

Spatiotemporal variation in resource selection: insights from the American marten (*Martes americana*)

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Abstract. Behavioral and genetic adaptations to spatiotemporal variation in habitat conditions allow species to maximize their biogeographic range and persist over time in dynamic environments. An understanding of these local adaptations can be used to guide management and conservation of populations over broad extents encompassing diverse habitats. This understanding is often achieved by identifying covariates related to species' occurrence in multiple independent studies conducted in relevant habitats and seasons. However, synthesis across studies is made difficult by differences in the model covariates evaluated and analytical frameworks employed. Furthermore, inferences may be confounded by spatiotemporal variation in which habitat attributes are limiting to the species' ecological requirements. In this study, we sought to quantify spatiotemporal variation in resource selection by the American marten (*Martes americana*) in forest ecosystems of the Pacific Northwest, USA. We developed resource selection functions for both summer and winter based on occurrence data collected in mesic and xeric forest habitats. Use of a consistent analytical framework facilitated comparisons. Habitat attributes predicting marten occurrence differed strongly between the two study areas, but not between seasons. Moreover, the spatial scale over which covariates were calculated greatly influenced their predictive power. In the mesic environment, marten resource selection was strongly tied to riparian habitats, whereas in the xeric environment, marten responded primarily to canopy cover and forest fragmentation. These differences in covariates associated with marten occurrence reflect differences in which factors were limiting to marten ecology in each study area, as well as local adaptations to habitat variability. Our results highlight the benefit of controlled meta-replication studies in which analyses of multiple study areas and seasons at varying spatial scales are integrated into a single framework.

Key words: American marten; canopy cover; forest fragmentation; limiting factor; *Martes americana*; mesic vs. xeric habitat; meta-replication; Pacific Northwest, USA; resource selection function; riparian habitat; scale.

INTRODUCTION

Species may evolve behavioral or genetic adaptations to local habitat conditions and thereby maximize their biogeographic range and ability to persist in dynamic environments (Holt 2003). To effectively manage and conserve species' habitat over broad scales therefore requires a comprehensive understanding of spatiotemporal variation in species–habitat relationships. This research need is generally met through meta-replication: multiple studies conducted in different locations, seasons, spatial scales, and often using different analytical approaches by different researchers (Johnson 2002).

However, comparison of species–habitat relationships across multiple studies may be challenging, for at least two reasons. First, independently conducted studies

often differ in the habitat covariates evaluated, sampling design, and statistical analysis. Consider, for example, the researcher's choice of the spatial extent over which covariates are calculated. Animals perceive and respond to variation in habitat conditions across a hierarchy of spatial scales (Johnson 1980, Wiens 1989, Orians and Wittenberger 1991). Recent studies have demonstrated that species–habitat relationships are only observable when the extent over which covariates are calculated matches the scale of the species' response (Thompson and McGarigal 2002, Grand and Cushman 2003, Wasserman et al. 2010). Thus, covariate scale differences between studies can confound consistent identification of the habitat factors driving species' occurrence.

Second, recent studies suggest that synthesis of habitat selection across multiple studies may also be affected by differences in factors limiting species' ecological requirements in different landscapes. Limiting factors have long been attributed to defining the limits of species biogeographic ranges, but rarely to factors driving variability in habitat selection or other ecological

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processes at finer scales within their range. However, Cushman et al. (2013) demonstrated through population genetic simulations that limiting factors control rates of gene flow in complex landscapes. Short Bull et al. (2011) conducted a replicated study of gene flow among American black bear across the northern Rocky Mountains, and confirmed that different landscape features were limiting gene flow in different study areas, depending on their composition and configuration in each landscape. Similarly, Cushman et al. (2011) showed that American marten movements were only related to canopy cover when it was limiting in the landscape after logging. Prior to logging, marten movements were driven by variation in forest types where prey was most abundant. These studies indicate that limiting factors drive species–habitat relationships at scales from individual movement path choices, to gene flow across large landscapes, up to the full species' range.

In this study, we sought to understand spatiotemporal variation in American marten habitat selection in the Pacific Northwest region, USA. Previous studies have commonly, but inconsistently, identified a number of American marten habitat requirements, including forests with high canopy cover (Hargis and McCullough 1984, Wynne and Sherburne 1984), abundant near-ground structure (Chapin et al. 1997, Payer and Harrison 2003, Godbout and Ouellet 2008), high prey densities (Fuller and Harrison 2005), and sufficient snow depth to provide subnivean spaces during winter (Wilbert et al. 2000). These habitats are thought to provide opportunities for foraging, resting, denning, thermoregulation, and avoiding predation. Although marten must meet these ecological requirements in all habitats, we hypothesized that related covariates would differ between study areas and seasons based on local adaptations and depending on which factors were limiting in each system.

We collected marten occurrence data and remotely sensed habitat attributes from two distinct marten habitats (mesic and xeric), in two seasons (summer and winter), over multiple spatial scales from the site (90 m) to the home range (1350 m). We analyzed these data with three objectives: (1) to identify key forest attributes related to marten occurrence in both mesic and xeric forest habitats of the Pacific Northwest, (2) to determine if selection for forest attributes differed between winter and summer, and (3) to determine the spatial scales at which marten occurrence was most related to these forest attributes.

