Research Article

Habitat Selection by American Martens in Coastal California

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ABSTRACT We investigated habitat selection using single- and mixed-scale modeling at 2 spatial scales, stand and home range, by the only known population of American martens (*Martes americana*) remaining in the historical range of the Humboldt subspecies (*M. a. humboldtensis*) in California, USA. During 2000 and 2001, we sampled a 12×14 grid with 2-km spacing, using 2 sooted track plates at each grid point. We detected martens at 26 of the 159 grid points. We used resource selection probability functions and an information-theoretic method to model habitat at detection locations. At the stand scale, martens selected conifer-dominated stands with dense, spatially extensive shrub cover ($\bar{x} = 74\%$ cover, SE = 4) in the oldest developmental stage. At the home-range scale, martens selected the largest available patches ($\bar{x}$ = 181 ha, SE = 14) of old-growth, old-growth and late-mature, or serpentine habitat. Mixed-scale models revealed that habitat characteristics from both scales best explained marten occurrence compared to one scale alone. Dense, spatially extensive shrub cover is a key habitat element for martens in coastal forests. Dense shrubs provide refuge from predators, cover for prey, and may also deter larger-bodied competitors. Managers can increase the likelihood of marten population persistence and encourage expansion in coastal forests by maintaining and restoring late-mature and old-growth, conifer-dominated forests with dense shrub cover in large, contiguous patches. (JOURNAL OF WILDLIFE MANAGEMENT 71(2):458–468; 2007)

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The contemporary distribution of the American marten (*Martes americana*) has declined since European settlement of North America (Gibilisco 1994), with the most dramatic declines occurring in the maritime regions of the Atlantic and Pacific coasts (Bergerud 1969, Dodds and Martell 1971, Gibilisco 1994, Zielinski et al. 2001). In coastal northern California, USA, martens appear to have been extirpated from >95% of the range they occupied in the early 1900s (Grinnell et al. 1937), with only a single known population occupying an area of about 400 km^2 (Zielinski et al. 2001, Slauson 2003). Conservation efforts and implementation of management alternatives favoring coastal marten populations are hampered by a lack of information on their habitat ecology and their response to forest management in coastal forests of California. Throughout most of their distribution, martens are associated with closed-canopy, late-successional, mesic coniferous forests with complex structure on or near the ground (Buskirk and Ruggiero 1994). However, no studies have been conducted on marten populations occupying coastal forests of the Pacific states.

There is considerable concern regarding the long-term persistence of marten populations within the coastal forests of the Pacific states due to the patterns of land ownership and forest management. Public lands are disjunct and represent small proportions of the total area of coastal forests in each state (United States Department of Agriculture, Forest Service [USFS] 1992, Noss et al. 2000). The 3 known populations of martens in coastal California (one population) and coastal Oregon, USA (2 populations), occur on the 3 largest areas of public lands in the region (Zielinski et al. 2001, Slauson and Zielinski 2004). However, these populations appear to be effectively isolated from each other due to the distance and the loss and fragmentation of suitable habitat in the intervening regions. These populations occur linearly along the coast, with distances between populations (approx. 50 km and 125 km) that are close to or exceed maximum reported dispersal distances for martens (Phillips 1994, Bull and Heater 2000, Fecske and Jenks 2002). Although these populations in California and Oregon were described as separate subspecies, *M. a. humboldtensis* in California and *M. a. caurina* in Oregon, recent genetic investigation questions this distinction (K. D. Stone, Southern Oregon University, unpublished data).

The structural composition of coastal forests has changed dramatically during the last century. More than 90% of coastal forests in northern California (Thornburg et al. 2000) and >70% in Oregon (USFS 1992) have been logged. The majority of coastal forests on private lands have been logged at least once, primarily using clear-cutting, and are currently managed under short-rotation (<60–70 yr), even-aged silvicultural regimes (Lettman and Campbell 1997, Thornburg et al. 2000), resulting in a structurally simplified, early to mid-seral landscape (USFS 1992, Bolsinger and Waddell 1993). Public lands harbor most of the remaining late-successional coastal forest, but it often occurs as a fragmented mosaic (USFS 1992). In contrast to

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their coastal distribution, martens remain fairly well distributed within the higher-elevation, largely true fir (*Abies* sp.) forests, of the Cascades and Sierra Nevada mountains of the Pacific states (Gibilisco 1994; Kucera et al. 1995; Zielinski et al. 2001; T. J. Sheets, Washington Department of Wildlife, unpublished data), where a large proportion of their range is a well-connected network of public lands (Bolsinger and Waddell 1993).

Responses of individuals to their environment vary with scale, with the smallest scale corresponding to the grain of the animal and the largest scale corresponding to the landscape in which the animal establishes its home range (Johnson 1980, Kotliar and Wiens 1990). Different aspects of an animal's life history (e.g., daily resting, winter foraging, finding mates) motivate selection at different scales (Bissonette et al. 1997). Martens appear to exhibit habitat selection at 4 primary spatial scales: the microhabitat, forest-stand, home-range, and landscape scales (Bissonette et al. 1997). At the microhabitat scale, martens select specific habitat elements that provide foraging, resting, or denning opportunities (e.g., large downed logs; Gilbert et al. 1997, Ruggiero and Pearson 1998). At the stand scale, martens select stands with the structural features that provide for one or more life-history requirements (e.g., prey populations, resting structures; Buskirk and Powell 1994). At the home-range scale, martens position their home ranges to include an array of forest stands that provide for year-round life-history needs (e.g., seasonal prey bases, access to mates; Katnik et al. 1994) and defend these against same-sex conspecifics. At the landscape scale, dispersing martens select home ranges from suitable areas that are unoccupied by same-sex conspecifics.

