

Developing and testing a landscape habitat suitability model for the American marten (*Martes americana*) in the Cascades mountains of California

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Abstract We used field surveys and Geographic Information System data to identify landscape-scale habitat associations of American martens (*Martes americana*) and to develop a model to predict their occurrence in northeastern California. Systematic surveys using primarily enclosed track plates, with 10-km spacing, were conducted across a 27,700 km² area of largely forested, mountain terrain. Martens were detected at 20/184 (10.8%) of the sample units, aggregated in three distinct regions. We investigated habitat selection at multiple scales using circular assessment areas of 3, 20, and 80 km². The model for the largest assessment area best fit the data and included the following predictors: amount of reproductive habitat, number of habitat patches and land ownership category. These results support the hypothesis that martens select habitat based upon broad scale landscape conditions and that these conditions vary

with ownership. We tested the model using an independent set of data, collected primarily during the winter. Poor fit of the test data in some locations raised concerns that our model, which was developed using data collected during the snow-free season, may not predict winter distribution well. We are investigating possible causes for the seasonal variation and until they can be incorporated our model represents a conservative view of marten habitat suitability based on summer occupancy. During the summer months, which is the reproductive season, martens are predicted to occur largely in relatively undisturbed landscapes where high-elevation, late-successional forests are common.

Keywords American marten · Habitat · Landscape pattern · GIS · *Martes americana* · Modeling · Landscape ecology · Model testing · Track plates · Conservation planning · California

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Introduction

The American marten (*Martes americana*) is a forest-dwelling member of the Mustelidae that is among the most habitat-specific mammals in North America (Buskirk and Powell 1994). Martens prefer late-successional, closed-canopy stands of mesic conifers with complex physical structure near ground level (Buskirk and Powell 1994). In the western United

States, martens are highly selective at the micro-habitat scale, preferring large diameter trees, snags and downed logs for resting and denning sites (Spencer et al. 1983; Spencer 1987; Minta et al. 1999). Research across North America demonstrates that martens avoid areas lacking sufficient overhead cover and which are in young forest condition (Soutiere 1979; Spencer et al. 1983; Snyder and Bissonette 1987; Payer et al. 2004; Slauson et al. 2007). Forest fragmentation reduces marten numbers, density and distribution (Soutiere 1979; Katnik 1992; Thompson and Harestad 1994; Phillips 1994).

Bissonette and Broekhuizen (1995) suggested a multiple-scale approach when investigating marten habitat selection to distinguish landscape-scale influences from those operating at finer scales. Landscape-scale studies conducted in boreal forests of Utah, Maine, and Quebec revealed sensitivity to fragmentation at levels as low as 25–35%, suggesting thresholds in amount and spatial arrangement of habitat (Bissonette et al. 1997; Chapin et al. 1998; Hargis et al. 1999; Potvin et al. 2000). The distribution of mature forest stands at the landscape-scale may be the primary determinant of marten distribution, and thus constrain habitat selection at finer scales (e.g., home range-scale) similar to other hierarchically organized systems (Allen and Starr 1982).

Significant declines in the distribution of endemic carnivore species have occurred across North America since the arrival of Europeans (Gibblisco 1994; Laliberte and Ripple 2004) with major reductions in marten populations resulting from the fur trade and timber harvest (Gibblisco 1994). Biologists first expressed alarm about declining marten populations in California during the 1920s (Grinnell et al. 1937). Despite protection from trapping since 1953, continued habitat loss has led to increased concern about martens in the West (Ruggiero et al. 1994; USDA 2001; Zielinski et al. 2001). In northeastern California, the marten has experienced an apparent loss of range over the last 75 years (Zielinski et al. 2005). We used the current distribution of martens to explore whether it may be explained by landscape-level sensitivity to forest conditions that have been reported elsewhere in North America. Specifically, we described landscape-scale habitat associations of martens, developed multivariate models to predict marten occurrence, and evaluated model performance

using an independent data set to assess the model's utility for conservation planning.

