12

Scale Dependency of American Marten (*Martes americana*) Habitat Relations

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ABSTRACT

Animals select habitat resources at multiple spatial scales; therefore, explicit attention to scale-dependency when modeling habitat relations is critical to understanding how organisms select habitat in complex landscapes. Models that evaluate habitat variables calculated at a single spatial scale (e.g., patch, home range) fail to account for the effects of other scales on the probability of species occurrence. Although single-scale approaches are common, we hypothesize that such models will be less predictive and incur greater risk of false inferences than multiscale models that account for the effects of habitat variables that are individually scaled to reflect their optimum relation with species occurrence. This follows from the knowledge that an animal's location is not well defined by the effects of habitat conditions occurring at any 1 spatial scale; rather, animal locations represent the cumulative influence of habitat selection across a broad range of spatial scales, from the landscape to the microsite. In this chapter, we describe an approach that uses bivariate scaling, logistic regression, and information theory to derive a multiscale model combining habitat variables at the scales that optimally predict species occurrence. We demonstrate the utility of this approach by investigating habitat relations of the American marten (*Martes americana*) in northern Idaho using 2 modeling approaches. By comparing how a multiscale model differs in terms of fit, performance, variable use, and spatial prediction from a single-scale model constrained to the scale of habitat patches (i.e., within 90 m of the sampling location), we reveal the importance of considering all relevant spatial scales in habitat models. Our results show that both the strength and the nature of apparent habitat relations are highly sensitive to the scale of predictor variables, and that models that are naïve to scale may easily misconstrue the nature of wildlife-habitat relations. We discuss this issue in the context of other marten

habitat studies and conclude by describing the implications of our findings for managing marten habitat.

Introduction

Previous studies of habitat selection by American martens (*Martes americana*) were often focused on the relation between marten occurrence and field data collected within a relatively small area centered on a sampling point. This approach has and continues to yield valuable insights about the factors determining marten habitat selection at relatively small spatial scales (e.g., Spencer et al. 1983; Bowman and Robitaille 1997). Recent advances in geographic information systems (GIS) and spatial statistics and the availability of remotely sensed spatial data have made it practical to model marten habitat relations at larger spatial scales. The importance of understanding ecological processes that occur across a range of relevant scales is a central tenet of landscape ecology (Urban 1987; Turner 1989) and has long been considered in studies of wildlife-habitat relations (Wiens 1976). Species respond to their environment across a hierarchy of spatial scales (Johnson 1980; Schaefer and Messier 1995; Rettie and Messier 2000). Johnson (1980) identified 4 levels within this hierarchy: (1) first-order selection is the species' geographic range; (2) second-order selection is the choice of home ranges within that range; (3) third-order selection is the choice of patches within a home range; and (4) fourth-order selection is the choice of habitat elements within a patch. Although this conceptual framework has been modified to account for additional scales of selection, including the location of populations within a geographic range and metapopulation dynamics (Baguette and Mennechez 2004; Meyer and Thuiller 2006), habitat-association models that have accounted for hierarchical selection have provided important insights about the ecological relations of a broad array of species (e.g., Bergin 1992; McIntyre 1997; Harvey and Weatherhead 2006).

The importance of scale and hierarchy in habitat selection has also been reported in studies of the American marten and other *Martes* species (Bissonette et al. 1997). For example, at the home-range scale, marten habitat selection has been related to canopy cover and habitat fragmentation (Chapin et al. 1998; Hargis et al. 1999; Potvin et al. 2000; Payer and Harrison 2003). At the stand scale, however, marten habitat selection has been related to forest structural characteristics such as age class, tree species, and understory composition (Chapin et al. 1997a). At smaller spatial scales, martens have been reported to select habitat in accordance with particular behaviors such as foraging, resting, denning, and predator avoidance. Fine-scale habitat selection related to these behaviors includes selection of structures based on the availability of coarse woody debris, vertical escape routes, tree cavities, and subnivean access sites (Buskirk et al. 1989; Corn and Raphael 1992; Taylor and Buskirk 1994).

The complexity of habitat selection at different spatial scales for martens and other wildlife species underscores the need to consider a multiscale approach for inferring habitat relations (Bissonette and Broekhuizen 1995; Bissonette et al. 1997; Cushman and McGarigal 2004). Thus far, the predominant approach to account for the influence of spatial scale on marten habitat selection has been first to identify 1 or more scales of interest (e.g., patch, stand, home range), and then to find relations between marten occurrence and habitat variables at each scale. Habitat variables sampled in the field are often collected and calculated at the patch scale. At broader spatial scales, habitat variables are frequently obtained from raster GIS models of landscape attributes, then calculated by taking the average value of that attribute within a given radius from locations where the study organism was either present or absent (Boyce 2006). Once habitat variables are calculated at the scale of interest, a resource selection function may be developed (Boyce and McDonald 1999; Manly et al. 2002; Johnson et al. 2006) to relate those variables to probability of occurrence.