Importantly, we evaluated a consistent set of model covariates within the same analytical framework for each study area, season, and scale. This removed analytical differences as a source of variation that could confound model comparisons. We also made a priori hypotheses regarding which factors would be limiting in each system (mesic and xeric) and explicitly interpreted model results with these in mind. Specifically, we hypothesized that covariates related to avoidance of

open forests and clearcuts would be apparent in the xeric study area (which was dominated by open forests and clearcuts), but not in the mesic study area (which was almost entirely forested, and therefore not likely to be a limiting factor).

MATERIALS AND METHODS

Study areas

The mesic study area was situated in the Mount Baker-Snoqualmie National Forest on the western slope of the Cascade Range, Washington, USA, about 40 km northeast of Mount Rainier (Fig. 1). Elevations over the area varied from 669 m to 1929 m. Mean annual temperature is 5.5°C. Mean annual precipitation is 2.7 m and snow accumulation averages 9.8 m. Topography is steep with deeply dissected slopes and many small streams. Forest cover is dominated by western hemlock (*Tsuga heterophylla*) and Pacific silver fir (*Abies amabilis*), with lesser amounts of noble fir (*A. procera*), subalpine fir (*A. lasiocarpa*), Douglas-fir (*Pseudotsuga menziesii*), and western red cedar (*Thuja plicata*). Much of the forest is mature, but past timber harvest has resulted in a mosaic of cutover and uncut forest patches.

The xeric study area was located in the Winema National Forest, Oregon, USA. This area is east of the Cascade crest on a high plateau 54 km northeast of Mount Mazama (Fig. 1). The plateau is about 1675 m in elevation. Mean annual temperature is 5.3°C with 0.68 m mean annual precipitation, and snow accumulation averages 4.2 m. Most streams are very low gradient and form a network of meadows. These streams are usually ephemeral; permanent water is isolated to one stream and artificial sources. The flat plateau's pumice soil supports lodgepole pine (*Pinus contorta*) interspersed with patches of ponderosa pine (*Pinus ponderosa*) or mixed conifer (*Abies* and *Pinus* species) on small hills and buttes. Much of the forest had been harvested at the time of data collection, resulting in a mosaic of clearcuts and regenerating forest.

Telemetry data and home range estimate.—We live-trapped martens year-round in the mesic study area from 1989 to 1994 and in the xeric study area from 1994 to 1998 (Raphael and Jones 1997). We used Tomahawk 202 or 205 single-door wire live traps (Tomahawk Live Trap, Hazelhurst, Wisconsin, USA) fitted with a waterproof plywood box at the opposite end from the trap door. We sedated each animal before attaching a neck-mounted VHF radio transmitter (Telonics Model MOD-70; Telonics, Mesa, Arizona, USA). We then followed each animal primarily from ground locations along roads, gathering at least three azimuth bearings to obtain an accurate location. We supplemented ground-based locations with flights by using fixed-wing aircraft fitted with H-type antennas mounted on wing struts. We classified each marten location as occurring in summer (1 June to 31 November) or winter (1 December to 31 May). We defined the two seasons based on the extent of snow cover, with the summer months generally snow-