Methods

Study area

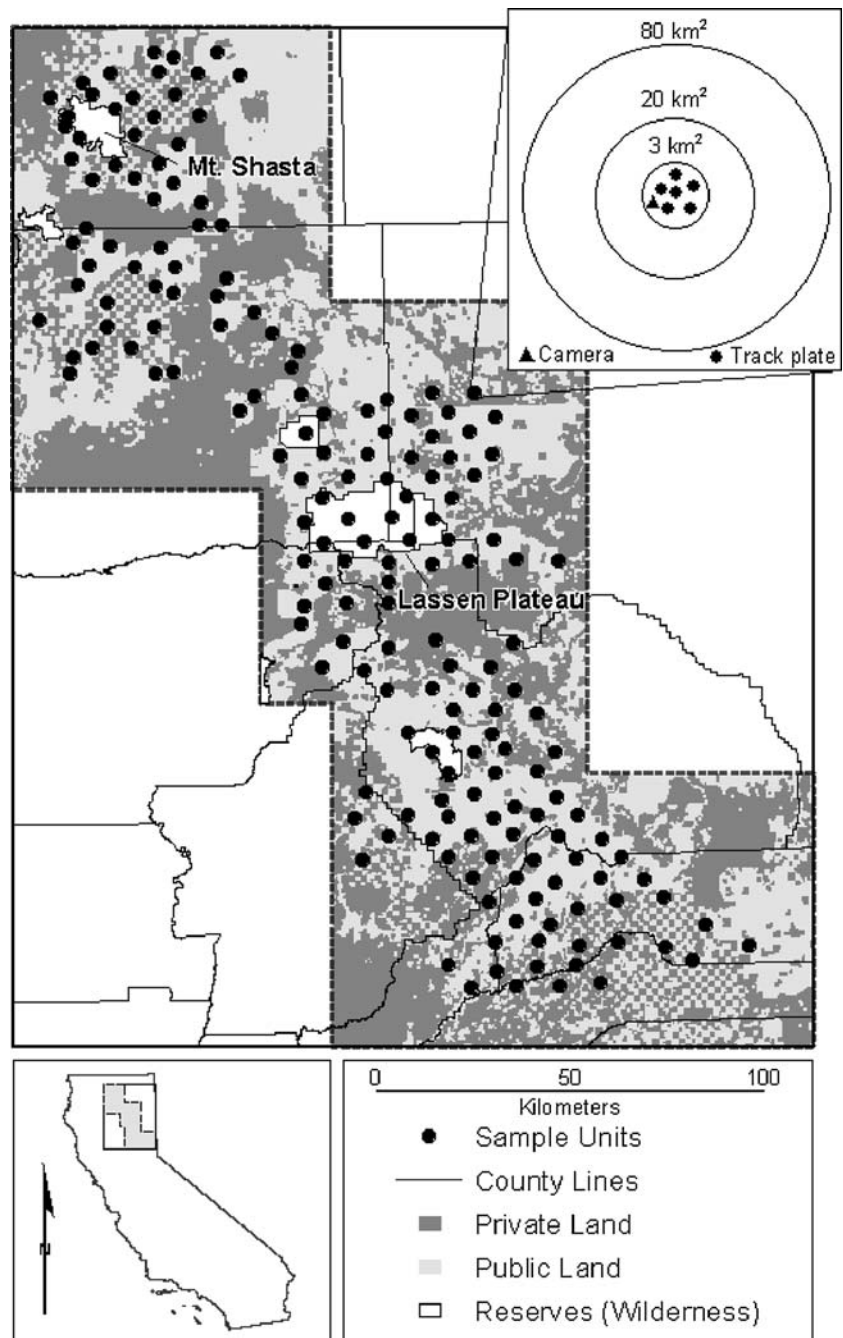
The study was located in the mountains of northeastern California including portions of Siskiyou, Shasta, Tehama, Lassen, Plumas, Butte, Nevada, Sierra, and Yuba counties (Fig. 1). The 27,700 km² area lies within the Sierran steppe–mixed forest–coniferous forest Province including the South Cascades, Sierra Nevada and the Klamath Mountains (Bailey et al. 1994) with elevations between 400 and 5,256 m. Precipitation ranges from 500 to 2,030 mm with most occurring as snow above 1,800 m (Bailey et al. 1994). The regional weather pattern is typical of California's Mediterranean climate with cool, wet winters and hot and dry summers.

Primary vegetation communities are Sierran mixed conifer, Douglas-fir (*Pseudotsuga menziesii*), Montane hardwood, Montane hardwood conifer, Ponderosa pine (*Pinus ponderosa*), Jeffery pine (*P. jefferyi*) and chaparral (Mayer and Laudenslayer 1988). At higher elevations red fir (*Abies magnifica*), white fir (*A. concolor*), lodgepole pine (*P. contorta*) and subalpine conifer forest types are dominant.

The majority of the study area (56%) is on land administered by the USDA Forest Service (USFS) including portions of Klamath, Shasta-Trinity, Lassen, Plumas, and Tahoe National Forests. Several protected areas are distributed throughout this region including a national park and seven designated wilderness areas (hereafter collectively referred to as “reserves”). Lassen Volcanic National Park and adjacent Caribou Wilderness are the largest contiguous protected lands in northeastern California, yet reserves account for only 3.6% of the study area. The remaining 40.4% is in private ownership.

Human activities including logging, mining, grazing, development, and fire suppression have greatly affected this region during the past 150 years (USDA 2001). Forests at higher elevations remained largely uncut until World War II, at which point cutting increased steadily and peaked in the 1950s. Selective logging was more common early in the cutting

Fig. 1 Study region and 10 km sampling grid with land ownership categories and county lines in northeastern California. *Inset* shows multiple scale assessment areas and a sample unit with its array of seven detection devices



period, with clearcutting becoming more frequent in the 1980s.

Marten sampling

We used a pre-existing systematic sampling grid, with points separated by 5.4 km, based on the Forest

Inventory and Analysis system (Bechtold and Patterson 2005). The final sampling grid was created by selecting every other point and each subsequent row was offset by one point, producing a grid with an interpoint spacing of roughly 11 km. Spatial independence of marten detections was likely using this distance because the average marten home range would fit

between points (Buskirk and McDonald 1989). Points at elevations below 600 m were excluded, as were several above 2,900 m which were considered inaccessible to survey personnel, resulting in 184 points.

We sought to detect martens at each grid point using enclosed sooted track plates and cameras (Ray and Zielinski 2008), following methods described in Zielinski et al. (2005). A sample unit consisting of six track plates and one remotely triggered camera (Trailmaster™ 500 or 1500, Goodson and Associates Inc., Lenexa, Kansas) was established at each of the 184 grid points (Fig. 1). One track plate was placed near the grid point and the remaining five were placed at 72° intervals approximately 500 m from the central track plate. The camera was randomly paired with a track plate and set 100 m away on a random azimuth. All detection devices were baited using raw chicken. Sample units were checked at 2-day intervals during a 16-day sampling period. A sample unit was considered occupied if any of the seven detection devices were visited by a marten at least once during the sampling period. Surveys were conducted from 1 June through 1 November 1999–2001 and 1 June through 15 August 2002.