There have been no investigations of habitat selection by martens in the coastal forests of the Pacific states and few in coastal forests of western North America (i.e., Baker 1992, Schumacker 1999). The purpose of this study was to investigate habitat selection by the only known population of American martens remaining in their historical range in coastal northwestern California. This information will enable managers to identify and retain suitable marten habitat and strategically restore key habitat elements where they have been lost in the coastal forests of California.

STUDY AREA

The study area was approximately 800 km^2 and was located in Del Norte, Humboldt, and Siskiyou counties in coastal northwestern California (123°45′00″N, 41°30′00″W; Fig. 1). It occupied portions of the Klamath-Siskiyou and Northern California Coastal Forest ecoregions (Ricketts et al. 1999). The study area ranged from 10 km to 38 km from the ocean from the western to the eastern edge, respectively, and from 10 m to 1,580 m in elevation. The climate was an inland expression of the maritime regime, characterized by moderate temperatures, distinct wet and dry periods throughout the year, and high rainfall during the winter months. Precipitation in the study area was mostly rainfall, totaling between 200 cm and 300 cm annually. Snowfall

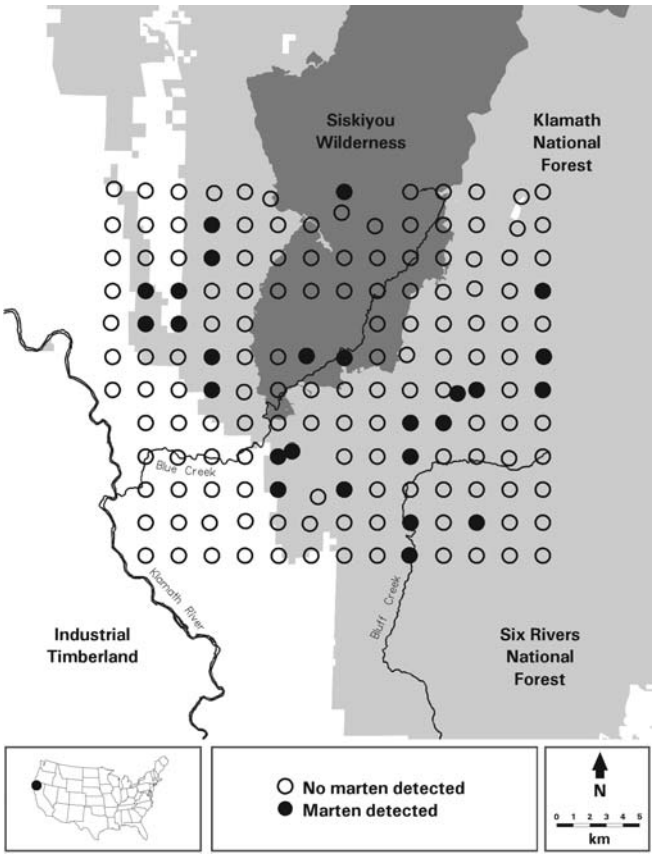


Figure 1. Study region and 2-km sampling grid with detection results for American martens in coastal northwestern California, USA, 2000–2001. Circles indicate sample unit locations and whether we did (black; $n = 26$) or did not (open; $n = 133$) detect martens at sooted track-plate stations.

occurred sporadically during the winter months and rarely persisted below 900 m in elevation. Summer fog was present within the western edge of the study area and further interior along major stream drainages, providing a source of moisture during the driest portions of the year.

The combination of moderate temperatures, high annual precipitation, and summer fog supported dense and continuous tree cover throughout most of the study area and dense shrub cover in mesic sites. Douglas-fir (*Pseudotsuga menziesii*) and tanoak (*Lithocarpus densiflora*) forest associations dominated the study area, with redwood (*Sequoia sempervirens*) associations becoming more prevalent on the western edge, and white fir (*Abies concolor*) associations occurring at higher elevations. Additionally, the presence of serpentine soil types fostered several structurally and compositionally unique forest types in the study area (serpentine habitats), which also harbored a rich diversity of plant species (Kruckeberg 1984). In these soil types, low levels of essential nutrients and high concentrations of detrimental elements offered a harsh growing environment for plants (Jenny 1980), resulting in open and rocky sites with slow-growing woody plants and stunted trees (Jimerson et al. 1995).

The USFS managed the majority (78%) of the study area, including portions of the Smith River National Recreation

Area and Six Rivers and Klamath national forests. The USFS lands in the study area were divided into 3 management designations: 18% were managed as congressionally designated wilderness where no logging has ever occurred, 20% were matrix lands currently available for logging and included a mosaic of stands in various developmental stages (logged and unlogged), and 40% were late-successional reserves. The latter were established under the Northwest Forest Plan (United States Department of Agriculture and United States Department of the Interior 1994), and although many are currently in mature forest conditions, others are being managed to develop late-seral conditions over time. The balance of the study area (22%) was owned by a private timber company and managed for wood products. These different management areas represented a gradient in the percentage of the areas that have been logged, with private lands extensively logged (83%), USFS matrix (16%) and late-successional reserves (13%) less extensively logged, and wilderness areas unaltered by logging. The majority of logging has been accomplished by clear-cut logging.

