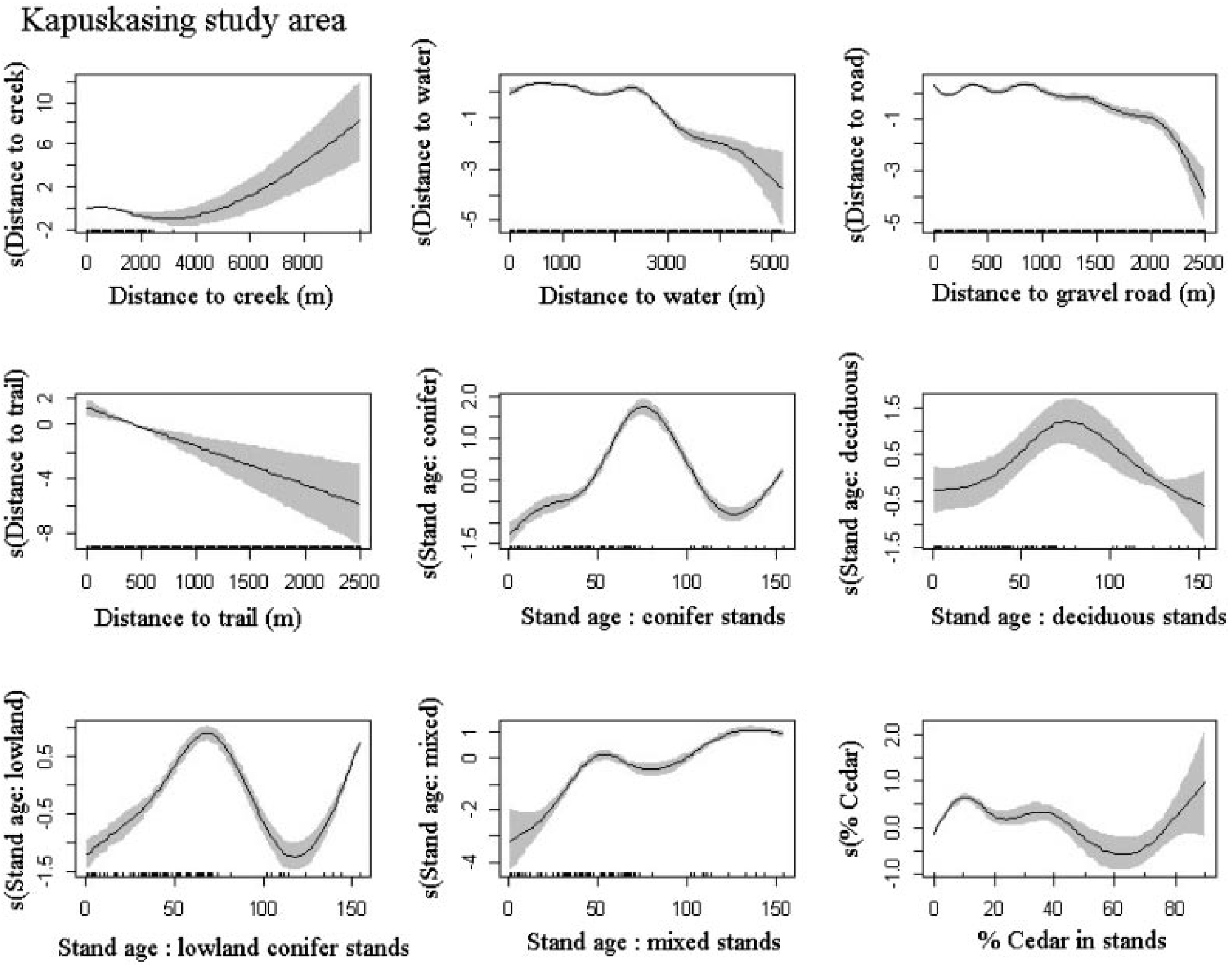

Figure 3. Graphical model outputs from resource selection models of marten from Kapuskasing, Ontario, Canada, 2004–2007, based on the most parsimonious logistic regression models. Outputs show the mean predicted response (line) with 95% confidence intervals (gray shading).

Table 4. Model selection results for marten resource selection at Kapuskasing and Ear Falls, Ontario, Canada, 2003–2007. The number of parameters for each model *i* is given as *K*. We present the difference in corrected Akaike's information criterion (AIC_c) values between the minimum value in the set and model *i* (ΔAIC_c), and AIC_c weights (w_i). We calculated true skills statistics (TSS), and area under the curve (AUC) values by 10-fold cross-validation.