Low detection probabilities can produce bias in estimates of species presence (MacKenzie et al. 2005). Thus, it was important to estimate, for the particular survey protocol applied, a per-visit probability that a marten is detected if present. A detection history was created for each sample unit visited by a marten and we generated an estimate of probability that a marten is detected, if present, across all stations in a sample unit and all eight visits using the equation:

$$1 - (1 - p)^m$$

where p is the per-visit probability of detection and m is the number of observations. This was executed using maximum likelihood methods via a program developed in SAS (J. Baldwin, USFS, unpublished data) which resembles the method advocated by MacKenzie et al. (2005).

Landscape analysis and model development

The spatial extents at which martens respond to habitat are unknown in northeastern California, we focused on broad scale measures of habitat features at 3, 20, and 80 km² (Fig. 1), maintaining a fixed grain size (100 × 100 m). All of the following procedures

of variable measurement, model development, and model evaluation were conducted separately at each of the 3 analysis scales. We used Geographic Information System (GIS) to measure 18 habitat features including land ownership, elevation, roads, hydrology, vegetation landscape pattern, and nearby marten detections (ArcInfo and ArcMap 8.3 Environmental Systems Research Institute, Redlands, California; Table 1). The California Department of Forestry's (CDF) Multi-Source Land Cover Data contained information on land ownership based on the 2000 Census (Fire and Resource Assessment Program (FRAP) 2002). We defined three categories of land ownership: 'private', all lands not owned by state or federal agencies; 'public' all lands in state and federal ownerships with the exception of congressionally designated wilderness and National Park Service lands, which were considered 'reserves'. The composition of each land ownership category was calculated using FRAGSTATS (McGarigal and Marks 1995).

Using a digital elevation model (DEM; 10 × 10 m) we determined the elevations at the center of each sample unit. We created a road layer across all land ownerships using data provided by the USFS, including primary highways, secondary roads, unimproved roads, and four-wheel drive roads. A hydrological model was created from the DEM mosaic; stream channel lengths were considered surrogate measures of riparian habitat. A weighting grid was used to determine precipitation values using PRISM climate data representing cumulative average annual rainfall (1960–1990) at 2 km² resolution (Daly et al. 1994).

Positive spatial autocorrelation occurs when the value of a parameter at a given site increases with its value at nearby sites, including the response variable (Lichstein et al. 2002). We modeled conspecific attraction (autocorrelation) in marten occurrence using a binary dummy variable. Marten detections within a search radius of 12.5 km were considered nearby, which included adjacent sample units, and is within known dispersal limits in western states (Bull and Heater 2001).

We obtained vegetation data with attribute information on forest composition and structure available from CDF's FRAP data set which were compiled from remotely sensed satellite imagery and field inventories of fine scale vegetation attributes (FRAP

Table 1 Description of predictor variables measured in three circular assessment areas for American marten, northeastern California, USA (1999–2002)

Variable	Description	Reference
ELEV	Elevation of sample unit in meters (center)	Buskirk and Powell (1994)
ROAD	Amount of road (km/km ²)	Robitaille and Aubry (2000)
STREAM	Amount of stream or riparian habitat (km/km ²)	Spencer et al. (1983)
AUTOCORR	Spatial autocorrelation (marten detections within 12.5 km)	Lichstein et al. (2002)
PLAND	Percent of habitat in landscape (ha)	Hargis et al. (1999), Chapin et al. (1998), Katnik (1992), Bissonette et al. (1997), Thompson and Harestad (1994)
NP	Number of habitat patches	Chapin et al. (1998), Snyder and Bissonette (1987)
LPI	Percent of landscape contained in the largest patch (ha)	Hargis et al. (1999), Chapin et al. (1998), Potvin et al. (2000), Thompson and Harestad (1994), Payer et al. (2004), Snyder and Bissonette (1987)
CPLAND	Percent of core-area in landscape (ha)	Hargis et al. (1999), Chapin et al. (1998), Potvin et al. (2000), Bissonette et al. (1997), Thompson and Harestad (1994), Payer et al. (2004)
NDCA	Number of disjunct (separate) core-area habitat patches	Potvin et al. (2000), Thompson and Harestad (1994)
AREA_MN	Average size of habitat patches (ha)	Chapin et al. (1998), Katnik (1992)
CORE_AM	Mean core-area per patch as percent of total core areas (ha)	Hargis et al. (1999), Chapin et al. (1998), Katnik (1992), Bissonette et al. (1997), Thompson and Harestad (1994)
DCORE_AM	Mean core-area per disjunct core as percent of disjunct core areas (ha)	Chapin et al. (1998), Potvin et al. (2000)
ED	Amount of edge habitat per unit area (m/ha)	Hargis et al. (1999), Potvin et al. (2000), Katnik (1992), Bissonette et al. (1997)
PROX_MN	Average proximity of patches (index: amount and distance)	Hargis et al. (1999), Chapin et al. (1998), Snyder and Bissonette (1987)
GYRATE_AM	Average amount of connected habitat per patch (ha)	Chapin et al. (1998), Katnik (1992)
PRIVATE	Percent of landscape in private ownership (ha)	Hargis et al. (1999), Phillips (1994), Soutiere (1979), Payer et al. (2004)
PUBLIC	Percent of landscape in public ownership (ha)	Hargis et al. (1999), Soutiere (1979), Payer et al. (2004)
WILD	Percent of landscape in reserves designated as wilderness (ha)	Phillips (1994), Payer et al. (2004)

Vegetation variables are composite measures of reproductive forest habitat

2002). These data coincided temporally with the field survey effort (1999–2002) and had good accuracy for forest type (89%), size class (81%), and canopy closure (75%) (USDA 2002).