METHODS

Sampling Design

We established a 12×14-point marten-sampling grid with 2-km spacing between grid points and a random point of origin for sampling (Fig. 1). We designed the grid to extend at least 2 km beyond the outermost locations at which martens were detected during previous baited track-plate surveys (Zielinski et al. 2001). The grid spacing was a compromise between maximizing detection of as many individuals as possible and covering the largest area possible. The southwestern portion of the grid (5 grid points) occurred in the Klamath River, and we excluded it from sampling. Additionally, we did not sample 5 sample units located in the Siskiyou Wilderness due to inaccessibility and we added one sample unit to the grid, resulting in 159 grid points. Due to hazardous terrain, we had to relocate a small number of sample-unit locations, resulting in a few grid points in close proximity (but $\geq$750 m apart; Fig. 1). Sample units ranged from 52 m to 1,457 m in elevation, with a mean of 911 m (SE = 22.5).

Animal Detections

We used sooted track plates (Barrett 1983, Zielinski and Kucera 1995) to determine presence of martens at each point on the grid. Each sample unit consisted of 2 track-plate stations. We established one track-plate station at the grid point and we placed one in the same stand 200 m from the grid point on a random bearing. Using the classification system of Jimerson et al. (1996), we defined stands by vegetation series and developmental stage. We attempted to place all track-plate stations $\geq$50 m from the edge of stands; however, the irregular shapes of many stands made this impossible in approximately 10% of the stands. We baited each station with chicken and checked them every other day for 16 consecutive days. We placed a commercial trapping lure (Gusto; Minnesota Trapline Products, Pennock, MN) at each station when we established it and reapplied on the eighth survey day if no marten detection had occurred at the sample unit.

We sampled 159 sample units from June to November in 2000 and 2001 and we detected martens at 26 (16.3%; Fig 1). Mean latency to first detection at the sample units was 9.1 days (SE = 3.2; range = 2–16). We detected martens at 2 of 36 (5.5%) sample units on private timberlands and 24 of 123 (19.5%) on lands administered by the USFS.

Habitat Selection Analysis

We used resource selection functions (Manly et al. 2002) to investigate habitat selection. In this study, we identified used and unused resources at the population level, and we simultaneously collected a random sample of each resource. This conforms to sampling design I, sampling protocol C in Manly et al. (2002), and involved estimating resource selection probability functions (RSPFs). This analysis assumes that the probability of a marten visiting a track-plate sample unit is constant across all sample units and that if a marten home range includes a track-plate sample unit, there is a reasonably high probability that the marten will visit it. This appears to be the case, as the mean probability of detecting a marten at least once, given the current sampling design, was 91.8% (95% CI = 84–96%; Mackenzie and Hinze 2006). We determined that probability of detection did not differ between our 2 most distinct habitat types (serpentine and non-serpentine; $t = 0.66$, $P = 0.5$). Furthermore, the relative bias (sensu McKenzie 2005:851) in detectability between these 2 types was only 6%. Thus, we assumed that probability of detection had very little effect on estimating occupancy in our study.

We considered a sample unit to be occupied if a marten detection occurred at one or both stations, resulting in a binomial response variable (0 = no detection, 1 = detection).

The RSPF conforms to standard logistic regression (Manly et al. 2002) and we used PROC GENMOD (Version 8; SAS Institute, Cary, NC) to estimate RSPFs.

Habitat Sampling

We investigated habitat selection by martens by comparing the habitat characteristics of detection and non-detection locations at 2 spatial scales, the stand and the home range, and we evaluated the contribution of variables from each scale in a mixed-scale analysis. Each grid point was encompassed by a single stand, a homogeneous vegetation polygon, which ranged from 1 ha to 137 ha in area ($\bar{x} = 24$ ha, SD = 23). We defined the home-range scale as the area within 1 km (314 ha) of each point on the grid, an area slightly smaller than the mean home-range sizes estimated for martens elsewhere in California (Simon 1980, Spencer 1981). Thus, we compared habitat characteristics measured at the stand and home-range scales between grid points where martens did and did not occur.

We selected variables for inclusion in our models by reviewing 29 published studies on the habitat ecology of American martens, and then adding variables that we hypothesized to have ecological importance unique to

Table 1. Definitions and abbreviations for variables measured at 2 spatial scales for each sample unit in the sampling grid during a study of American martens in coastal northwestern California, USA, 2000–2001.

Scale	Variable	Abbreviation	Source, measurement technique, and definition
Stand	Developmental stage[a]	SERAL	EP coverage[b]; shrub, pole, early mature, mid-mature, late mature, old growth
	Tree canopy cover	TREE_COV	EP coverage; total tree cover in 5% increments
	Shrub cover	SHRUB_C	Mean of 2 0.49-ha plot ocular estimates of % shrub cover/stand, centered on each station
	Relative % conifer cover	CONIF	EP coverage; % conifer cover/total tree cover
	Aspect–slope position	ASP-MSP	Digital elevation model; macro aspect at 1 of 3 macro slope positions (bottom, mid, upper)
Home range	Old-growth patch	OG_PATCH	EP coverage; area (ha) of the largest patch of old growth
	Old-growth and late-mature patch	OLM_PATCH	EP coverage; area (ha) of the largest patch of old growth and late mature
	Amount of serpentine habitat	SERP	Six Rivers National Forest soils coverage; total area of serpentine soils, a surrogate for serpentine habitat
	Amount of riparian habitat	STREAM	United States Geological Survey 1:100,000 digital line graph coverage of streams; sum of linear distance of streams
	% area logged	LOGGED	EP coverage; total area (ha) of old growth

[a] The developmental stage variable had 6 categories, with "old growth" being coded as a dummy variable.
[b] EP coverage = vegetation coverage produced by the Ecology Program (EP) of the Six Rivers National Forest.

martens in coastal California. We screened each potential variable for inclusion on the basis of its relevance to the study area, ease of measurement (especially in a Geographic Information System [GIS]), biological interpretability, scale appropriateness, its value as determined by previous marten habitat studies, and whether it was highly correlated with other variables ($r > 0.6$). We excluded variables that did not meet one or more of these criteria from further consideration.