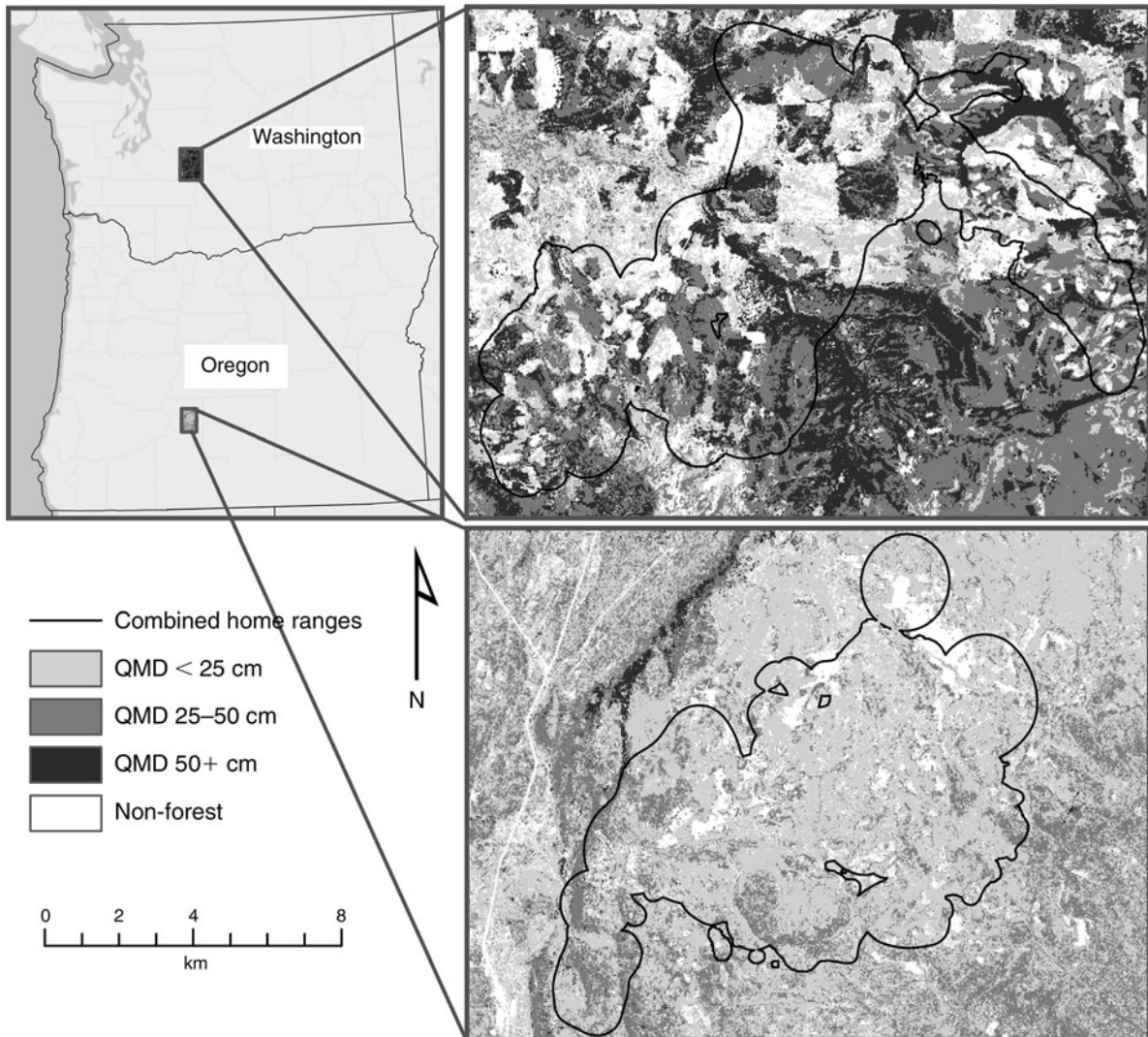


FIG. 1. The mesic Mount Baker-Snoqualmie National Forest (upper right) and xeric Winema National Forest (lower right) study areas in the Pacific Northwest, USA, are depicted, with gray tones representing four tree size classes from white (non-forest) to black (large quadratic mean diameter or QMD). The outer extent of all marten home ranges merged together in each study area is outlined in black.

free over most of the study area and the winter months characterized by generally deep snow. In summer, we obtained 1853 observations from 34 martens in the xeric study area and 1424 observations from 15 martens in the mesic study area. In winter, we obtained 3140 observations from 47 martens in the xeric study area and 975

observations from 14 martens in the mesic study area. The number of observations per marten ranged from 25 to 157 (Table 1).

To define the spatial extent and estimate the area of marten home ranges, we used a 95% kernel density estimate method (Silverman 1981) implemented in

TABLE 1. Male and female American marten year-round home range area, number of individuals, and number of observations for the mesic and xeric forest study areas in summer and winter in the Pacific Northwest, USA.

Study area	Sex	Home range (km ²)	Individuals		Locations	
			Summer	Winter	Summer	Winter
Mesic	male	12.9	8	7	645	540
Mesic	female	10.1	7	7	779	435
Xeric	male	12.6	16	26	846	1454
Xeric	female	9.3	18	21	1007	1686

TABLE 2. Covariates (mean with SD in parentheses) based on marten occurrence in winter, summer, or availability year-round, in xeric and mesic study areas.

Covariate	Units	Xeric			Mesic		
		Summer	Winter	Available	Summer	Winter	Available
CANCOV	%	32.6 (10.3)	33.8 (9.8)	30.4 (12.7)	73 (20.4)	75.3 (19.3)	69.8 (21.8)
QMD	cm	17.6 (5.3)	17.8 (4.9)	16.8 (6.1)	35.3 (16)	35.3 (13.9)	31.3 (16.2)
Elevation	m	1689 (31.6)	1690.4 (30.7)	1689 (46.2)	1177.5 (191.2)	1241.3 (177)	1301.4 (204.5)
Slope		3.2 (2.6)	3.3 (2.8)	2.8 (3)	22.7 (6.5)	21.1 (7.1)	22.5 (7.8)
TCI	NA	5.1 (1.2)	5.1 (1.2)	5.3 (1.3)	3 (1)	2.9 (1)	2.5 (0.8)
TPI	m	87 (11.8)	88 (13.3)	86.5 (12.8)	137.4 (76.4)	163.6 (84.5)	212.5 (80.5)
SUMRAD	kWH/m/d	838.6 (13.5)	839.1 (15.0)	838.5 (16.1)	657.3 (82.3)	688.8 (81.7)	713.5 (89.7)
WINRAD	kWH/m/d	581.8 (13.7)	582.2 (15.2)	581.3 (15.7)	436.4 (70.8)	460.7 (71.1)	481.7 (79.6)
LPI_NF	ha	9.1 (14.4)	8.4 (12.5)	14.7 (22.3)	15.4 (23.6)	13.5 (22.5)	18.4 (26.5)
LPI_sQMD	ha	69.7 (25.1)	70.9 (23.9)	63 (28.8)	17.3 (21.1)	15.6 (18.2)	22 (24.6)
LPI_mQMD	ha	14.6 (19.5)	13.9 (18.6)	15 (19.7)	33.4 (31.3)	37.4 (29.6)	29.3 (29.7)
LPI_lQMD	ha				25 (27.3)	23.9 (25)	21.4 (27.6)
PD_NF	patches/100 ha	47.4 (41.3)	46.5 (40.5)	47 (39.2)	34.3 (34.4)	28.8 (32.5)	33.2 (34.9)
PD_sQMD	patches/100 ha	51.3 (27.4)	50.5 (25.3)	53.5 (30.5)	47.5 (36.9)	51.6 (38.2)	49.9 (37.1)
PD_mQMD	patches/100 ha	49.8 (40.3)	49.5 (41.3)	50.5 (41)	51.4 (33.4)	56.6 (31.6)	49.8 (35.1)
PD_lQMD	patches/100 ha				45.7 (33.6)	52 (35.6)	41.3 (36.8)
PLAND_NF	%	11.3 (15.2)	10.6 (13.7)	16.9 (22.6)	16.9 (24)	14.7 (23.1)	19.9 (26.9)
PLAND_sQMD	%	71.6 (22.7)	73 (21.1)	65.4 (26.5)	19.8 (21.7)	18.4 (19)	24.7 (24.9)
PLAND_mQMD	%	17 (20)	16.3 (19.3)	17.6 (20.3)	35.9 (30.8)	40.3 (28.7)	31.9 (29.5)
PLAND_lQMD	%				27.4 (27.5)	26.6 (25)	23.5 (27.9)