Although this approach has yielded important insights about habitat selection for many species (including martens) across a hierarchy of spatial scales, it does not consider the cumulative influence of all scales of habitat selection in a single model or resource selection function; instead, it constrains all the variables to act at a single scale. Just as early habitat-association studies that focused on the patch scale did not account for potential influences at larger spatial scales, more recent studies constrained to analyses at the largest spatial scales do not account for influences occurring at finer scales. Developing several models at different spatial scales using the same data does not fully address this issue. Rather than referring to a series of scale-constrained models (e.g., individual models scaled to the patch, stand, and home range) as representing multiscale habitat selection, as is commonly reported in the literature, we refer to each as a *single-scale* model. We reserve the term *multiscale* for a single model that accounts for the cumulative influences of habitat associations occurring across a range of relevant scales.

We hypothesize that a predictive model of species occurrence based on the influence of habitat variables acting at all relevant spatial scales would generally offer greater specificity, sensitivity, classification accuracy, and predictive power than a model based on variables constrained to a single scale. We also predict that such multiscale models may provide new insights into species habitat associations that would not be apparent when variables were constrained to a single scale. Indeed, recent studies based on a multiscale approach have yielded highly predictive models of bird and moth rarity (Grand et al. 2004) and bald eagle (*Haliaeetus leucocephalus*) habitat selection (Thompson and McGarigal 2002). Among marten habitat studies, Slauson et al. (2007) found that a model combining stand- and home-range scale habitat selection was more predictive of marten occurrence in coastal

California (USA) than either a stand- or home-range scale model alone. These examples suggest the power of a multiscale approach.

Although previous studies and expert knowledge can suggest scales that might be important to consider for evaluating the influence of habitat variables, it is not possible to know a priori the spatial scale at which a species perceives a particular habitat variable. Constraining these variables to 1 or a few potential spatial scales and ignoring the cumulative effects of habitat selection at all possible scales is likely to reduce the predictive power of the model and may lead either to invalid inferences or to obscure valid ones. Instead, we propose an approach that does not make unsupportable assumptions regarding the scale at which potential habitat predictor variables may be acting.

Our objectives in this chapter are (1) to assess whether the multiscale modeling approach reveals hierarchical habitat relations and (2) to compare this multiscale approach with a single-scale approach and evaluate differences between model performance, interpretation, predictive power, and probability maps of species occurrence. We use bivariate scaling, logistic regression, and information theory to examine marten occurrence in northern Idaho with respect to relevant habitat variables across multiple spatial scales. We then repeat the analysis using the same occurrence data and habitat variables, but restrict the analysis to a single spatial scale. We then discuss the differences between the multiscale and single-scale models in the context of previous marten habitat models and conclude with a discussion of the implications of our findings for managing marten habitat.

Methods

Study Area

The study area is a 3000 km^2 section of the Selkirk, Purcell, and Cabinet mountains, encompassing the Bonners Ferry and Priest River ranger districts of the Idaho Panhandle National Forest (Figure 12.1). Elevation ranges from about 700 to 2400 m above sea level. The climate is characterized by cold, wet winters and mild summers. The area is heavily forested, with subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) codominant above 1300 m, and a diverse, mixed forest of Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), ponderosa pine (*Pinus ponderosa*), western white pine (*Pinus monticola*), grand fir (*Abies grandis*), western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), western larch (*Larix occidentalis*), paper birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), and black cottonwood (*Populus trichocarpa*) dominating below 1300 m.