Stand-scale variables.—The 5 explanatory variables retained for analysis at the stand scale described structural, compositional, and topographic characteristics (Table 1). We derived all of the stand-scale variables, except shrub cover, from GIS coverages. We derived 3 of these variables (developmental stage, tree canopy closure, relative percent conifer cover) from a vegetation coverage developed by the Six Rivers National Forest Ecology Program (EP) during the mid-1990s (see Jimerson et al. 1996). The EP vegetation layer has a classification error of <10% (J. E. Hunter, United States Fish and Wildlife Service, unpublished data) and was developed through a combination of plot data, air photo interpretation, polygon typing based on the classification system, and ground truthing. Private timberland was not included in the original EP coverage but was mapped and classified under our direction by the same individual who classified the original vegetation data (J. Jones, Six Rivers National Forest Ecology Program).

Home-range scale variables.—The 5 variables that we retained for home-range scale analysis included compositional and management-related characteristics within each 1-km-radius circle (Table 1). We measured all home-range scale variables using GIS. We measured 4 of the 5 variables from the EP coverage and the one other from a USFS stream channel coverage for the region.

Analysis

We conducted 3 analyses: one at the stand scale, one at the home-range scale, and one considering these 2 scales simultaneously. We conducted the single-scale analyses first to thoroughly investigate selection at each scale. Then, building on what we learned from the single-scale analysis, we conducted the mixed-scale analysis to thoroughly investigate the relative importance of, and interactions between, the 2 scales. For the stand- and home-range scale analyses we used an information-theoretic method of model evaluation (Burnham and Anderson 2002). This method involves development of a small set of a priori models based on the careful consideration of potential biologically meaningful variables. We used all variables meeting the screening criteria to develop competing models representing alternative hypotheses for habitat selection at each spatial scale. The first stage in this process involved the development of conceptual models describing marten habitat selection based on existing information and our hypotheses about habitat selection in coastal forests of northwestern California. We then translated conceptual models into logistic regression models using the selected variables for each scale. The resulting models represented competing hypotheses about scale-specific characteristics that influence marten habitat selection. During model development, we limited the total number of variables per model to 4 to maintain interpretability of the results for each variable. We also constrained the number of parameters per model to ≤ 15, to allow a minimum of 10 observations per parameter and to maintain interpretability of the process involved; most models had <10 parameters. Using this process, we developed a set of 15 stand and 13 home-range models. We ranked each set of models from the stand and home-range scales separately using Akaike's Information Criterion for small sample sizes, (AIC_c), recommended for use when the sample size divided the total number of parameters is <40 (Burnham and Anderson 2002).

We interpreted models by the comparison of ΔAIC_c values, which provides a measure of strength of evidence and a scaled ranking for candidate models (Anderson et al. 2000). To further interpret the relative importance of a model, given the a priori model set, we calculated Akaike weights (w_i) using ΔAIC_c values and created a 95%

confidence set of models by summing all the w_i until we reached 0.95 (Burnham and Anderson 2002).

To assess the relative importance of each variable in the selected models, we calculated their adjusted importance weights (Anderson et al. 2001). Because we considered >1 model when making inferences about the data, we also assessed the importance and interpretation of each variable by examining the range and direction of coefficient values for variables in the best models for each spatial scale. We did not use model averaging because we were interested in understanding the relationships among variables included in the top models and not in developing the best estimate of parameters common to all top models (Burnham and Anderson 2002).

For the mixed-scale analysis, we used the 3 variables having the highest-importance weights from each scale-specific analysis to create an orthogonal set of competing models ($n = 63$). This departs from the a priori approach used previously and constitutes a post hoc analysis step. Thus, we only considered the relative importance of each variable and did not attempt additional interpretation of their coefficients unless there was a change in sign or significant change in coefficient. We ranked and interpreted models in this analysis using the same methods previously described for the stand and home-range analyses.

Model Evaluation

For each best model developed at the stand, home-range, and mixed scales, we evaluated the distribution of predicted probabilities and correct classification rates and compared the chance-corrected classification rates using Cohen's kappa (Manel et al. 2001) at both standard (0.5) and optimized probability cut points (Neter et al. 1989:609–610). Then we conducted a 10-fold cross-validation procedure for each of the 3 top models by randomly dividing the original data into 10 equal-sized subsets, estimating model coefficients using 9 subsets (training data), and classifying the remaining (10%) subset (test data; see Boyce et al. 2002). We repeated this procedure 10 times. To evaluate the stability of each model's predictions, we evaluated the distribution of the probabilities for the test data, the correct classification rates, and compared kappa statistics for each cross-validated model.