Model[a]	*K*	AIC_c	ΔAIC_c	w_i	% Deviance explained	TSS	AUC
Kapuskasing study area							
s(A:E) + s(B) + s(C) + E + s(G × H) + H + s(N)	40.7	5048.29	0.00	1.00	15.90	0.421	0.775
s(G × H) + H + s(N)	27.9	5203.82	563.17	0.00	5.96	0.248	0.657
Ear Falls study area							
s(A) + s(B) + s(G × H) + H	66.9	9451.04	0.00	1.00	13.40	0.347	0.738
s(G × H) + H	45.4	9572.22	381.57	0.00	9.50	0.290	0.691

[a] A, distance to nearest road; B, distance to nearest water; C, distance to nearest creek; E, road class; G, stand age (continuous); H, species composition (categorical); N, percent cedar in stand.

than the next best model. As with Kapuskasing, the best model that did not include distance to linear features contained the same age and species composition components as the most parsimonious model and had substantially less predictive power (Table 4). Selection was less for deciduous (β 95% CI: −1.56 to −0.504, $Z = -3.91$, $P < 0.001$) and mixed stands (β 95% CI: −1.67 to −0.269, $Z = -2.77$, $P < 0.01$), when compared to upland conifer stands. Selection for lowland conifer stands was not significantly different from selection for upland conifer stands (β 95% CI: −0.775 to 0.457, $Z = -0.51$, $P > 0.1$).

Recalculating the TSS and AUC goodness-of-fit tests with observed to random point ratios close to 1:1 resulted in no difference. All 4 ANOVA tests reported differences not significantly different from zero with $P > 0.25$ in all cases while controlling for differences among models.

DISCUSSION

Vehicular access to traps was the most influential factor affecting trap placement and the motive is easily understood. Pick-up trucks, ATVs, snowmobiles, and motor boats were all used by trappers in our study areas and, in our experience, this is typical of most trappers throughout northern Ontario. Trappers clearly minimized the effort required to check traps by placing traps close to the access routes.