The FRAP data were reclassified to generate vegetation-based habitat predictors using the California Wildlife Habitat Relationships (CWHR) system, which uses vegetation information to predict habitat suitability for 256 species, including the marten, in California (CDFG 2002). In CWHR, vegetation is classified into 6 tree size classes, 4 canopy closure classes, and a variety of vegetation types (Mayer and Laudenslayer 1988). Each combination of vegetation type, size class, and canopy closure is assigned a suitability value equivalent to none, low, medium, and high, respectively, for each of three different life history requirements: cover, foraging, and reproduction. We used the CWHR system to identify vegetation types that are associated with the marten's most important life history requirement, reproduction. Female martens are highly selective for reproductive habitat features such as natal and maternal den sites, which typically occur in large diameter trees and snags. Such structural attributes are closely associated with dense, late-seral forest types, making them disproportionately important (Buskirk and Powell 1994). We assumed these forests were more critical to marten persistence than those providing cover or foraging opportunities. We considered all vegetation type/size class/canopy closure combinations receiving high values for reproduction. Based on our field experience, we excluded two forest types

and included one more closely associated with marten presence in this region (Table 2).

We combined these 5 forest types with the 3 largest size classes and the 2 densest canopy closure classes to describe marten reproductive habitat. Vegetation patches were classified as reproductive habitat if they were one of these types and non-reproductive habitat if not. We generated habitat predictor variables using landscape pattern analysis (FRAGSTATS) to describe the composition and configuration of reproductive habitat patches surrounding each sample unit. Due to the binary nature of landscape patterns in this study, all metrics were calculated at the class level, which aggregated similar focal patch types. Grid cells were considered connected when side-by-side.

Landscape metrics were carefully selected based on their reported importance in the marten literature (Table 1). If two metrics were strongly correlated (e.g., $|r| \geq 0.8$), the one most difficult to interpret was excluded. This yielded four vegetation variables: percent of reproductive habitat in the landscape (PLAND), average reproductive patch size (AREA_MN), area-weighted mean proximity of reproductive patches (PROX_AM), and number of reproductive habitat patches, (NP).

Statistical analyses

We used multiple logistic regression to predict marten occurrence using environmental covariates measured at the landscape-scale (SAS Institute Inc.,

Table 2 Summary of the California Wildlife Habitat Relationships (CWHR) system high suitability forest types, size classes, and canopy closures for the American marten

CWHR forest type	CWHR high suitability reproductive habitat		Modified reproductive habitat	
	Size class ^a	Canopy closure ^b	Size class ^a	Canopy closure ^b
Montane hardwood conifer (MHC)	4, 5	M, D	–	–
Douglas-fir (DFR)	4, 5, 6	M, D	–	–
Lodgepole pine (LPN)	4, 5	M, D	4, 5	M, D
Red fir (RFR)	4, 5	M, D	4, 5	M, D
Subalpine conifer (SCN)	4, 5	M, D	4, 5	M, D
White fir (WFR)	–	–	4, 5, 6	M, D
Montane riparian (MRI)	5, 6	M, D	5, 6	M, D

^a Diameter at breast height (DBH) class 4 = (28–60 cm), class 5 = (>61 cm), class 6 = (>61 cm with multi-layered canopy)

^b Canopy closure M = moderate (40–60%), D = dense (>60%)

Cary, NC). The resulting function is considered a resource selection probability function because use and non-use of sample units was known with certainty (Manly et al. 2002) and takes the following form:

$$W_{(x)} = \frac{\exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_n x_n)}{1 + \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_n x_n)}$$

$W_{(x)}$ is the predicted probability of resource use given the covariates x_i . Maximum likelihood estimates were obtained for the slopes β_1 and the intercept β_0 . A small candidate set of a priori models was created based on previous research, landscape ecology literature and our field experience (Burnham and Anderson 2002). This set of 89 multivariate and univariate models was evaluated using information-theoretic methods (Burnham and Anderson 2002). We used Akaike's Information Criteria corrected for small sample size (AIC_c) to rank the best fitting models (Akaike 1973) and used the differences (ΔAIC_c), and Akaike weights (w_i) to interpret their relative importance and assess model selection uncertainty (Burnham and Anderson 2002). We defined a 95% confidence set representing the top models by summing w_i until the total was 0.95 or greater. We also investigated the relative significance of each variable in the top models (Anderson et al. 2001). Adjusted individual importance weights were calculated by summing normalized w_i values for every model in which the variable was present using the formula:

$$\text{Adjusted } w_i = \frac{(\# \text{ models} \times w_i)}{(\# \text{ models with variable}) \times (\text{total } \# \text{ variables})}$$

Model performance was assessed using several diagnostics, including classification of an independent set of test data. We report classification success using Cohen's Kappa statistic (Cohen 1960) and integrate the Area under the Receiver Operating Characteristic (ROC) curve (AUC) to evaluate the classification skill (Altman and Bland 1994; Fielding and Bell 1997). A model with no classification skill produces an AUC of 0.5; a perfect model corresponds to an AUC of 1.0.