RESULTS

Habitat Characteristics

Stand scale.—The stand-scale model with the lowest ΔAIC_c value (Table 2; model 1) contained the 3 variables with the highest importance weights (Table 3): shrub cover, developmental stage, and relative percent conifer cover. This model was 2.32 times more likely than the model with the next lowest ΔAIC_c value (Table 2). All 4 models within the 95% confidence set included the shrub cover and developmental stage variables, which also had 2 of the highest importance weights (Table 3). The odds of marten occurrence increased with shrub cover, relative percent conifer cover, and in certain developmental stages. Specifically, a 10% increase in shrub cover was associated with a 43% increase in marten occurrence (odds = 1.43, 95% CI = 1.13–1.81), after accounting for developmental stage and relative percent conifer cover. Relative to the old-growth developmental stage, the shrub developmental stage was associated with a 21% increase (odds ratio = 1.21, 95% CI = 0.21–7.05), the pole stage an 89% decrease (odds ratio = 0.11, 95% CI = 0.02–0.66), the early mature stage a 92% decrease (odds ratio = 0.08, 95% CI = 0.009–0.87), the mid-mature stage a 96% decrease (odds ratio = 0.048, 95% CI = 0.008–0.27), and the late-mature stage an 81% decrease in marten occurrence after accounting for shrub cover and relative conifer cover. A 10% increase in relative percent conifer was associated with a 27% increase in marten occurrence (odds ratio = 1.27, 95% CI = 0.98–1.64), after accounting for seral stage and shrub cover.

Selection patterns for developmental stages differed between non-serpentine and serpentine stands. In non-serpentine stands, martens used the old-growth developmental stage highly disproportionate to availability, used the late-mature stage similar to availability, and made little or no use of all other developmental stages (Fig. 2a). Although we detected martens at only 8 sample units in serpentine habitats, the shrub and old-growth developmental stages appeared to be used disproportionately, although every developmental stage except the pole was used in serpentine sites at least once (Fig. 2b). Although selection for developmental stages differed, percent shrub cover and relative percent conifer cover were similar for both serpentine and non-serpentine stands (Slauson 2003).

Home-range scale.—At the home-range scale, 5 models are included within the 95% confidence set, 3 of which (Table 4; models 1–3) are strongly competing for the best model based on ΔAIC_c values and relative weights. The serpentine variable had the highest importance weight (Table 3), occurred in every model in the 95% confidence set (Table 4), and was positively associated with marten occurrence. Using model 1, a 20-ha increase in serpentine area was associated with an 18% increase in the probability of marten occurrence (odds ratio = 1.18, 95% CI = 1.07–1.29). The top 5 models had 1 of 2 variables associated with late-successional forest, both of which were positively associated with the probability of marten occurrence. In model 1, a 20-ha increase in old-growth patch size was associated with a 26% increase in marten occurrence (odds ratio = 1.26, 95% CI = 1.05–1.51), after accounting for the amount of serpentine habitat. In model 2, a 20-ha increase in the old-growth and late-mature patch size was associated with a 19% increase in marten occurrence (odds ratio = 1.19, 95% CI = 1.03–1.37), after accounting for the amount of serpentine habitat. The best models suggest that home-range areas with larger patch sizes of old-growth, old-growth plus late-mature, or serpentine habitat within a 1-km radius of each sample unit are important for marten occurrence. Martens disproportionately used sample units within these largest patch sizes (Fig. 3). The mean maximum patch sizes within a 1-km radius of sample units where we detected ($\bar{x} = 181$ ha, SE = 14) and did not detect

Table 2. Resource selection probability functions (RSPFs) for American martens studied in coastal northwestern California, USA, 2000–2001, at the stand scale, ranked according to ΔAIC_c[a] value.

	Variable								
RSPF[b]	Seral stage	Shrub cover	% conifer	Canopy cover	Slope position-aspect	K[c]	ΔAIC_c	w_i[d]	Relative wt
1	X[e]	X	X			8	0.00	0.535	1.00
2	X	X				7	1.68	0.230	2.32
3	X	X		X		8	2.63	0.143	3.74
4	X	X			X	11	4.41	0.059	9.06
Null						1	30.99	0.000	>535.0

[a] ΔAIC_a = difference in the Akaike's Information Criterion value, adjusted for small sample sizes, relative to the top-ranked model's value.
[b] We only included models in the 95% confidence set.
[c] K = no. of parameters in a model.
[d] w_i = Akaike wt, corrected for small sample sizes.
[e] An X indicates that a variable is included within a model.

martens ($\bar{x}$ = 101 ha, SE = 16) differed significantly (t = 4.99, df = 157, $P < 0.0005$). The smallest maximum patch sizes of either old-growth, old-growth plus late-mature, or serpentine habitat within a 1-km radius of sample units used by martens were 83.4 ha, 89.4 ha, and 88.9 ha, respectively, but many of the patches were actually larger than our analysis suggests because sizes were truncated by the perimeter of the 1-km radius circle used to characterize the home-range area. The amount of area logged within a 1-km radius had the fourth-most importance (Table 3) and was negatively associated with marten occurrence. A 10% increase in the amount of area logged was associated with a 23% decrease in the odds of marten occurrence (odds ratio = 0.77, 95% CI = 0.58–1.03), after accounting for amount of serpentine and old-growth patch size. Sixty percent of the sample units where we detected martens had ≤13% of the 1-km radius logged, and we did not detect any martens at a sample unit with >50% of the total area within a 1-km radius logged.