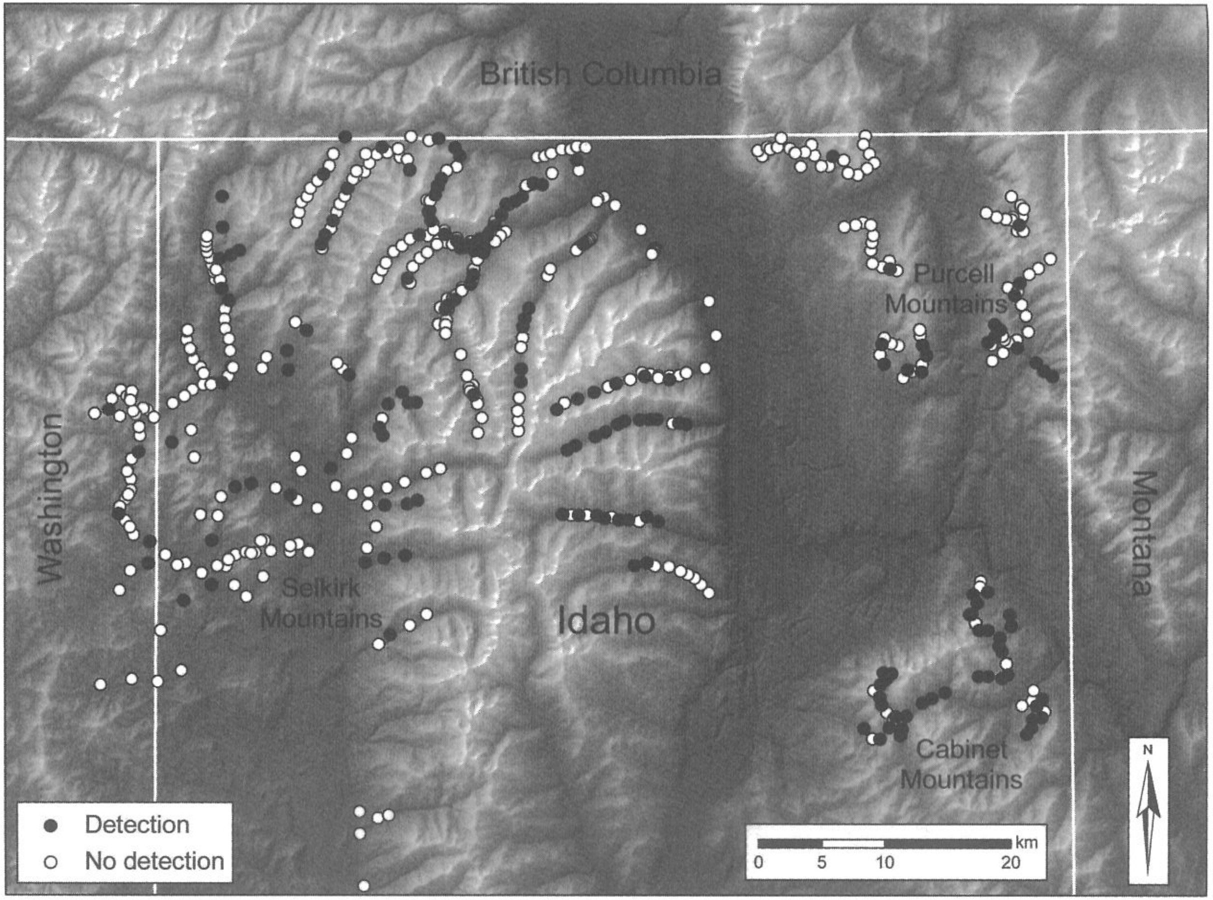

Figure 12.1. Study area extent and digital elevation model in the panhandle of northern Idaho where marten surveys were conducted. Lighter shades indicate higher elevations and darker shades indicate lower elevations. The Kootenai River valley is oriented north to south and is bordered by the Selkirk Mountains on the west, the Purcell Mountains to the east, and the Cabinet Mountains to the southeast.

American Marten Occurrence Data

To document marten occurrence, we set hair snares to collect genetic samples along transects in various portions of the study area from January through March 2005–2007. We selected sampling transects to provide near-complete coverage in all areas of federal or state ownership that are accessible via snowmobile. We set snares for 2 weeks, after which we revisited each station to collect hair samples and rebaited each for another 2-week cycle. Altogether, we surveyed for martens at 361 different locations.

Species identifications from hair-snare samples were based on genetic analyses conducted at the Rocky Mountain Research Station (RMRS) Wildlife Genetics Lab in Missoula, MT using the method of Riddle et al. (2003). Briefly, DNA was extracted with the DNeasy tissue kit (Qiagen) from hair samples taken from each detection station and amplified by polymerase chain reaction (PCR) using primers specific to the mitochondrial gene cytochrome *b*. After PCR products were digested with the restriction enzymes *Hinf* I, *Hae*III, and *Mbo*I, restriction fragments were separated by agarose gel electrophoresis and compared with those that are diagnostic for the American marten.