Model robustness was tested using tenfold cross-validation of the fitted models. Both detection and

non-detection data were divided into ten equal partitions, one partition was withheld for testing and the model was fit using the balance. The process was repeated 10 times and the mean value was calculated (Boyce et al. 2002). When the model is sensitive to moderate changes in the input data set, the cross-validated score will be substantially lower than that from the full data set. Classification success was evaluated using a 0.5 cutpoint (Manel et al. 2001).

Model testing

The statistical model with the best mean performance over the tenfold cross-validation was implemented spatially in GIS using moving window functions in FRAGSTATS. We tested this model using an independent set of forest carnivore survey data provided by the Lassen National Forest (M. Williams, personal communication). These test data were not collected using a systematic sampling grid, but in a haphazard manner based on the location of planned timber harvests. They also differed from the data used to develop the model in that they were largely collected during the winter, primarily used cameras and were typically a single-device sample unit. We screened these data to assure detections were valid, that sites were surveyed to established protocols, and were conducted within a 10-year window (1995–2005) centered on the period when the data used to develop the model were collected. We evaluated model performance using two versions of these test data: the full dataset and a subset using data collected from June to November, corresponding to the same period when survey data were collected to develop the model.

Results

The total survey effort resulted in 20,592 survey nights; 166 sample units (90%) were located on public lands, 13 (7%) in reserves, and 5 (3%) on private land. Martens were detected at 20 of 184 sample units (10.8%) and in each ownership category. The probability of detection, when a marten was present, was 0.465 per visit to a sample unit. When compounded over all 8 visits it was 0.99

(95% confidence interval: 0.97–0.999). Because probability of detection was so high, we did not adjust for it in the occurrence models. Detections were clustered in three distinct population centers: the eastern side of Mt. Shasta, the Lassen Plateau, and near the border of the Plumas and Tahoe National Forests (Fig. 2). Mean elevations were 1,949 and 1,463 m for sample units with and without marten detections, respectively (Appendix 1—see Supplementary material).

Fig. 2 Predicted probability surface of top performing model (80 km² scale) with detection results for American martens in northeastern California. Sample unit locations with marten detections (*white circles*, $n = 20$) and without (*plus signs*, $n = 164$) at track plates and/or cameras. *Inset* depicts the region where independent test data were available

Three km² assessment area

The model with the lowest AIC_c value included the variables PLAND, NP, PUBLIC, ELEV, and STREAM (Table 3). Six models were in the 95% confidence set, however, this model was clearly best ($w_i = 0.90$). The number of reproductive habitat patches and percent of land in public ownership were in 4 of 6 top models, elevation and stream density occurred in 3 of the 6.

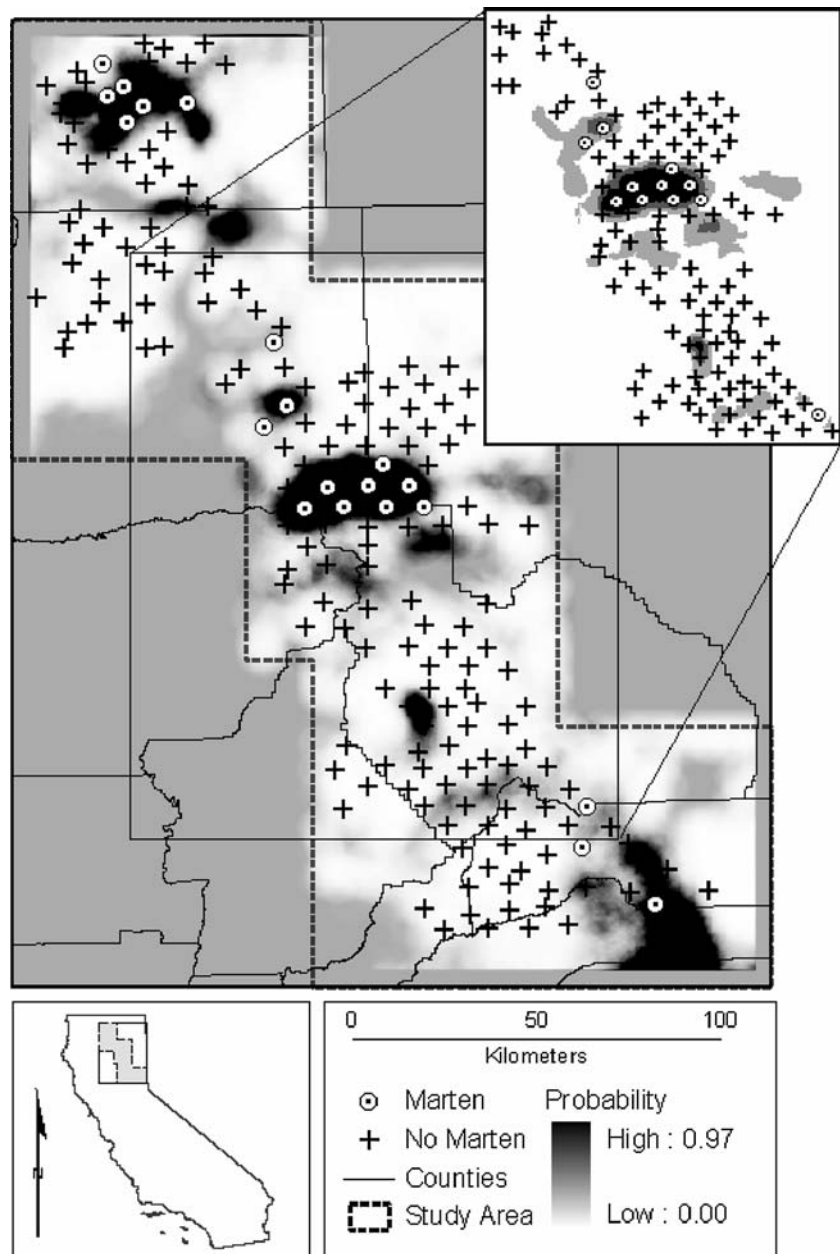


Table 3 Summary of AIC_c selected logistic regression models within 95% confidence set for the American marten in northeastern California, USA (1999–2002) for the three assessment areas