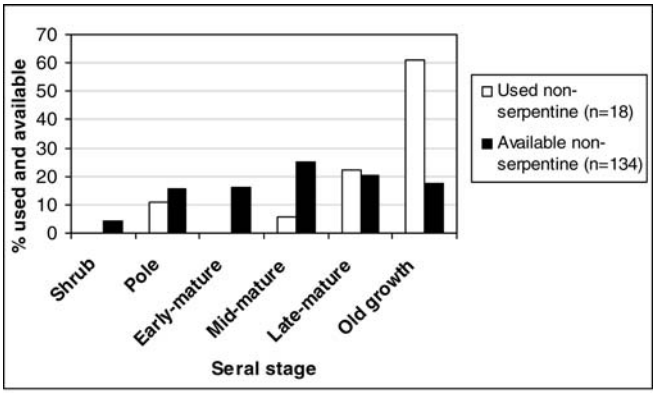
Mixed scale.—For the mixed scale, 16 models are included in the 95% confidence set, 9 of which are strongly competing for the best model based on ΔAIC_c values and relative weights (Table 5). Fourteen of the 16 models included at least one variable from both the stand and the home-range scales, demonstrating that the variables from each scale contribute importantly to the explanation of marten occurrence. However, the normalized importance weights reveal that 2 stand-scale variables, developmental stage and shrub cover, are the most influential variables of the 6 included in the mixed-scale analysis (Table 3). The old-growth patch variable had the lowest importance weight of all mixed-scale variables due to its correlation with the old-growth developmental stage of the stand. The signs and coefficients for the top variables in the mixed-scale analysis did not differ appreciably from those generated in the single-scale analysis.

Model evaluation.—Cross-validation revealed that the best a priori models for each scale continued to have high correct

Table 3. Normalized importance weights for stand- and home-range scale variables for both single-scale and mixed-scale analyses for American martens studied in coastal northwestern California, USA, 2000–2001.

	Scale		
Variable	Stand	Home range	Mixed
Shrub cover	0.199[a]		0.316
Seral stage	0.169		0.328
% conifer	0.119		0.144
Tree canopy cover	0.029		
Slope position–aspect	0.016		
Serpentine		0.429	0.169
Old-growth patch		0.235	0.086
Old-growth–late-mature patch		0.196	
Amount logged		0.109	0.175
Stream		0.063	

[a] Normalized importance wt for all home-range scale variables based on Akaike wt, corrected for model redundancy.



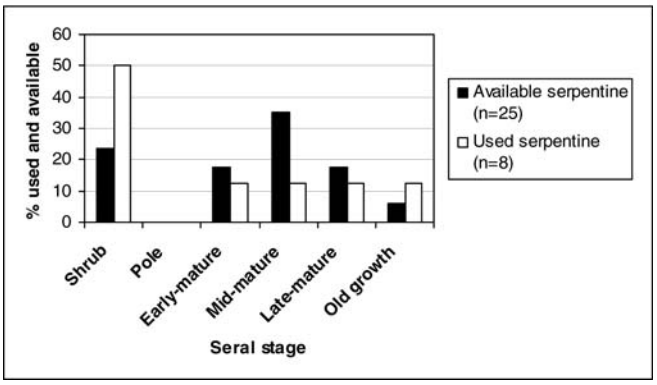


Figure 2. Use and availability of seral stages for (top) non-serpentine and (bottom) serpentine stands where we detected American martens using sooted track-plate stations in coastal northwestern California, USA, 2000–2001.

Table 4. Resource selection probability functions (RSPFs) for American martens studied in coastal northwestern California, USA, 2000–2001, at the home-range scale, ranked according to ΔAIC_c[a] value.

RSPF[b]	Serpentine	OG patch[c]	OLM patch[d]	Amount logged	Stream	K[e]	ΔAIC_c	w_i[f]	Relative wt
1	X[g]	X				3	0.00	0.314	1.00
2	X		X			3	0.07	0.302	1.03
3	X	X		X		4	1.26	0.167	1.88
4	X		X	X		4	2.07	0.111	2.82
5	X	X		X	X	5	3.39	0.057	5.50
Null						1	13.42	0.000	826

[a] ΔAIC_c = difference in the Akaike's Information Criterion value, adjusted for small sample sizes, relative to the top-ranked model's value.
[b] We only included models in the 95% confidence set.
[c] OG patch = area of the largest old-growth patch.
[d] OLM patch = area of the largest old-growth and late-mature patch.
[e] K = no. of parameters in a model.
[f] w_i = Akaike wt, corrected for small sample sizes.
[g] An X indicates that a variable is included within a model.

classification rates for non-detection sites at both standard and optimized cut points (Table 6). However, correct classification rates for detection sites for all a priori models were originally low and showed some change in rates when compared to cross-validated models. The low correct classification rate for detection sites is not surprising given our relatively small proportion of detections ($n = 26$, 16.3%) relative to non-detections ($n = 133$, 83.6%). Also expected is the generally higher classification success when we selected cut points optimally. The home-range model appears to perform poorer than either the stand- or mixed-scale models. However, because martens selected either large areas of serpentine habitat dominated by early developmental stages or large patches of non-serpentine forest in the old-growth developmental stage, predicted probabilities for this model are skewed low because of the spatially segregated nature of these habitats.

DISCUSSION

Habitat Selection at the Stand Scale

Martens selected conifer-dominated stands with dense shrub cover in the oldest developmental stage in non-serpentine areas and in various seral stages in serpentine areas. The results for non-serpentine areas are consistent with the hypothesis that martens specialize on late-developmental stands of mesic coniferous forest in the western United States, especially those with complex physical structure near the ground (Buskirk and Powell 1994). Stands with these characteristics typically provide the key structural elements (e.g., large woody structures for resting and denning) and prey populations (e.g., *Clethrionomys* sp., *Tamaisciurus* sp.) required by martens. Late-mature and old-growth developmental stages in the tanoak and Douglas-fir vegetation series in northwestern California have the highest mean densities of large-diameter (>80-cm) snags relative to all other developmental stages (Jimerson et al. 1996). In Douglas-fir stands in the coast ranges of the Pacific states, large downed logs are most abundant in the old-growth developmental stage (Franklin et al. 1981, Spies et al. 1988). Thus, the non-serpentine stands selected by martens contain the elements that probably provide key life-history needs, which include overhead and escape cover, suitable resting and denning structures, and prey populations.