Variable Selection

We selected a set of variables a priori that we believed would be strongly related to American marten occurrence based on previous research (e.g., Buskirk and Ruggiero 1994; Hargis et al. 1999; Mowat 2006). These variables include elevation, landscape metrics based on seral stage, percent canopy cover, road density, and predicted habitat suitability for tree species associated with riparian habitats (western redcedar), warm and xeric habitats (Douglas-fir), and cool and mesic habitats (subalpine fir) in the study area

Table 12.1. Candidate habitat variables

Habitat variable	Description
ELEVxSDy	Gaussian function of elevation (x = optimum, y = SD)
CWED	Contrast-weighted edge density
PLAND_LST	Percentage of focal area in large sawtimber
PROX_AM_LST	Area-weighted mean proximity index for large sawtimber
AREA_AM_LST	Area-weighted mean patch size for large sawtimber
PD_NST	Patch density of nonstocked timber
PLAND_NST	Percentage of focal area in nonstocked timber
CANCOV	Percentage canopy cover
ROADS	Road density
HAB_DF	Predicted habitat suitability for Douglas-fir
HAB_WRC	Predicted habitat suitability for western redcedar
HAB_SF	Predicted habitat suitability for subalpine fir

(Table 12.1). We co-rectified all input variables to a UTM projection with a 30-m cell size.

We obtained elevation source data from the Shuttle Topographic Radar Mission downloaded from the USGS national map (available at http://nationalmap.gov). We modeled the influence of elevation on the probability of marten occurrence as a Gaussian function based on the expectation that martens should show a unimodal optimum in habitat quality with respect to elevation. Specifically, we generated a factorial combination of elevation variables that differed in the optimum elevation (ranging from 1200 to 2000 m in 100-m increments) and the standard deviation of the optimum elevation (ranging from 300 to 1000 m in 100-m increments). We named these elevation variables ELEVxSDy, where x represents the optimum elevation and y represents the SD of the optimum elevation.

We created a seral-stage GIS layer by merging the Idaho Panhandle National Forest forest stands map (A. Zack, USDA Forest Service, unpublished data) with the Idaho Department of Lands timber type map (Idaho Department of Lands 2006). Seral stage was defined based on tree diameter at breast height (dbh) and included 6 categories: nonforest, nonstocked forest land (<10% stocked with trees after logging), seedling/sapling (<1.4 m high, <8 cm dbh), pole timber (8–21 cm dbh), small sawtimber (21–41 cm dbh), and large sawtimber (>41 cm dbh).

We used FRAGSTATS 3.3 (McGarigal et al. 2002) to derive 2 landscape metrics based on the seral-stage map. These included patch density (PD) and contrast-weighted edge density (CWED). We selected these variables based on previous work showing that martens avoided fragmented landscapes with a large amount of high-contrast edges (Hargis et al. 1999). We also used FRAGSTATS 3.3 (McGarigal et al. 2002) to calculate 4 stand-scale metrics for seral stages believed to influence marten habitat associations (Buskirk and Ruggiero 1994). Specifically, we calculated the percentage of the focal landscape (PLAND_LST), area-weighted mean patch size (AREA_AM_LST), and area-weighted mean proximity index (PROX_AM_LST) for large sawtimber, because previous work has shown strong effects of area, patch size, and connectivity of late-seral forests on the probability of marten occurrence (Hargis et al. 1999). Likewise, we calculated the percentage of the landscape (PLAND_NST) and patch density (PD_NST) for nonstocked timber land consisting of unregenerated timber-harvest areas, because previous work has shown that martens avoid landscapes with even moderate amounts of recent clear-cuts (Hargis et al. 1999). We calculated all landscape metrics at multiple, nested spatial scales using FRAGSTATS 3.3 (McGarigal et al. 2002) to define 12 circular analysis windows with radii ranging from 90 to 1080 m in 90-m increments around each marten detection station.

We derived a canopy-cover GIS layer from the National Landcover Database (2001). We calculated percent canopy cover (CANCOV) within focal landscapes centered on each marten detection station. To model the effect of roads on marten habitat selection, we calculated the kernel density of all road classes following procedures used by Cushman et al. (2006). Roads within the study area include both maintained and unmaintained roads (including abandoned roads in various stages of recolonization by vegetation). We identified unmaintained roads from previous road layers; these represent roads that have been abandoned but may still affect landscape processes, such as habitat selection by wildlife. We calculated the kernel density of roads within focal landscapes centered on each marten detection station.

We created variables representing the habitat suitability of 3 dominant tree species, including Douglas-fir (HAB_DF), western redcedar (HAB_WRC), and subalpine fir (HAB_SF), using a random forest-ensemble modeling approach based on climatic, topographic, and spectral predictor variables (Evans and Cushman 2009). We determined the dominant tree species within focal landscapes centered on each marten detection station.