Notes: Abbreviations include CANCOV, canopy cover; QMD, quadratic mean diameter; TCI, topographic convergence index; TPI, topographic position index; SUMRAD, solar radiation from June through November; WINRAD, solar insolation from December through May; LPI, largest patch index; PD, patch density; PLAND, percentage of the landscape; sQMD, small QMD < 25 cm; mQMD, medium QMD 25–50 cm; and lQMD, large QMD > 50 cm. Empty cells for three covariates in the xeric study area indicate that trees of the largest size class (dbh > 50 cm) were not present.

Abode (Laver 2005), an ArcGIS (ESRI) toolbox. We used all marten locations for a year-round estimate and selected the least-squares cross-validation option (Seaman and Powell 1996) to calculate an adaptive smoothing parameter.

Resource selection function (RSF) covariates

Forest structure, forest habitat configuration, and topography are frequently cited as important factors driving marten habitat selection (Buskirk and Ruggiero 1994, Hargis et al. 1999, Mowat 2006, Kirk and Zielinski 2009). A priori, we selected 20 covariates related to these factors as candidates for use in marten RSFs (Table 2). We obtained forest structure raster GIS data at 30-m resolution from the Interagency Mapping and Assessment Project (IMAP; Weyerhann and Fassnacht 2000). IMAP uses the gradient nearest-neighbor method (Ohmann and Gregory 2002) to impute various forest structure attributes across a defined study area from empirical data collected from proximate U.S. Forest Service Forest Inventory Analysis plots (Nelson et al. 2007). From IMAP data (based on imagery from 2000 in Oregon and 2006 in Washington), we selected indices of percent canopy cover (CANCOV) and quadratic mean diameter (QMD) to characterize forest structural conditions within the two study areas.

To characterize forest habitat configuration, we first reclassified the QMD raster into four size classes: non-forest (NF), small QMD (≤ 25 cm; sQMD), medium QMD (> 25 cm and ≤ 50 cm; mQMD), and large QMD (> 50 cm; lQMD). We then used FRAGSTATS 3.3

(McGarigal et al. 2002) to calculate the following class-level metrics: largest patch index (LPI), patch density (PD), and percentage of the landscape (PLAND) for each of the four QMD size classes. Calculating these three metrics for each of four QMD size classes yielded a total of 12 habitat configuration indices.

We also evaluated topographic indices that potentially influence marten habitat suitability. We obtained a digital elevation model from the U.S. Geological Survey at 30-m resolution (*available online*).⁵ We evaluated elevation (ELEV) as a covariate, as well as several metrics calculated in ArcGIS (ESRI) based on the elevation model, including slope (SLOPE), topographic position index (TPI; a measure of elevation relative to the average elevation of the surrounding area), topographic convergence index (TCI; a measure of upslope area), and solar radiation during summer or winter months (SUMRAD and WINRAD, respectively; based on the angle of the sun relative to the slope over the season). In total, we evaluated the relationship of two forest structure, 12 habitat configuration, and six topographic indices to marten occurrence. We projected raster data representing each of these indices in NAD27 UTM zone 10 at a 30-m cell size.

Resource selection functions

We generated resource selection functions for each study area (mesic and xeric) and season (summer and winter) using a mixed-effects general linear model with a

⁵ <http://earthexplorer.usgs.gov/>

logit link. We included a random intercept term (grouped by individual marten), thus allowing the magnitude of the response to differ among marten (Gillies et al. 2006). The general form of the model was

$$g(x) = \beta_0 + \beta_1 x_1 + \gamma_{0j}$$

where the logit $g(x)$ is a function of the intercept β_0 , observations $i = 1, \dots, n$ clustered by group j (the individual marten), the covariate x , the fixed-effect coefficient β , and the random intercept γ_{0j} .

Because the telemetry data that we collected only detected the presence of marten, absence was unknown. Rather than relate model covariates to marten presence and absence, we compared marten presence to randomly generated “available” locations at a density of 200 available locations/km² within each marten’s 95% kernel density estimated home range. In such use–availability study designs, RSFs are interpreted as a ratio of density functions for used and available resource units rather than a probability of use (Seber 1984, Keating and Cherry 2004).

RSF development for each season and study area occurred in two steps. In the first step, we sought to identify which covariates listed in Table 2 exhibited the strongest univariate relationship with marten occurrence, and the spatial scale at which each of these covariates was optimally related to marten occurrence (Shirk et al. 2012). We evaluated a range of spatial scales for each covariate by calculating their mean values within a circular moving window with a radius of 90 m to 1350 m in 180-m increments. For this we used the FOCALMEAN function in ArcGIS (ESRI; for the forest structure and topographic covariates) or a moving-window analysis implemented in FRAGSTATS (when calculating habitat configuration metrics). We then extracted the values of these covariates for each marten location and random available location.