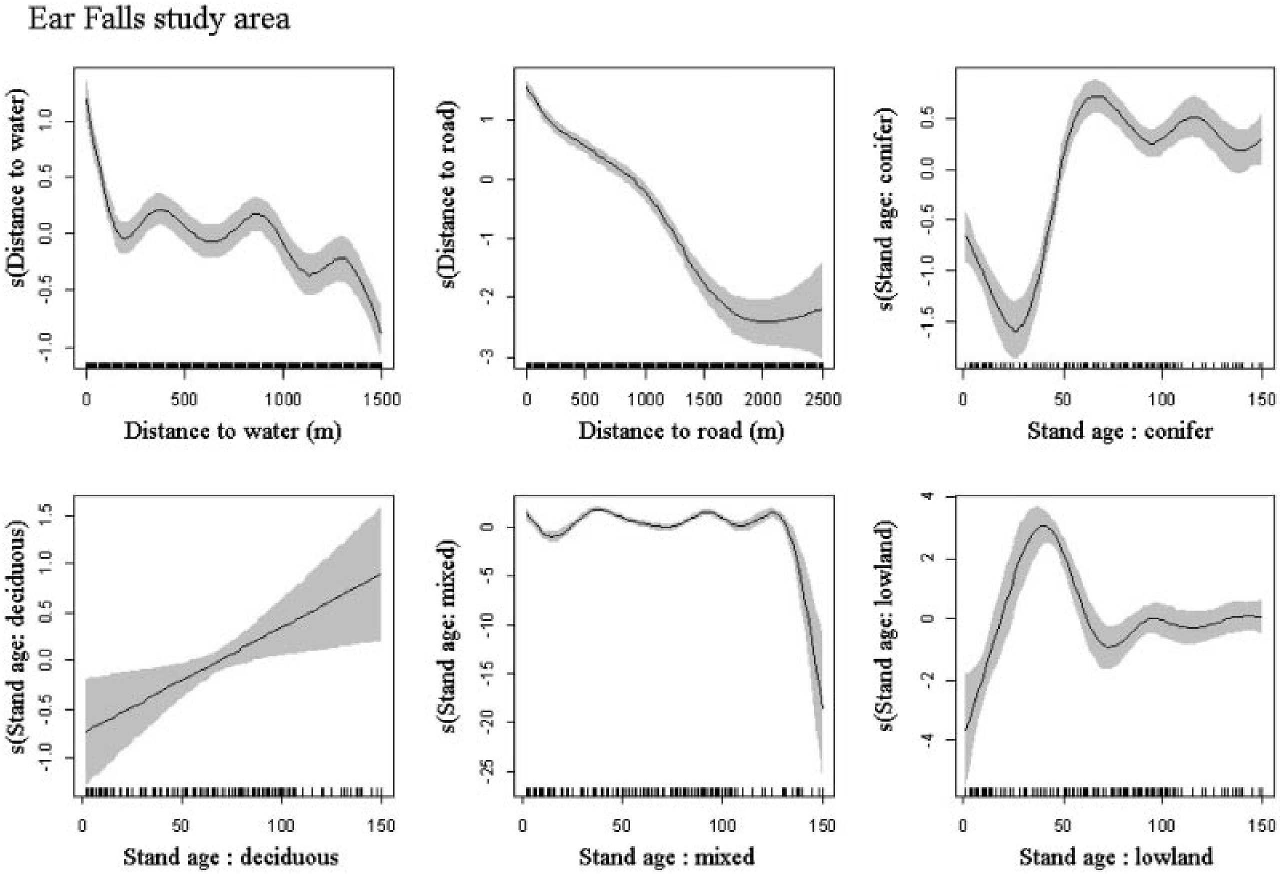

Figure 4. Graphical model outputs from resource selection models of marten from Ear Falls, Ontario, Canada, 2004, based on the most parsimonious logistic regression models. Outputs show the mean predicted response (line) with 95% confidence intervals (gray shading).

Trappers also appeared to select trap sites in stands with low black spruce and conifer proportions, based on the coarse resolution FRI data. This pattern of selection contrasted with their selection at fine spatial resolution, where trappers selected for greater proportions of black spruce and other coniferous trees. Trappers chose mixed stands in which to place traps and upon entering a stand, selected specific trap locations near black spruce and other conifers. Alternatively, GIS data may not adequately identify species composition at a resolution that matches the decision-making process used by trappers. The apparent avoidance of conifer stands could simply be an issue of resolution. Trappers are far more likely to be making decisions about trap placement based on what they can see from their travel routes, than from what appears on FRI maps. Furthermore, the fact that the species composition component had low model fit (deviance explained = 5.1% and 3.4%, for Kapuskasing and Ear Falls, respectively) and was not included in the best model for coarse resolution trap selection at Ear Falls, suggested that species composition from FRI data were not a good predictor of trap presence.

Both the Ear Falls and Kapuskasing study areas were composed of a mixture of forest types, ranging from stands logged 40–60 years ago, to areas originating from fire 80–120 years ago, with some recent clear cuts at Ear Falls. Marten selected the oldest stands in the study area, consistent with the majority of previous findings that marten prefer older, unlogged stands (Thompson and Colgan 1994, Bull et al. 2005, Godbout and Ouellet 2008) in northern boreal and montane forests, but see Hearn et al. (2010). Marten selected upland and lowland conifer stands more than others at Ear Falls but only upland conifer stands more than others at Kapuskasing. This was consistent with earlier studies in boreal forests that found marten preferred conifer dominated and mixed wood forests (Raine 1983, Thompson and Colgan 1987, Bowman and Robitaille 1997, Potvin et al. 2000).

Trappers and marten selected old forest stands over stands <40 years old, consistent with many previous studies of marten (Thompson and Colgan 1987, Bull et al. 2005, Gosse et al. 2005, Slauson et al. 2007, Baldwin and Bender 2008). Selection for species composition of forest stands was only important for trappers on the Kapuskasing study area, where they selected mixed stands. In marten selection models, conifer stands were selected more than any others. This result was consistent with some studies on marten (Raine 1983, Baldwin and Bender 2008), but not others (Chapin et al. 1997, Payer and Harrison 2003, Poole et al. 2004). Trappers apparently learn the habitat preferences of their prey species within their own trap lines and adjust their trapping techniques accordingly to improve trapping success.