We used a presence-absence statistical design (Fielding and Bell 1997) whereby we compared habitat variables at stations where martens were detected with those at stations where they were not detected. For each candidate habitat variable listed in Table 12.1, we identified the scale that showed the greatest difference in the means between occupied and unoccupied sites using a nonparametric difference in means test (PROC NPAR1WAY Wilcoxon; SAS Institute 1999–2000) following procedures used by Grand et al. (2004). Next, for each candidate variable, we selected the scale that produced the smallest P value <0.05, and excluded all other scales from further analysis. If all scales of a variable produced a $P < 0.05$, that variable was eliminated from further analysis. We refer to this process as "bivariate scaling." After the scale-selection process was completed, we identified pairs of correlated variables (Pearson's $r > 0.5$) and eliminated the variable with the higher P value in each pair.

Logistic Regression Analysis

We used R version 2.8 (Venables and Smith 2008) to conduct 2 logistic regression analyses. Both analyses were based on the presence or absence of martens at detection stations. The first analysis, a multiscale model, included logistic regressions for the full factorial combination of all habitat variables remaining after the bivariate-scaling analysis described above. The second, a single-scale model, included logistic regressions for the full factorial combination of all habitat variables calculated only at the patch scale (90-m radius).

For both the multiscale and single-scale analyses, we selected the model with the smallest AIC_c for further analysis. For both models, we calculated several measures of model performance, including sensitivity, specificity, Kappa statistic (Cohen 1968), area under the receiver operator curve (AUC), and the percentage of observations that were classified correctly. We also calculated the sign and coefficent of each habitat variable in the model as well as odds ratios representing the effect size of each variable's influence on the probability of marten occurrence. We calculated the odds ratio as the percent change in probability of occurrence, given a change from the 25th to the 75th percentile for each habitat variable. We then used ArcGIS 9.1 (ESRI) to generate a spatial map of predicted marten occurrence for both the multiscale and single-scale models, based on the model intercept and coefficients. We then calculated the difference between the 2 prediction maps to evaluate spatial differences in model predictions.

Results

We detected martens at 159 of the 361 (44% detection rate) hair-snare stations located throughout the study area (Figure 12.1). There were large differences in the scale at which habitat variables optimally predicted marten occurrence in the multiscale model compared with the single-scale model derived from these presence-absence observations (Table 12.2). Although the 90-m radius (patch scale) was the optimum radius for ELEV, HAB_WRC, and PLAND_LST in the multiscale model, the other variables, including CANCOV, ROADS, PD_NST, AREA_AM_LST, and PLAND_NST, were most related to marten habitat selection at much larger spatial scales approximating the size of marten home ranges (990- and 1080-m radii; Table 12.2).

In addition to differences in the optimum scale for habitat variables, 2 variables (CANCOV and ROADS) changed signs between the multiscale and single-scale models, and there were large differences in the optimum elevation

Table 12.2. Multiscale and single-scale model variables, scale at which the variable was calculated, variable coefficients, and *P* values for evaluating statistical significance ($P \leq 0.05$)

	Multiscale model			Single-scale model		
Habitat variable	Scale (m)	Coefficient	*P* value	Scale (m)	Coefficient	*P* value
(Intercept)		−0.320	0.0066		−0.153	0.138
CANCOV	990	0.398	0.0085	90	−0.046	0.716
ROADS	1080	−0.218	0.0798	90	0.002	0.106
ELEV1400SD400	90	0.381	0.0058			
ELEV2000SD900				90	0.181	0.015
HAB_WRC	90	0.198	0.0822	90	0.319	0.009
PD_NST	990	−0.269	0.0478	90	−0.001	0.991
AREA_AM_LST	990	−0.335	0.0330	90	−0.326	0.833
PLAND_NST	990	−0.394	0.0948	90	−0.911	0.986
PLAND_LST	90	0.284	0.1069	90	0.013	0.750

Table 12.3. Differences in odds ratios between the multiscale and single-scale models

	Odds ratio	
Habitat variable	Multiscale	Single-scale
CANCOV	0.73	−0.94
ROADS	−0.78	1.40
ELEV1400SD400	1.66	—
ELEV2000SD900	—	1.65
HAB_WRC	1.27	1.19
PD_NST	−0.69	−1.00
AREA_AM_LST	−0.54	−0.46
PLAND_NST	−0.02	−0.00
PLAND_LST	1.64	3.20

and standard deviation of elevation (Table 12.2). Moreover, only 2 of 8 variables in the single-scale model were significantly different from 0 ($P < 0.05$), whereas in the multiscale model, 4 of 8 variables were significantly different from 0 (Table 12.2).

Based on odds ratios, we detected a large apparent difference in variable importance between the multiscale and single-scale models (Table 12.3). This change in apparent effect size was particularly large for PLAND_LST, which decreased from 3.2 to 1.64 from the single-scale to the multiscale model, and for ROADS and CANCOV, which reversed sign and changed from 1.4 to −0.78 and from −0.94 to 0.73, respectively.