We used the occurrence data to fit mixed-effects logistic regression models with the lme4 package (Bates et al. 2012) in the R statistical software environment, including a random intercept grouped by individual marten. We then plotted Akaike information criterion (AIC) scores for each covariate across the range of moving-window scales and identified the scale at which AIC was minimized. From the 20 covariates initially evaluated, we selected the eight with the lowest AIC scores (at the scale at which they were optimally related to marten occurrence) for possible inclusion in multivariate models generated in the second step in developing RSFs. If two covariates exhibited a correlation >0.70, we excluded the covariate with the higher AIC score and added the covariate with the next lowest AIC to keep the list of candidates for inclusion in the multivariate model fixed at eight. The choice of eight covariates was driven by the bimodal distribution of univariate model AIC scores, which indicated that no more than eight covariates had strong univariate

relationships with marten occurrence in a particular season or study area.

In the second step of RSF development, we produced multivariate logistic regression models (with the same general form as previously described) by first starting with the covariate with the lowest AIC score in the univariate analysis, and then stepwise adding each of the remaining seven covariates stepwise based on minimizing AIC in each step. Once all eight covariates were included in the multivariate model, we then reversed the process by omitting one covariate at a time (selected based on minimizing AIC), until there were only two covariates remaining. This forward and backward stepwise selection procedure produced a range of multivariate models with between two and eight covariates. For each study area and season, we then selected the model (among both the univariate and multivariate models) with the lowest AIC as the RSF most related to marten occurrence. If the difference in AIC score between the optimal model and any alternative models evaluated per season and study area was less than 10, we used model averaging to derive the final model coefficients (Burnham and Anderson 2002).

Model performance and cross-validation

We used the presence–absence package (Freeman and Moisen 2008) in the R statistical environment to measure the area under the receiver operator curve (AUC), a measure of model performance based on the trade-off between sensitivity (the probability of the model correctly predicting marten presence where they were observed by telemetry) and specificity (the probability of the model correctly predicting marten absence at randomly “available” locations). We also calculated the true skill statistic (TSS), a measure of model skill that is particularly suited for comparisons between models that differ in prevalence (Allouche et al. 2006). TSS is calculated as sensitivity + specificity – 1, given a particular threshold value for classification. We used a threshold value at which specificity and sensitivity were equal. Finally, we calculated the percentage of observations correctly classified (PCC) based on a threshold value at which specificity and sensitivity were equal.

RESULTS

Landscape and home range differences between study areas

We observed substantial differences in forest structural attributes between the two study areas (Table 2). In general, forests in the xeric study area had low canopy cover and were composed mainly of small QMD trees (<25 cm dbh, most commonly lodgepole pine), but also numerous patches of non-forest, including clearcuts and meadows along ephemeral streams. In contrast, forests in the mesic study area had very high canopy cover and were composed of roughly equal proportions of non-forest (mainly clearcuts) and small (<25 cm), medium (25–50 cm), or large QMD (>50 cm) stands.

There were also important differences in topography between the two study areas (Table 2). The mesic location was topographically complex, with high variation in elevation, slope, topographic position, topographic convergence, and solar radiation. Conversely, the xeric study area was situated on a plateau, and topographic variation in each of these indices was very low. Moreover, the vegetation communities associated with variation in these topographic indices varied in important ways between study areas (described in the *Discussion*).

Finally, the configuration of forests on the landscape also differed between the two study areas. The mesic location consisted of a mosaic of young, regenerating forests (small QMD), early to mid-seral stands (medium QMD), and mature forests (large QMD), with a few large clearcuts interspersed. In the xeric location, forests were generally large patches of small-diameter lodgepole pine interspersed with a few small stands of larger QMD ponderosa pine and mixed-conifer trees, and many small clearcuts or open meadows. Forests in the xeric study area also tended to be sparse, with canopy cover averaging only 30% compared to 68% in the mesic study area.

Despite the major differences in habitat, we observed very similar home range sizes in the two study areas. Marten home range area estimated by a 95% kernel density function was 12.6 km² for males and 9.3 km² for females in the xeric study area and 12.9 km² for males and 10.1 km² for females in the mesic study area.

Univariate RSFs

For each season and study area, we evaluated all covariates based on their univariate relationship with marten occurrence (based on AIC scores) at each spatial scale (i.e., the moving-window radius over which the covariate was calculated). For all covariates, we observed a unimodal peak of support for a single spatial scale at which the covariate was optimally related to marten occurrence. As an example, the AIC values for two covariates (topographic position and canopy cover) that exhibited a large effect size in the multivariate models are shown in relation to the range of scales evaluated (Fig. 2). The optimal scale frequently varied between seasons and between study areas (Table 3).

Multivariate RSFs

The summer RSF for the mesic study area included several topographic covariates, including a negative relationship with topographic position (90 m), a positive relationship with topographic convergence (90 m), a negative relationship with summer insolation (270 m), and a positive relationship with slope (990 m; Table 3). In addition, forest configuration indices such as largest patch index of small QMD forests (negative relationship, 1170 m) and patch density of small QMD forests (positive relationship, 1350 m) were also included. The winter RSF for the mesic study area was similar to that