Scale	Model	Variables	K	ΔAIC _c	w _i	Model likelihood
3 km ²	82	PLAND + NP – PUBLIC + ELEV + STREAM	6	0.000	0.901	1.000
	21	PLAND + NP – PUBLIC	4	7.780	0.018	0.020
	46	AREA_MN + NP – PUBLIC	6	7.884	0.017	0.019
	73	ELEV + STREAM	3	8.820	0.011	0.012
	68	PROX_AM + NP – PUBLIC	4	9.332	0.008	0.009
	74	ELEV – ROAD + STREAM	4	9.681	0.007	0.007
20 km ²	46	AREA_MN + NP – PUBLIC	4	0.000	0.584	1.000
	21	PLAND + NP – PUBLIC	4	1.318	0.302	0.517
	68	PROX_AM + NP – PUBLIC	4	4.676	0.056	0.096
	82	PLAND + NP – PUBLIC + ELEV + STREAM	6	4.738	0.054	0.094
80 km ²	21	PLAND + NP – PUBLIC	4	0.000	0.489	1.000
	82	PLAND + NP – PUBLIC + ELEV – STREAM	6	1.051	0.289	0.591
	46	AREA_MN + NP – PUBLIC	4	2.996	0.109	0.220
	68	PROX_AM + NP – PUBLIC	4	3.845	0.071	0.146

Table 4 Adjusted importance weights for all variables in the top models for the American marten in northeastern California, USA (1999–2002)

Variable	3 km ²	20 km ²	80 km ²
PUBLIC	0.421	0.444	0.437
PLAND	0.267	0.103	0.231
NP	0.244	0.254	0.242
ELEV	0.468	0.027	0.149
STREAM	0.399	0.023	0.121
AREA_MN	0.007	0.190	0.035
PROX_AM	0.006	0.019	0.023
PLAND × WILD	0.008	0.018	0.023
ROAD	0.006	0.000	0.004
WILD	0.002	0.000	0.002

All associations are positive except PUBLIC at all scales and STREAM at 80 km² scale

Importance weights indicate that elevation was the most important variable, followed by percent in public ownership, and stream density (Table 4). All variables were positively associated with marten occurrence except PUBLIC.

Twenty km² assessment area

The model with the lowest AIC_c value was AREA_MN, NP, and PUBLIC (Table 3). Four models were included in the 95% confidence set and each

included an area-based measure of reproductive habitat, number of reproductive habitat patches, and percent of landscape in public ownership. Model selection uncertainty was greater at this scale, based on the top model's Akaike weight, $w_i = 0.58$. The variable with the highest importance weight was PUBLIC which exhibited a negative association with marten occurrence (Table 4). Elevation and stream density, two variables important at the 3 km²-scale, showed little influence at this extent.

Eighty km² assessment area

The model that included PLAND, NP, and PUBLIC had the lowest AIC_c value (Table 3) and 4 models were in the 95% confidence set. However, model selection uncertainty was high ($w_i = 0.49$). The percent of land in public ownership had the highest importance weight, followed by number of reproductive habitat patches, and percent of reproductive habitat, each with roughly half the importance of PUBLIC (Table 4). Variables derived from landscape pattern were more influential than topographic variables at this broad scale, compared to the 3 km² extent.

Kappa values for the top model at the 3 and 20 km² assessment areas indicate 'moderate' agreement with the data using standards described by Landis and Koch (1977), whereas the model for the

Table 5 Classification success and Kappa for full (developmental) dataset and cross-validations for the top models in each assessment area for American marten in northeastern California, USA (1999–2002)

Assessment area (model)	Kappa	Classification success (%)	
		Marten detection	No detection
3 km ² (−9.0667 + 0.00253 PLAND + 0.0982 NP −0.0295 PUBLIC + 0.00457 ELEV + 1.7982 STREAM)			
Full dataset	0.57	50.0	98.1
Cross-validation	0.56	49.9	97.8
20 km ² (−2.6424 + 0.0280 AREA_MN + 0.1281 NP −0.0502 PUBLIC)			
Full dataset	0.44	40.0	96.9
Cross-validation	0.47	43.8	96.9
80 km ² (−2.2786 + 0.0622 PLAND + 0.0261 NP −0.0549 PUBLIC)			
Full dataset	0.61	55.0	98.1
Cross-validation	0.60	52.8	98.5

80 km² area showed ‘substantial’ agreement (Table 5).

Classification skill was greatest for the broadest scale model (AUC = 0.866 and CV AUC = 0.833), resulting in an ‘excellent’ AUC score (Hosmer and Lemeshow 2000). The cross-validated Kappa and AUC scores indicate model stability. We implemented the model in GIS to map the probability of occurrence (Fig. 2). The map indicates a patchy distribution of high predicted probability areas separated by larger regions of very low probability, especially between Mt. Shasta and the Lassen Plateau.