We found a substantial difference in model fit and performance between the multiscale and single-scale models. The multiscale model had a significantly lower AIC_c value and higher sensitivity, specificity, Kappa statistics,

Table 12.4. Comparison of model parameters between the multiscale and single-scale models

Model parameter	Multiscale model	Single-scale model
AIC_c	468.70	484.34
ΔAIC_c	0	15.64
Threshold	0.50	0.50
PCC[a]	0.665	0.576
Sensitivity	0.579	0.421
Specificity	0.733	0.698
Kappa statistic	0.314	0.122
AUC[b]	0.70	0.64

[a] Percentage classified correctly
[b] Area under the receiver operator curve

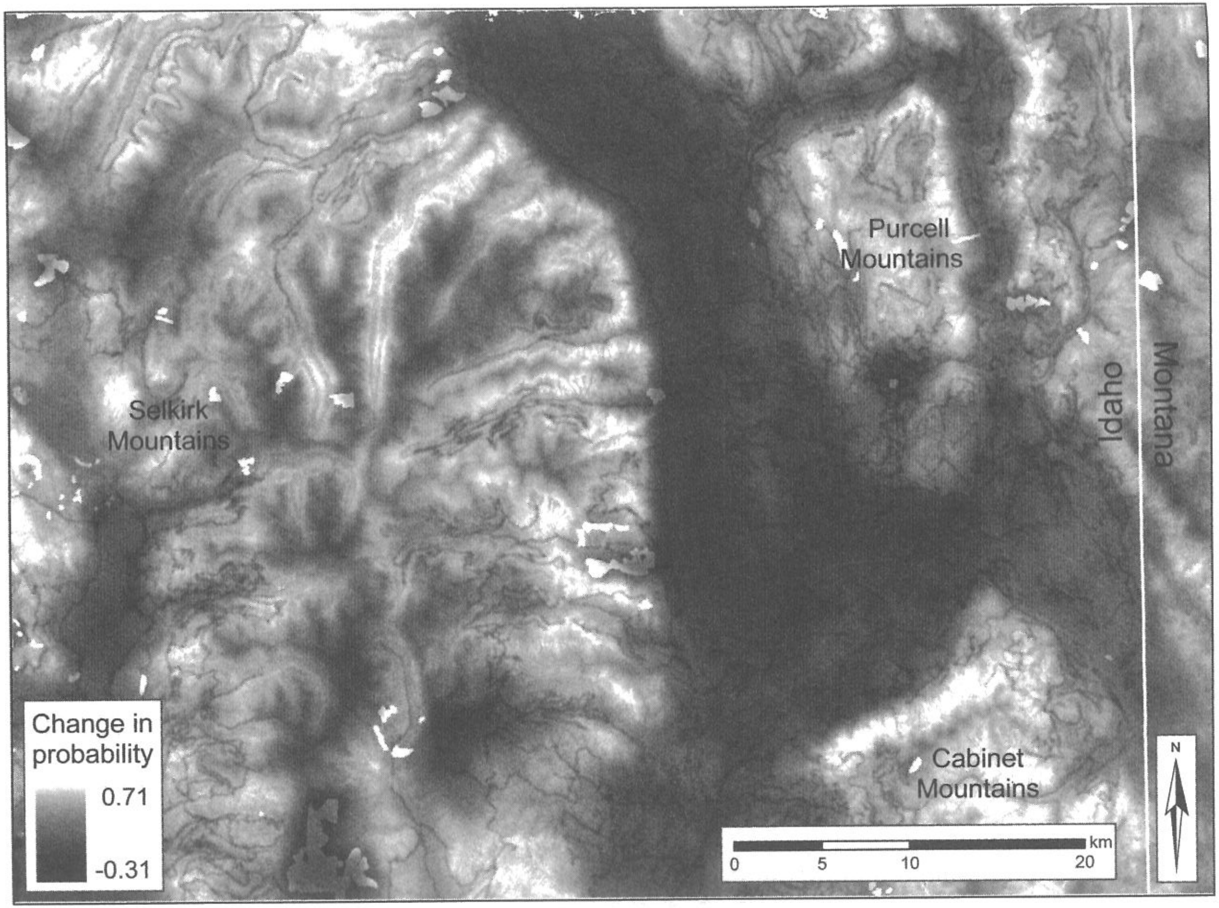

Figure 12.2. Difference in probability of occurrence between multiscale and single-scale models. Darker shades indicate areas where the multiscale model predicts higher probability of occurrence than the single-scale model. The single-scale model would make substantial errors of omission in those areas. Lighter shades indicate areas where the multiscale model predicts lower probability of occurrence than the single-scale model. The single-scale model would make substantial errors of commission in those areas.