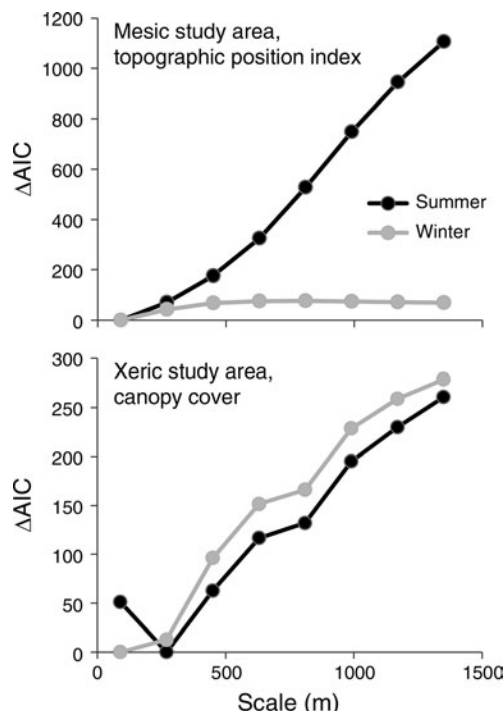


FIG. 2. Each plot shows the change in Akaike's information criterion (ΔAIC) among resource selection functions (RSFs) relating marten occurrence to the indicated model covariate calculated over varying spatial extents (x-axis). The top plot shows the topographic position index in the mesic study area. The bottom plot shows canopy cover in the xeric study area. The black and gray lines represent the summer and winter RSFs, respectively.

for the summer model except that a positive relationship with patch density of large QMD forests (1170 m) and a negative relationship with the percentage of the landscape in small QMD forests (270 m) were included and slope was not included (Table 3).

In the summer RSF for the xeric study area, we observed a negative relationship with topographic convergence (630 m) and positive relationships with patch density of non-forest (990 m), canopy cover (270 m), percentage of the landscape in small QMD forests (630 m), and slope (270 m). The winter RSF for the xeric study area was similar except that negative relationships with largest patch index of non-forest (270 m) and patch density of small QMD forests (810 m) were included and topographic convergence was not included.

Model performance and cross-validation

In both study areas, the AUC, TSS, and PCC scores were slightly higher in summer compared to winter. All RSFs had an AUC > 0.70, indicating fair to good model accuracy. In both seasons and study areas, *k*-fold cross-validation of RSFs resulted in only slightly lower AUC, TSS, and PCC values relative to the model based on all the data (Table 4).

TABLE 3. Model covariates, optimal scale, standardized coefficient (β), coefficient standard deviation (SD β), and effect size (change in odds ratio from the 10th to 90th percentile) for summer and winter seasons in the mesic and xeric study areas.

Study area and season	Covariate	Optimal scale (m)	β	SD β	Effect size
A) Mesic					
Summer	LPI_sQMD†	1350	-0.30	0.03	3.00
	PD_sQMD	1170	0.28	0.03	2.76
	SUMRAD	270	-0.19	0.02	1.95
	TCI	90	0.17	0.03	1.69
	SLOPE	990	0.15	0.04	1.52
Winter	TPI	90	-0.20	0.02	2.17
	PD_sQMD	1170	0.28	0.03	2.70
	PD_lQMD	1170	0.21	0.02	2.06
	LPI_sQMD	1170	-0.15	0.04	1.96
	TCI	90	0.31	0.04	2.98
	WINRAD	630	-0.14	0.03	1.30
	PLAND_sQMD	270	-0.06	0.02	1.15
B) Xeric					
Summer	TCI	630	-0.25	0.03	3.04
	PD_NF	990	0.15	0.01	1.47
	PLAND_sQMD‡	630	0.09	0.02	0.78
	SLOPE	270	0.10	0.03	0.69
Winter	CANCOV§	90	0.22	0.02	1.96
	PD_NF	1170	0.16	0.02	1.91
	SLOPE	90	0.28	0.04	2.46
	PLAND_sQMD¶	270	0.05	0.03	1.37
	LPI_NF#	270	-0.11	0.04	1.72
	PD_sQMD	810	-0.11	0.04	1.70

† PLAND_sQMD excluded due to 0.83 correlation.

‡ LPI_NF excluded due to 0.92 correlation.

§ QMD excluded due to 0.77 correlation.

¶ LPI_sQMD excluded due to 0.98 correlation.

PLAND_NF excluded due to 0.96 correlation.

DISCUSSION

A major limitation of meta-replication as a means to infer spatiotemporal variation in habitat selection is that results from independent studies may be difficult to reconcile when the habitat attributes evaluated and analytical methods employed are not directly comparable. Canopy cover, for example, was found to be an important predictor of American marten occurrence during winter in second-growth forests in Ontario, Canada (Bowman and Robitaille 1997), but not in Newfoundland (Thompson and Curran 1995). Important differences between these studies in terms of the habitat characteristics, scale of analysis, and experimental design make it difficult to discern whether the differences in selection were due to local adaptations,

differences in which factors were limiting in each system, or differences in the analysis.

For management and conservation of species over a narrow range of spatiotemporal variation in habitat conditions, small, directed studies of species-habitat relations offer very specific insights appropriately scaled to the local research needs. However, as the example just described demonstrates, piecing together these local insights from independent studies into a broader understanding to manage species over large extents can be difficult. For this purpose, large analyses of multiple study areas, seasons, and spatial scales under a consistent analytical framework provide more direct inferences, yet we found no example meeting all of these criteria in the current literature.

TABLE 4. Model performance metrics for the mesic and xeric study areas in summer and winter for the optimal multivariate model and the mean of a fivefold cross-validation of the optimal model.

Study area	Season	Optimal model			<i>k</i> -fold validation		
		AUC	TSS	PCC	AUC	TSS	PCC
Mesic	summer	0.84	0.51	0.78	0.81	0.49	0.75
Mesic	winter	0.77	0.41	0.71	0.75	0.40	0.69
Xeric	summer	0.72	0.32	0.68	0.70	0.31	0.67
Xeric	winter	0.71	0.30	0.67	0.70	0.29	0.66

Note: Metrics include area under the receiver operator curve (AUC), true skill statistic (TSS), and percentage correctly classified (PCC).