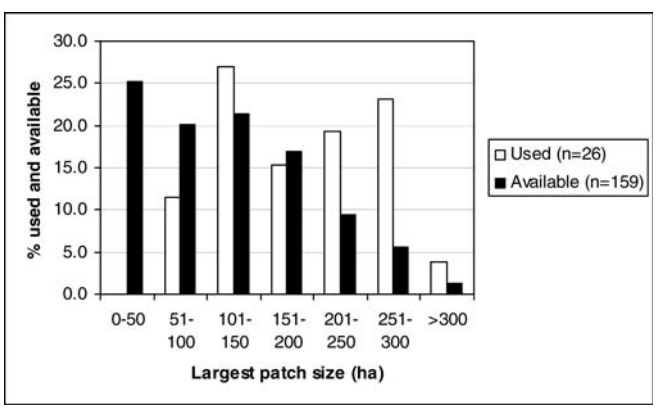


Figure 3. Use and availability of size classes of the maximum contiguous old-growth, old-growth plus late-mature, or serpentine patch within a 1-km radius for each sample unit where we detected American martens using sooted track-plate stations in coastal northwestern California, USA, 2000–2001.

Our results that demonstrate selection for the oldest seral stages and against younger stages differ from those of Baker (1992), who found that martens in coastal forests of Vancouver Island, British Columbia, Canada, selected for second growth (10–40 yr) and used mature (40–120 yr) and old-growth (>120 yr) forest types less than expected. However, the second-growth stands in Baker's study were structurally complex due to the presence of large amounts of residual large wood (potential resting and denning locations) and abundant overhead shrub and herb cover. Marten use of second-growth sites on Vancouver Island may also be influenced by the relative abundance of potential prey associated with early successional forests (e.g., deer mouse [*Peromyscus maniculatus*]) and the paucity of old-growth-forest–associated microtine rodents that are typical marten prey (Nagorsen et al. 1989).

The use of serpentine habitats by martens was one of the most interesting findings of our work. Martens used stands on serpentine sites that had very sparse tree cover and a variety of seral stages, many of which had few large-

Table 5. Resource selection probability functions (RSPFs) for American martens studied in coastal northwestern California, USA, 2000–2001, for the mixed (stand- and home-range) scale, ranked according to ΔAIC_c[a] value.

	Variable									
RSPF[b]	Shrub cover	Seral stage	% conifer	Serpentine	Old-growth patch	Amount logged	K[c]	ΔAIC_c	w_i[d]	Relative wt
1	X[e]	X		X		X	4	0	0.135	1
2	X	X	X				3	0.37	0.112	1.2
3	X	X				X	3	0.47	0.106	1.27
4	X	X		X			3	0.67	0.096	1.4
5	X	X	X			X	4	1.13	0.076	1.77
6	X	X	X	X			4	1.27	0.071	1.9
7	X	X	X	X		X	5	1.85	0.053	2.54
8	X	X		X	X	X	5	2.03	0.048	2.81
9	X	X					2	2.05	0.048	2.81
10	X	X			X	X	4	2.25	0.043	3.13
11	X	X	X		X		4	2.51	0.038	3.55
12	X	X		X	X		4	2.82	0.032	4.21
13	X	X	X		X	X	5	3.15	0.027	5
14	X	X	X	X	X		5	3.48	0.023	5.86
15	X	X	X	X	X	X	6	3.97	0.018	7.5
16	X	X			X		3	4.03	0.018	7.5
Null							1	31.36	0.000	0

[a] ΔAIC_c = difference in the Akaike's Information Criterion value, adjusted for small sample sizes, relative to the top-ranked model's value.
[b] We only included models in the 95% confidence set.
[c] K = no. of parameters in a model.
[d] w_i = Akaike wt, corrected for small sample sizes.
[e] An X indicates that a variable is included within a model.

diameter trees, snags, or logs. In the serpentine habitats, large boulder piles and rocky outcropping with interstitial spaces occurred quite regularly where we detected martens (Slauson 2003). It is likely that these rocky structures provide for the life-history needs that large live and dead woody structures typically provide (e.g., resting structures). Martens have been found resting in and associated with these rocky structures (K. M. Slauson and W. J. Zielinski, USFS, unpublished data) and likely prey species (e.g., *Tamias* spp., *Spermophilus lateralis*) are often observed emerging from and escaping to these features (K. M. Slauson, personal observation).

Martens sometimes use shrub cover as resting locations (Martin 1987), foraging locations (Buskirk and MacDonald 1984), and as overhead cover following disturbances from fire (Magoun and Vernam 1986, Paragi et al. 1996) and spruce budworm (*Choristoneura fumiferana*) defoliation (Chapin et al. 1998). In our study, dense shrub cover was the most consistent habitat element at sites selected by martens in both serpentine and non-serpentine stands, and it represents a distinct layer that continues unbroken throughout entire stands and into adjacent stands. Dense, spatially extensive shrub layers occurred under the coastal forest canopy and were dominated by shade-tolerant, long-lived, mast-producing ericaceous species (e.g., *Gaultheria shallon*, *Vaccinium ovatum*, *V. californica*, *Rhododendron macrophyllum*) and shrub oaks (*Quercus vaccinifolia*, *Lithocarpus densiflora echinoides*; Jimerson et al. 1996, Mahony

Table 6. Classification success and kappa values for the top model at each spatial scale for American martens studied in coastal northwestern California, USA, 2000–2001.