AUC values, and percent classified correctly (Table 12.4). In addition, differences in the spatial prediction of marten occurrence between the multiscale and single-scale models ranged from 0.712 to −0.317, respectively (Figure 12.2).

Discussion

Hierarchical Habitat Relations of the American Marten

As in previous studies that identified hierarchical habitat relations for the American marten, we found strong evidence of habitat preferences at both the patch and home-range scales. Rather than impose these scales on the analysis, the bivariate scaling approach allowed us to infer the appropriate scale based on the optimum relation with marten occurrence. By evaluating the full factorial of possible models across a range of relevant spatial scales, we were able to construct a single model that accounted for the hierarchical effects of multiple predictor variables acting at the scales at which martens perceive habitat conditions in the study area.

Based on the multiscale analysis, habitat variables were most related to marten occurrence at 2 hierarchical levels. At a scale approximating the size of marten home ranges (1080-m radius), we observed a negative relation with ROADS (Table 12.2). Avoidance of areas where low-use roads occur at high densities has been reported for other *Martes* species (Goszczyński et al. 2007), but previous results have been equivocal for the American marten (e.g., Mowat 2006). We expected martens to avoid heavily roaded areas because of increased risk of predation or mortality, and perhaps because of behavioral avoidance of road-related disturbances (Forman and Alexander 1998; Coffin 2007). We also found a positive relation with CANCOV at the home-range scale (990-m radius). Dense canopy cover and avoidance of clear-cuts have been positively related to marten occurrence in North America (Bissonette et al. 1997; Potvin et al. 2000) and linked to greater prey availability, subnivean access, resting sites, den sites, and vertical escape routes for predator avoidance (Corn and Raphael 1992; Buskirk and Ruggiero 1994; Bissonette et al. 1997).

We found negative habitat relations at the home-range scale for PD_NST, AREA_AM_LST, and AREA_PROX_LST. In accordance with other home range-scale studies of habitat selection by martens (Chapin et al. 1998; Potvin et al. 2000; Payer and Harrison 2003), these relations indicated that, at large spatial scales, martens avoided areas where stands of large-diameter trees were fragmented into small or less-proximal patches, and where regenerating clear-cuts represented a large proportion of the landscape.

We found positive selection occurring at the patch scale (90-m radius) for ELEV1400SD400, HAB_WRC, and PLAND_LST. Together, these results indicate selection for riparian habitats in montane forests (where western redcedar predominate) dominated by mature closed-canopy forests. Such habitats are likely to provide for finer-scale winter habitat requirements related to prey availability, subnivean access, and cavities or coarse woody debris suitable for resting, denning, and predator avoidance (Buskirk et al. 1989; Bowman and Robitaille 1997; Mowat 2006).

Variables analyzed at the stand scale (180–360-m radii) were absent from the multiscale model. This may reflect the absence of significant stand-level heterogeneity within the sampled portions of the study area. This is likely because all detection stations were within national forest land consisting of relatively homogeneous montane forest managed using similar forest practices. The lack of a stand-scale effect may also simply reflect the lack of a limiting habitat factor at this scale (Rettie and Messier 2000). Interestingly, Minta et al. (1999) found weak stand-scale habitat selection to be a general phenomenon among marten studies (see I.D. Thompson et al., this volume).

Habitat Relations Based on Multiscale vs. Single-Scale Models

We hypothesized that constraining a habitat-selection model for martens to a single spatial scale of analysis could result in false inferences or obscure valid habitat relations. This hypothesis was based on the knowledge that martens select habitat across a range of spatial scales (Bissonette et al. 1997; Nams and Bourgeois 2004), and our expectation that a model incorporating all scales of influence would more accurately predict marten occurrence. The differences between the multiscale and single-scale models in this analysis provide support for this hypothesis. For example, the single-scale analysis found a positive relation between marten occurrence and ROADS, and a negative relation with CANCOV (Table 12.2). These inferences contrast with previous work showing strong habitat preferences for roadless areas with high canopy cover at small spatial scales (Spencer et al. 1983; Robitaille and Aubry 2000). As expected, however, the multiscale model identified a negative relation with road density and a positive relation with canopy cover. Similarly, the multiscale analysis indicated a significantly lower optimum elevation with a smaller standard deviation than the single-scale analysis.