At a fine spatial resolution, trappers selected trap sites in forest stands with high basal area of trees, high proportions of black spruce, and high canopy cover in both study areas when compared to random locations. High basal area of trees is characteristic of mature and old boreal forest stands. Several studies investigating habitat use by marten at a fine resolution have identified positive associations with high basal area (Spencer et al. 1983, Payer and Harrison 2003, Bull et al. 2005), suggesting that trappers selected preferred marten habitat in this respect.

Trappers selected trap sites with greater proportions of black spruce and coniferous trees than were available at random locations. Marten have also been shown to select habitats with a high proportion of conifer at a fine resolution (Bowman and Robitaille 1997, Poole et al. 2004). In Kapuskasing, trappers also selected trap sites in stands with greater proportions of eastern white cedar, as do marten in this area (McKague 2007). Trappers selected areas with trees >10 cm in diameter more than those with smaller trees when making decisions about trap placement. This may be because attaching traps to larger trees was easier, or because trappers perceived larger trees as better habitat for marten. Trap site selection at locations with high proportions of canopy cover was consistent with many studies on habitat selection by marten (Spencer et al. 1983, Hargis and McCullough 1984, Payer and Harrison 2003, Poole et al. 2004, Bull et al. 2005), although Baldwin and Bender (2008) found no selection for high canopy cover. With respect to forest maturity, species composition, and forest structure, trappers appeared to be targeting habitats frequently selected by marten in both study areas.

At the Ear Falls study area, trappers also selected trap sites with greater than random densities of coarse woody debris, as marten often do (Spencer et al. 1983, Bowman and Robitaille 1997, Payer and Harrison 2003). At Kapuskasing, however, we found no significant relationship between trap site use and coarse woody debris and shrub density was not a significant predictor of trap presence in either study area. Marten have been found to select high shrub densities in some studies (Spencer et al. 1983, Poole et al. 2004, Porter et al. 2005) but not in others (Payer and Harrison 2003). The best predictive models at fine resolution contained all 3 habitat components: forest maturity, species composition, and forest structure. Thus, all influential factors affecting trap placement were consistent with what is generally known about marten habitat selection in northern Ontario.

Differences in resource selection at coarse versus fine resolutions might indicate problems for using FRI data for habitat selection studies and for planning forest management relative to marten. Fine resolution models had more explanatory power than coarse resolution models with respect to habitat variables. Similar results were observed in a study comparing coarse versus fine resolution resource selection by marten on the same study areas (McKague 2007). Forest stands from FRI data average tree species composition over an area that is probably larger than that perceived by fur trappers. The edges of stands that are close to travel routes within the perceptual range of trappers may not be representative of the entire stand. Consequently, stands that are correctly identified as deciduous from FRI may appear coniferous when viewed from a road or river. Errors in species composition also exist within FRI datasets (Thompson et al. 2007). Regardless of which explanation is true, this study offers evidence that habitat managers should be cautious about their level of precision when making decisions based on forest species composition obtained from FRI data.

In summary, trappers in northern Ontario take advantage of available access routes to use motorized vehicles for trapping marten. Within the areas of their trap lines that are easily accessible, they tend to select trap sites where they perceive that marten are most likely to occur. Although FRI data, including road layers, are appropriate for predicting trap presence based on access and stand age, they are not effective at predicting trap presence with respect to other aspects of marten habitat. To accurately predict trap presence based on species composition and forest structure, more detailed measurements are required from the ground.

MANAGEMENT IMPLICATIONS

Forest managers establishing required sanctuaries or core habitat areas for marten should consider that trappers seldom trapped far from roads or water used for vehicular access. Consequently, the effectiveness of sanctuaries depends on not only the age and species composition of forest stands left unlogged, but also on the degree to which they are accessible to trappers. Trappers are well aware of the habitats that marten use and trap accordingly. If marten populations are to be sustained in northern Ontario, the management of commercial forests and of marten should be integrated so that the needs of harvesters of both commercial forests and of fur bearing mammals are considered.

ACKNOWLEDGMENTS

We thank J. Oaks, N. Romanow, J. Ellis, B. Beadow, M. Latos, A. Dussault, D. Wiebe, G. Nagorski, W. Williamson, J. Couette, and D. Kott for field support and data collection. We thank J. Shuter and C. Johnson for assistance during analysis. We thank R. Norris, T. Avgar, and D. Kueffler for project proposal input and review and early stages of the manuscript. Funding was provided by the Natural Sciences and Engineering Research Council of Canada, Canadian Forest Service, Ontario Ministry of Natural Resources, Forest Ecosystem Science Cooperative Inc., and Sustainable Forest Management Network. We also thank 2 anonymous reviewers and the journal editors whose constructive criticism led to a much improved manuscript.