In the test data set, martens were detected at 75 of 589 stations (12.7%). Classification skill was poor for the model when using all the test data (AUC = 0.597; Fig. 3a). Further exploration revealed a strong seasonal difference in the model’s ability to accurately predict marten occurrence, performing better when evaluated against test data that were collected during ‘summer’ (June–October; AUC = 0.875; Fig. 3b).

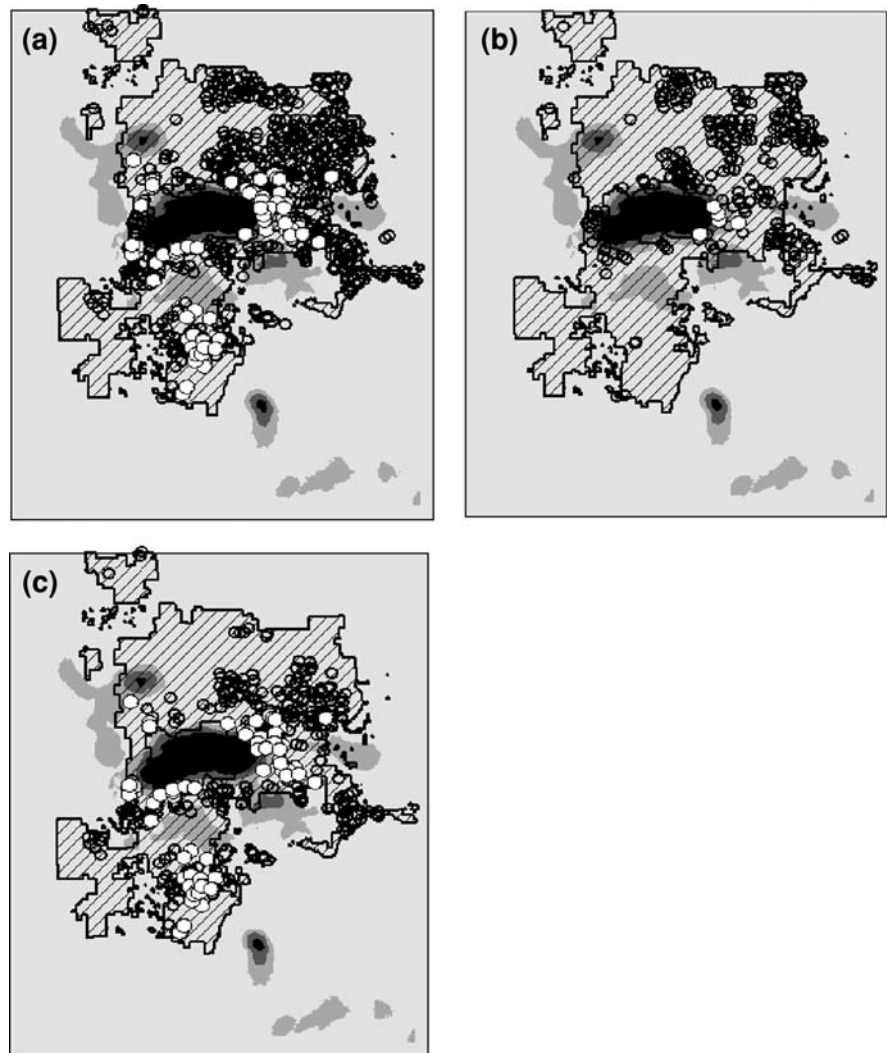
Discussion

The aim of this study was to model American marten occupancy across a large geographic region using landscape-scale habitat associations and test model predictions with an independent data set. We found that marten populations were influenced by the distribution of habitat at or above the home range-scale, similar to findings elsewhere in North America

(Chapin et al. 1998; Hargis et al. 1999; Potvin et al. 2000; Slauson et al. 2007; Baldwin and Bender 2008). Bissonette et al. (1997) suggested that fragmentation acted as an upper level constraint on habitat selection, affecting martens at relatively low levels; a conclusion drawn from studies in Maine, Ontario, and Utah. Despite substantial differences between forest types, landscape structure, and topography in our study and the boreal forests of the east and inter-mountain west, several of our findings are consistent with these previous studies. These found that more habitat, larger patch sizes, and larger areas of interior forest were important predictors of occurrence (Chapin et al. 1998; Hargis et al. 1999; Potvin et al. 2000). Similarly, our marten sites had 3 times as much reproductive habitat and interior forest, over twice as many reproductive habitat patches, and larger mean reproductive habitat patch sizes (Appendix 1—see Supplementary material).

Although thresholds in environmental conditions tend to be specific to a given landscape’s structure and composition, at the largest spatial extent nearly all our marten sites (95%) contained at least 17% of vegetation types we defined as reproductive habitat and 5% interior forest. Thus, we would expect to find martens present in landscapes with approximately 17% reproductive habitat (i.e., 1,360 ha), within an 80 km² assessment area, and roughly a third of this unfragmented forest. However, the *mean* percentages of reproductive habitat and interior forests were 34% (e.g., 2,700 ha) and 15% (e.g., 1,200 ha), representing more conservative management targets.

Fig. 3 Predicted probability surface and test data detection results for American martens (*white circles*, $n = 75$) and non detections (*open circles*, $n = 589$) using **a** the full data set, **b** summer-only data, **c** winter-only data in the vicinity of Lassen National Forest, northeastern California where test data were available (*hatched area*)



Marten distribution

Marten distribution appears patchy with frequent detections at high elevations, in or near designated wilderness, and in ‘checker board’ regions of mixed public–private ownership. Surveys detected marten populations densely clustered near Mt. Shasta and on the Lassen Plateau. Despite reproductive habitat being well distributed throughout the southern half of the study area, a smaller, more dispersed population of martens was found near the southern border of the Plumas National Forest (Fig. 2).