There were also differences in the relative importance of habitat variables in the multiscale and single-scale models. Based on odds ratios, the single-scale model was most influenced by PLAND_LST (Table 12.3), yet the coefficient of this variable was not significantly different from 0, indicating uncertainty about its influence on marten habitat selection. Notably, only 2 of 8 variables in the single-scale model were significantly different from 0 (ELEV2000SD900 and HAB_WRC), and both were optimally related to marten occurrence in the multiscaled model within the 90-m radius. In contrast, the multiscale model comprised 4 variables with coefficients significantly different from 0. Together, these differences highlight the greater emphasis of the single-scale model on 1 significant variable (PLAND_LST) at 1 spatial scale, whereas the multiscale model accounts for the influences of an array of habitat variables acting across multiple spatial scales. In other habitat-selection studies that have compared multiscale and single-scale models, results were similar in that the multiscale models were generally better predictors of species occurrence (Poizat and Pont 1996; Graf et al. 2005; Slauson et al. 2007).

We observed significant differences in spatial predictions between the multiscale and single-scale models. Given that the multiscale model is more sensitive, specific, and predictive, large differences in spatial predictions suggest that the single-scale model is likely to result in major errors of omission and commission across much of the study area. These differences in spatial prediction suggest that restricting the analysis to 1 spatial scale not only alters variable selection and model performance but also affects the ability of the model to predict marten occurrence.

Limitations of Our Analysis

We acknowledge that there are 2 important limitations of our analyses. First, optimizing the scale at which each habitat variable was calculated in the multiscale model may result in overfitting of the model. Although the multiscale model predicted habitat relations that were strongly supported by previous research, the generality of this model should be tested with novel data through cross-validation. In a similar multiscale analysis of marten habitat selection in Oregon and Washington, we found that scale-optimized models were highly predictive of marten occurrence based on k-fold cross-validation (A. Shirk, unpublished data). Second, stronger relations may occur at larger spatial scales than those included in our analyses. The multiscale model revealed that martens avoided areas with high road densities at the largest radius we evaluated (1080 m); however, had we included larger radii, we might have found a unimodal peak of support for a single optimum scale at which roads influence marten occurrence.

Implications for Managing American Marten Habitat

Decades of research on marten habitat relations, including this study, indicate that martens select habitat based on the cumulative influence of many factors acting across a hierarchy of spatial scales, from the landscape to microsites. We have demonstrated that constraining an analysis to a single spatial scale may result in false inferences, weaker models, and poorer spatial predictions of marten occurrence. Conducting multiple single-scale analyses of the same occurrence data (e.g., evaluating 3 separate models constructed at the patch, stand, and home range scales) does not eliminate these risks because such an approach does not produce a single model that simultaneously accounts for the potential influences of habitat variables occurring at multiple spatial scales.

For resource managers, the consequences of false inferences could be significant. For example, in this study, inferences from the single-scale model that marten habitat selection at the patch scale was negatively related to canopy cover and positively related to road density might be interpreted as providing empirical support for forest practices (i.e., intensive harvest and clear-cutting) and road development that have been shown in other studies to cause declines in marten populations. In addition to stronger inferences, the greater predictive power of the multiscale approach provides a more accurate depiction of the areas within a landscape that are likely to support martens. This improved spatial understanding of marten habitat can help guide conservation efforts by enabling managers to better identify habitat areas important for population persistence and for maintaining habitat connectivity.

Furthermore, the multiscale approach explicitly seeks to optimize the scale at which each habitat variable is related to occurrence, and in a way that does not constrain variables to 1 spatial scale, or that ignores the potential influence of habitat conditions occurring at other scales. This attention to spatial scale and flexibility in optimization provides resource managers with strong inferences regarding the scale at which martens perceive each habitat variable, enabling them to more appropriately match the scale of management activities to the scale at which the habitat variable influences marten occurrence. For example, in this study, the multiscale model suggests that, to improve habitat conditions for martens, managers should limit road density and forest fragmentation at the home-range scale while preserving patches of large western redcedars (found mainly in riparian habitats) at elevations centered around 1400 m.

Much of what we have learned about the hierarchical habitat relations of the American marten has been based on models that do not simultaneously account for the influence of habitat variables at all relevant scales. We suggest that future studies of marten habitat selection incorporate a multiscale approach to facilitate the identification of novel habitat associations, and produce better predictive models of marten occurrence that will help to elucidate our understanding of marten ecology and conservation.

Acknowledgments

We thank the editors and anonymous reviewers for their comments and help in preparing this manuscript. We also thank David Wallin, Western Washington University, and Jim Hayden, Idaho Department of Fish and Game, for their assistance. This work was supported by the USDA Forest Service Rocky Mountain Research Station and Pacific Northwest Research Station.