LITERATURE CITED

Akaike, H. 1973. Information theory as an extention of the maximum likelihood principle. Pages 267–281 *in* B. N. Petrov, and F. Csaki, editors. Second international symposium on information theory. Akademiai Kiado, Budapest, Hungary.

Allouche, O., A. Tsoar, and R. Kadmon. 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). Journal of Applied Ecology 43:1223–1232.

Andruskiw, M., J. M. Fryxell, I. D. Thompson, and J. A. Baker. 2008. Habitat-mediated variation in predation risk by the American marten. Ecology 89:2273–2280.

Baldwin, R. A., and L. C. Bender. 2008. Distribution, occupancy, and habitat correlates of American martens (*Martes americana*) in Rocky Mountain National Park, Colorado. Journal of Mammalogy 89:419–427.

Bissonette, J. A., R. J. Fredrickson, and B. J. Tucker. 1989. American marten: a case study for landscape-level management. Transactions of the North American Wildlife and Natural Resources Conference 54: 89–101.

Boos, J. D., and W. R. Watt. 1997. Small mammal habitat associations in the Lake Abitibi Model Forest of northeastern Ontario. Queen's Printer for Ontario, Sault Ste Marie, Ontario, Canada.

Bowman, J. C., and J.-F. Robitaille. 1997. Winter habitat use of American martens (*Martes americana)* within second-growth forest in Ontario, Canada. Wildlife Biology 3:97–105.

Bull, E. L., T. W. Heater, and J. F. Shepherd. 2005. Habitat selection by the American marten in northeastern Oregon. Northwest Science 79: 37–43.

Burnham, K. P., and D. R. Anderson, editors. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Chapin, T. G., D. J. Harrison, and D. M. Phillips. 1997. Seasonal habitat selection by marten in an untrapped forest preserve. Journal of Wildlife Mangement 61:707–717.

Cottam, G., and J. T. Curtis. 1956. The use of distance measures in phytosociological sampling. Ecology 37:451–460.

Fryxell, J. M., J. B. Falls, E. A. Falls, R. J. Brooks, L. Dix, and M. A. Strickland. 1999. Density dependence, prey dependence, and population dynamics of martens in Ontario. Ecology 80:1311–1321.

Godbout, G., and J.-P. Ouellet. 2008. Habitat selection of American marten in a logged landscape at the southern fringe of the boreal forest. Ecoscience 15:332–342.

Gosse, J. W., R. Cox, and S. W. Avery. 2005. Home-range characteristics and habitat use by American martens in eastern Newfoundland. Journal of Mammalogy 86:1156–1163.

Hargis, C. D., and D. R. McCullough. 1984. Winter diet and habitat selection of marten in Yosemite National Park. Journal of Wildlife Management 48:140–146.

Hearn, B. H., D. J. Harrison, A. K. Fuller, C. G. Lundrigan, and W. J. Curran. 2010. Paradigm shifts in habitat ecology of threatened Newfoundland martens. Journal of Wildlife Management 74:719–728.

Hodgman, T. P., D. J. Harrison, D. D. Katnik, and K. D. Elowe. 1994. Survival in an intensively trapped marten population in Maine. Journal of Wildlife Management 58:593–600.

Hodgman, T. P., D. J. Harrison, D. M. Phillips, and K. D. Elowe. 1997. Survival of marten in an untrapped forest preserve in Maine. Pages 86–99 *in* G. Proulx, H. N. Bryant, and P. M. Woodard, editors. Martes: taxonomy, ecology, techniques and management. Provincial Museum of Alberta, Edmonton, Alberta, Canada.

Lemmon, P. E. 1956. A spherical densiometer of estimating forest overstory density. Forest Science 2:314–320.

Liu, C., M. White, and G. Newell. 2011. Measuring and comparing the accuracy of species distribution models with presence–absence data. Ecography 34:232–243.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson, editors. 2002. Resource selection by animals: statistical design and analysis for field studies. Second edition. Kluwer Academic Publishers, Dordecht, The Netherlands.

Marshall, W. H. 1951. Pine marten as a forest product. Journal of Forestry 49:899–905.