Although martens are territorial animals, territories are often in close proximity. The high proportion of nearby marten detections and their clustered nature

suggest conspecific attraction in the response variable (Appendix 1—see Supplementary material). Our initial candidate model set included AUTOCORR and all models with this variable were in the 95% confidence set at each scale. However, model selection uncertainty increased and Akaike weights were lower in the two smallest scales. Subsequent model performance diagnostics indicated that AUTOCORR did not increase predictive ability. Therefore, we dropped this variable to focus on environmental variables.

Landscape habitat suitability model

Our best predictive model was developed at the broadest scale (80 km²) and included three variables:

PLAND, NP, and PUBLIC. That reproductive habitat composition was an important predictor suggests these forests may be a limiting factor for marten populations, constraining habitat selection at finer scales. The number of reproductive habitat patches was also key, and because late-successional forests in this region are largely fragmented, every patch represents additional structural elements important for martens life requisites (Andruskiw et al. 2008); marten populations require many structures of this type for denning and resting sites, this may explain the positive correlation with their occurrence.

Land ownership was the most important variable indicating that landscape context, where habitat is located relative to administrative boundaries, may influence its use by martens. Sample units with detections had, on average, 14 times as much of the landscape in reserves as those without (Appendix 1—see Supplementary material). Increased habitat quality within reserves and less relative disturbance/alteration of habitat provide possible explanations. Land ownership and administrative boundaries have been identified in several landscape-scale studies as the central factor in modifying landscape pattern due to different land use practices (Turner et al. 2003). The highest density of martens were located in the largest protected area in the region, 60% of detections occurred in or near designated wilderness, which constitutes less than 5% of the study area. Thus, when ownership is viewed as an index of management history, the marten's preference for wilderness indicates an association with less anthropogenic disturbance. Marten detections in wilderness areas throughout the Cascades and Sierra Nevada and their association with 'wild places' is consistent with historic and more recent anecdotal descriptions (Minta et al. 1999).

Model testing

Habitat suitability models are rarely subjected to evaluation using independent test data and those that are often exhibit little predictive ability (Beutel et al. 1999; Manel et al. 1999). We tested model predictions with data not used in the development of the model to evaluate its utility for conservation planning (Manel et al. 1999). Our findings revealed a potentially important influence that the season of data collection has on predicted marten occurrence. The

poor fit of the model to the test data collected during winter has raised concerns that model performance diagnostics may be overly optimistic and that the model does not accurately predict marten occurrence. However, the predictive power of the model is good when evaluated against summer survey data.

Marten behavioral responses offer several possible reasons for seasonal differences in occupancy, including juvenile dispersal, source-sink/metapopulation dynamics, unequal detection probabilities, and seasonal changes in home range size or location. Juveniles disperse from natal territories in fall and early winter and may move into marginal or sink habitats where winter snow provides a competitive advantage. Thus, these may be the martens that are being detected in winter but then succumb before the summer survey season. Similarly, metapopulation dynamics operating in areas of high quality habitat may require emigration of some individuals when densities are at or near capacity. Martens may also expand or shift their home ranges or be more willing to visit detection devices during winter than during summer, making them easier to detect. We plan to conduct surveys during both seasons to compare occupancy rates and detection probabilities in areas with the greatest seasonal discrepancies in prediction success. A radio telemetry study may be required to investigate marten movements, detectability, and survival.

Conclusions

The results of this study indicate high-elevation, lateral forests appear important for marten population persistence. Marten detections were clustered in three distinct regions and at elevations that are largely consistent with the distribution reported over a decade ago (Kucera et al. 1995), suggesting that gaps in their contemporary distribution may not be recent occurrences (Fig. 2). However, historic records indicate marten populations were more widespread and in closer proximity 75 years ago (Grinnell et al. 1937). The combined effects of trapping depression and habitat loss are hypothesized to be responsible for their reduced distribution (Zielinski et al. 2005). It was Joseph Grinnell and colleagues who first warned that the precipitous decline in the number of martens in California was a result of overtrapping and that:

If this species continues to decline in numbers, and if efforts are not made to give it more adequate protection, in a short time it will be scarce or entirely absent in the State except in such protected areas as national parks (Grinnell et al. 1937, pg. 206).

His prophetic words accurately describe the clustered pattern of detections we report here, despite a closure of the trapping season over 50 years ago.

The test data suggest that we can do better at developing a model that will apply to the occurrence of martens year-round. Reduced model performance may be related to sampling design and choice of predictor variables. First, our coarse-scale sampling may have failed to detect some smaller populations. Such populations may be dependent on emigration from a larger population center and are vulnerable to local extirpation. Second, predictor variables that have direct ecological significance are preferred to surrogate variables, such as land ownership, which have only indirect association to causal factors driving marten distribution (Guisan and Zimmerman 2000). However, we also need to determine whether marten occurrence during winter should be considered as influential in habitat modeling as the places where they maintain home ranges in summer. Until we understand the reasons for seasonal differences in occurrence this model represents a conservative view of marten habitat based on summer occupancy. Given their current distribution, both public and private land managers have important roles in maintaining functional connectivity to ensure viable marten populations. The results presented here are sufficient, in our view, to heighten concern about the conservation of American martens in northeastern California that currently reside in high-elevation oases which contain significant amounts of late-successional forests.

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