	Standard 0.5 cut point		Optimized cut points	
Scale	Original	Cross-validated	Original	Cross-validated
Stand			Cut point = 0.15	
Detection (%)	38.4	50.0	80.7	53.8
Non-detection (%)	96.2	96.2	76.3	78.3
Kappa	0.435	0.543	0.417	0.282
Home range			Cut point = 0.14	
Detection (%)	3.80	0	69.2	69.2
Non-detection (%)	97.7	100	67.6	74.6
Kappa	0.03	0.0	0.239	0.320
Mixed			Cut point = 0.16	
Detection (%)	46.1	69.2	76.9	88.4
Non-detection (%)	94.7	91.0	85.0	83.5
Kappa	0.475	0.571	0.521	0.547

1999, Sawyer et al. 2000). Importantly, this shrub community does not include the shade-intolerant and short-lived *Ceanothus* shrub species (e.g., *C. veluntinus*, *C. thyrsiflorus*) that occur in more xeric sites and dominate sites immediately after logging or natural disturbances.

The dense shrub layers in our wet, coastal study area created a spatially extensive and highly complex environment near the ground, formed by dense stems and foliage. This environment may help explain the paucity of detections of larger-bodied mesocarnivores such as the fisher (*Martes pennanti*) and gray fox (*Urocyon cinereoargenteus*). We rarely detected these latter 2 species in our study area (7.5% and 5.0% of sample units, respectively), but they are commonly detected adjacent to the study area where drier climates cannot sustain dense mesic shrub cover (fisher and gray fox detections at 54% and 54% of sample units, respectively; Slauson and Zielinski 2004) and where shrub cover is reduced and fragmented due to forestry practices (fisher and gray fox detections at 30–60% and 30% of sample units, respectively; Klug 1996, Slauson and Zielinski 2004). Furthermore, fishers and gray foxes appear to avoid areas with the density of the shrub cover (>70%) where martens typically occur (K. M. Slauson and W. J. Zielinski, unpublished data). Weir and Harestad (2003) have also found that fishers in Douglas-fir forests of British Columbia selected against stands with dense (>80%) low shrub cover and hypothesized that complex structure near the ground may reduce their likelihood of capturing prey. Dense, spatially extensive shrub layers may provide martens an advantage over larger-bodied carnivores in coastal California, much like soft, deep snow is hypothesized to limit competitively dominant fishers from winter access to marten habitats in the Sierra Nevada of California and in eastern North America (Krohn et al. 1997, 2004).

Habitat Selection at the Home-Range Scale

At the home-range scale, martens selected the largest available patch sizes of old-growth, old-growth and late-mature, and serpentine habitat. Selection for larger contiguous patch sizes of suitable habitat at the home-range scale is consistent with the results of other studies on martens. For example, Chapin et al. (1998) found that martens incorporated the largest residual forest patches into their home ranges and used larger patches significantly more than small patches in an industrial forest landscape in Maine, USA. In the present study, martens showed the strongest selection for sample units with the largest available patch sizes of serpentine or late-developmental forest (Fig. 3). Chapin et al. (1998) found that the largest residual patch comprised a median of 75% (range 30–90%) of the home ranges of 13 male martens and a median of 80% (range 51–93%) of 14 female martens. We found similar results in this study, where the largest maximum patch comprised a median of 50% (range 26–100%) of the 1-km-radius circles around sample units where we detected martens. The minimum patch sizes of late-developmental and serpentine where we detected a marten were very similar, suggesting that a minimum patch size of suitable habitat may be required for marten occupancy.

MANAGEMENT IMPLICATIONS

Managers can have direct effects on marten habitat by maintaining or restoring dense, spatially extensive cover of mesic shrub species. Maintenance or restoration of dense shrub cover in stands where it has been lost can be achieved by maintaining lower tree densities or by thinning early developmental stands, and possibly some mid-developmental stands. Restoration of dense shrub cover can be rapid, within 10–15 years after thinning 30-year-old redwood (*Sequoia sempervirens*) stands, dense shrub cover resembling that in adjacent old-growth stands had returned (S. D. Veirs, Redwood National Park, unpublished data). Importantly, the recommendations regarding shrubs apply only to the community of relatively shade-tolerant and long-lived mast-producing shrubs, not to shrub species that typically occur in xeric sites or only in early successional communities (e.g., *Ceanothus* sp., *Arctostaphylos* sp.). Although managers can use thinning to increase shrub cover, it should not overshadow the benefit of developing old-growth stand conditions. Management actions that have the dual goals of restoring or maintaining dense and productive shrub layers in the short term and accelerating of the growth of remaining trees to hasten the development of large live trees, a multilayered canopy, and to recruit large snags and logs that will likely benefit martens over the long term. While most management occurs at the stand scale, we believe that marten conservation will require the consideration of larger scales. Strategic locations for stand-scale restoration are those that enlarge small suitable patches so they exceed the minimum patch size occupied by martens (>83 ha), reconnect suitable patches currently separated by unsuitable habitat, and increase the overall size of suitable patches toward the mean size of 181 ha. Our mixed-scale models will help identify areas of suitable habitat and areas for restoration.

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