McKague, C. I. 2007. Winter resource selection by the American marten (*Martes americana*): the effect of model resolution. Thesis, University of Guelph, Guelph, Ontario.

Payer, D. C., and D. J. Harrison. 2003. Influence of forest structure on habitat use by American marten in an industrial forest. Forest Ecology and Management 179:145–156.

Poole, K. G., A. D. Porter, A. de Vries, C. Maundrell, S. D. Grindal, and C. C. St. Clair. 2004. Suitability of a young deciduous-dominated forest for American marten and the effects of forest removal. Canadian Journal of Zoology 82:423–435.

Porter, A. D., C. C. St. Claire, and A. de Vries. 2005. Fine-scale selection by marten during winter in a young deciduous forest. Canadian Journal of Forest Research 35:901–909.

Potvin, F., L. Bélanger, and K. Lowell. 2000. Marten habitat selection in a clearcut boreal landscape. Conservation Biology 14:844–857.

Quick, H. F. 1956. Effects of exploitation on a marten population. Journal of Wildlife Management 20:267–274.

Raine, R. M. 1983. Winter habitat use and response to snow cover of fisher (*Martes pennanti*) and marten (*Martes americana*) in southeastern Manitoba. Canadian Journal of Zoology 61:25–34.

Slauson, K. M., W. J. Zielinski, and J. P. Hayes. 2007. Habitat selection by American martens in coastal California. Journal of Wildlife Management 71:458–468.

Smith, A. C., and J. A. Schaefer. 2002. Home-range size and habitat selection by American marten (*Martes americana*) in Labrador. Canadian Journal of Zoology 80:1602–1609.

Snyder, J. E., and J. A. Bissonette. 1987. Marten use of clear-cuttings and residual forest stands in western Newfoundland. Canadian Journal of Zoology 65:169–174.

Soukkala, A. M. 1983. The effects of trapping on marten populations in Maine. Thesis, University of Maine, Orono, USA.

Soutiere, E. C. 1979. Effects of timber harvesting on marten in Maine. Journal of Wildlife Management 43:850–860.

Spencer, W. D., R. H. Barrett, and W. J. Zielinski. 1983. Marten habitat preferences in the Northern Sierra Nevada. Journal of Wildlife Management 47:1181–1186.

Strickland, M. A., and C. W. Douglas. 1987. Marten. Pages 530–546 *in* M. Novak, J. A. Baker, M. E. Obbard, and B. Malloch, editors. Wild furbearer management and conservation in North America. Ontario Trappers Association, North Bay, Ontario, Canada.

Sugiura, N. 1978. Further analysis of the data by Akaike's information criterion and the finite corrections. Communications in Statistics, Theory, and Methods A7:13–26.

Thompson, I. D. 1994. Marten populations in uncut and logged boreal forests in Ontario. Journal of Wildlife Management 58:272–280.

Thompson, I. D., and P. W. Colgan. 1987. Numerical responses of martens to a food shortage in northcentral Ontario. Journal of Wildlife Management 51:824–835.

Thompson, I. D., and P. W. Colgan. 1990. Prey choice by marten during a decline in prey abundance. Oecologia 83:443–451.

Thompson, I. D., and P. W. Colgan. 1994. Marten activity in uncut and logged boreal forests in Ontario. Journal of Wildlife Management 58:280–288.

Thompson, I. D., and W. J. Curran. 1995. Habitat suitability for marten of second-growth balsam fir forests in Newfoundland. Canadian Journal of Zoology 73:2059–2064.

Thompson, I. D., S. C. Maher, D. P. Rouillard, J. M. Fryxell, and J. A. Baker. 2007. Accuracy of forest inventory mapping: some implications for boreal forest management. Forest Ecology and Management 252:208–221.

van Wagner, C. E. 1968. The line intersect method in forest fuel sampling. Forest Science 14:20–26.

Watt, W. R., J. A. Baker, D. M. Hogg, J. G. McNichol, and B. J. Naylor. 1996. Forest management guidelines for the provision of marten habitat. Queen's Printer for Ontario, Sault Ste Marie, Ontario, Canada.

Wood, S. N. 2006. Generalized additive models: an introduction with R. Chapman and Hall/CRC Press, Boca Raton, Florida, USA.

Yeager, L. E. 1950. Implications of some harvest and habitat factors on pine marten management. Transactions of the North American Wildlife Conference 15:319–334.

Associate Editor: Stan Gehrt.