In this study, we conducted an analysis of marten habitat selection in two common classes of Pacific Northwest forest habitat (mesic and xeric) during two biologically distinct seasons (summer and winter) at multiple spatial scales (from the site to the home range) using a consistent modeling framework. This allowed us to make robust comparisons between study areas and seasons, and thereby improve our understanding of spatiotemporal variation in marten habitat selection in this region. As expected, resource selection in these biologically distinct habitats and seasons was driven by very different factors. Indeed, no covariates were consistently related to marten occurrence across all study areas and seasons.

Resource selection in the mesic study area

Covariates in the top RSF models for the mesic study area indicate strong selection for areas of low topographic position, low solar insolation, and high topographic convergence in both summer and winter. Such areas correspond to narrow bands of riparian forests in the valley bottoms of the major drainages, where the largest trees tend to grow (due to nutrient and water flow into the drainage bottoms) and coarse woody debris tends to accumulate (due to nearby large diameter trees and the flow of debris downslope; Harmon et al. 1986). A previous fine-scale analysis of resting and denning site selection in this study area revealed that marten preferentially used large-diameter trees and coarse woody debris (CWD) primarily from western red cedar, which is mainly found in riparian portions of this study area (Raphael and Jones 1997). The lush understory vegetation of riparian forests has been associated with high marten prey densities (Doyle 1990), and the ample near-ground structure affords suitable sites for resting, denning, thermoregulation, and avoiding predation. For these reasons, riparian forests have been associated with the American marten throughout its range (Spencer et al. 1983, Buskirk et al. 1989, Baldwin and Bender 2008, Wasserman et al. 2012).

The abundant near-ground structure in riparian forests also provides subnivean spaces in winter. Marten are sensitive to winter low temperatures because of their elongated body shape, limited body fat reserves, and short pelage (Buskirk and Powell 1994, Feldhamer et al. 2003). They maintain thermotaxis in winter in the more stable microenvironments found beneath the snowpack (Wilbert et al. 2000). Thus, riparian forests in this study area would be expected to improve thermoregulation when temperatures dip below their critical temperature (Buskirk et al. 1989). Moreover, complex near-ground structure also provides winter habitat for important marten prey species, including voles and mice (Sherburne and Bissonette 1994).

The deep valley bottoms that harbor riparian forests also develop a deep snowpack in winter within the study area. The prevailing winds during winter storms

generally originate from the southwest, making leeward northeast slopes in valleys below exposed ridges places of deep snow accumulation. Although we did not measure snow depth directly, the selection for valley bottoms with low solar radiation (northerly aspects) in winter is consistent with the need for sufficient snow depth in winter.

In addition to selection for riparian forests within the mesic location, in both summer and winter, marten avoided large patches of regenerating forests (represented by the small QMD size class in our models) or areas where regenerating forests were not mixed with other forest types (i.e., low patch density of small QMD trees). Forests regenerating from harvest generally have limited coarse woody debris and understory vegetation due to the lack of large trees and a closed canopy shading the forest floor. Avoidance of this forest type is probably driven by the absence of near-ground structure, and has also been linked to lower prey density compared to mature forests (Koehler et al. 1990).

Resource selection in the xeric study area

The strong selection for riparian forests and avoidance of regenerating forests that was so apparent in the mesic location was undetectable in the xeric location, where these forest types were extremely rare. Instead, the top RSF models indicate that marten occurrence was driven by other habitat attributes prevalent in xeric landscapes like the Winema National Forest. In both summer and winter, marten avoidance of large clearcuts and wet meadows (limited to areas of very low slope) is consistent with most marten studies in other landscapes (Spencer et al. 1983). Indeed, the avoidance of large canopy openings appears to be a nearly universal feature of marten habitat selection.

Our study indicates that, in addition to the size of forest openings, their configuration in the landscape also strongly influences marten occurrence. In the mesic study area, clearcuts were few but large, and marten home ranges could generally be positioned to avoid them. In contrast, the numerous small clearcuts in the xeric location made it difficult for them to be avoided entirely within home ranges. Instead, marten appeared to limit their impact by selecting areas where clearcuts were small and fragmented (rather than large and unfragmented). Conversely, marten in the xeric study area selected forests that were unfragmented and composed of the largest tree size class (25–50 cm in this area). The importance of clearcuts and forest patch configuration has been widely observed in other studies of the American marten as well (e.g., Chapin et al. 1998, Hargis et al. 1999, Wasserman et al. 2012).

In addition to avoidance of large canopy openings, marten occurrence in the xeric study area was also strongly influenced in both seasons by selection for greater canopy cover and larger tree diameter. Because these two covariates were highly correlated in this landscape, it was not possible to know if one or both

factors was influencing habitat selection. However, both have been frequently tied to marten occurrence in other studies. Avoidance of sparse, open canopy forests is thought to be motivated by the same reasons that marten avoid clearcuts and other non-forest areas (previously described). Selection for large-diameter trees has been frequently related to suitable nesting and resting sites because they provide tree cavities, snags, and coarse woody debris.

During summer in the xeric site, marten occurrence was strongly tied to the driest portions of the study area (where topographic convergence was very low). These sites were dominated by ponderosa pine stands. In a previous fine-scale habitat analysis in the same study area (Raphael and Jones 1997), such forest types were also found to be preferentially utilized by marten for resting and denning, probably because they afforded larger diameter trees compared to the more common lodgepole pine forests that predominate on the plateau. That this relationship was only observed during summer is consistent with marten preferring subnivean resting sites during the winter months in this study area (Raphael and Jones 1997) and elsewhere.

Scale of selection

We and others (Thompson and McGarigal 2002, Grand and Cushman 2003, Shirk et al. 2012) have demonstrated the inferential value of evaluating species-covariate relationships at multiple spatial scales. In an American marten population in northern Idaho, for example, we found that marten occurrence was strongly related to road density, forest structure, patch configuration, and elevation (Shirk et al. 2012), each at characteristic scale. Models that were constrained to a single scale had lower accuracy, sensitivity, and specificity by comparison. The present analysis confirms this result in two new study areas, because marten habitat relations in the Washington and Oregon study areas were unimodally related to marten occurrence at a single optimal scale (Fig. 2). The strong relationship with riparian forests in low-TPI and high-TCI areas of the mesic location, for example, was only apparent at the finest extent over which covariates were calculated (90 m; Table 3). This agrees with the findings of Wasserman et al. (2012), who found a similar association with western red cedar forests at fine scales. Similarly, the preferences for forests with high canopy cover and high slope in the xeric location were manifest at among the finest scales we evaluated. The selection for these forest attributes at fine scales matches the fine-scale variation in forest type. Riparian forests in the mesic location, for example, occupy narrow valley bottoms, and marten there appear to respond to this variation at corresponding scales. In contrast, marten generally responded to the landscape-scale metrics (patch density, largest patch index, and percentage of the landscape) at much broader scales. This relationship between marten occurrence and patch configuration at broad scales was also observed in

Wasserman et al. (2012). Together, these findings demonstrate that American marten respond at characteristic spatial scales to a range of habitat attributes influencing their occurrence.

Limiting factors

Consistent with our hypothesis, covariates related to canopy cover were not present in the top RSF models for the mesic study area, despite their prominence in the RSF model for the xeric study area, and the widely reported avoidance of these habitats in many studies. In the mesic study area, canopy openings included relatively few, but often very large, clearcuts that marten could generally position their home ranges to avoid. Additionally, a few small canopy openings were present mainly on southerly aspects in higher elevation parkland. Otherwise, the landscape was largely (80%) covered by dense canopy cover (approaching 100%) forest of varying age, from young, regenerating stands to late-seral forests. In this environment, our analysis of home range habitat selection would not be expected to detect avoidance of open areas or sparse forests because it was not likely to be limiting to marten avoidance of predators. Cushman et al. (2011) recently demonstrated how an unobserved relationship between marten and clearcuts in an unlogged forest could be made observable by repeating the analysis post-logging in the same landscape, providing strong evidence for the role of limiting factors in shaping RSF inferences.

Despite the importance of limiting factors in driving which covariates appear to be related to species occurrence, few published articles address this issue. A literature search using the term “habitat selection” in the Web of Science database returned 7205 articles, but only 28 of them (0.39%) mentioned hypotheses regarding which habitat factors might be limiting in the system under study. This lack of explicit hypotheses and discussion of limiting factors greatly impedes the synthesis of inferences between different study areas (and potentially seasons) into a comprehensive understanding of spatiotemporal variation in habitat selection.

Conclusion

The consistent analytical framework that we employed across multiple study areas and seasons allowed us to attribute differences in habitat selection between the mesic and xeric sites to local adaptations, with the caveat that some habitat relationships were not likely to be observed because they were not limiting in the landscape. We conclude that multi-scale, spatially replicated studies such as this facilitate clear inferences regarding spatiotemporal variation in habitat selection that are valuable to wildlife management and conservation over broad extents in heterogeneous landscapes.

Our analysis indicates that riparian forests provide important habitat for marten in mesic montane environments common on the west slopes of the Cascade

Range. Current forestry practices of limiting logging in riparian buffers would therefore be expected to conserve marten habitat, provided that the broadscale context of forest configuration is suitable (i.e., low fragmentation and high canopy cover). The fine scale at which marten appeared to select riparian habitat suggests that even small disturbances in riparian forests could have a large effect on their suitability. At broad scales, marten avoidance of large patches of young, regenerating forests and selection for areas where they are fragmented by more suitable forest types suggests that limiting clearcuts to small, dispersed patches (low patch density within an 1170-m window) may improve suitability.

In xeric habitats consisting mainly of lodgepole pine forests highly impacted by logging (a common habitat type on the east slopes of the Cascade Range), marten appear to be strongly limited by sparse canopy cover, small tree diameter, and numerous forest openings (clearcuts and meadows). This combination of natural and anthropogenic habitat limitations depicts an extreme environment that may test the limits of their adaptations. One indication of this comes from a fine-scale study in this same xeric landscape, which revealed that marten relied heavily on slash piles for resting and denning sites because natural cavities in large trees and coarse woody debris were extremely rare (Raphael and Jones 1997). Forestry practices that limit clearcuts or thinning in the preferred ponderosa pine stands and reduce the size and density of clearcuts elsewhere would be expected to improve suitability of this habitat for marten, based on the importance of patch size and density in our models. Importantly, we expect large patches of sparse forest and open canopy to be unsuitable marten habitat throughout the range of the American marten in both mesic and xeric habitats, but their impact may not be apparent if they are not sufficiently limiting, as appeared to be the case in the mesic study area.

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