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Research Article

Decline in American Marten Occupancy Rates at Sagehen Experimental Forest, California

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ABSTRACT We compared the distribution and frequency of American marten (*Martes americana*) detections during historic surveys and a recent survey on the Sagehen Experimental Forest (SEF) in the Sierra Nevada Mountains, California. This area has been the location of 9 previous marten surveys during 1980–1993, each involving a systematic detection/non-detection survey on the same grid. These data are a time series of information on the occupancy of martens that can be related to habitat change in the study area. Our objectives were to 1) resurvey martens in SEF using methodology similar to previous studies to assess current marten occupancy; 2) evaluate changes in marten occupancy during the period 1980–2008; and 3) examine associations between marten occurence and changes in habitat and landscape metrics. Current marten occupancy was estimated using surveys conducted in summer 2007, winter 2007–2008, and summer 2008. From 1978 to 2007 there was a decrease in predicted habitat patch size, core area, and total amount of marten habitat in the study area, as well as an increase in distance between patches. Marten detections in 2007–2008 were approximately 60% lower than in surveys in the 1980s. We detected no martens in the summers of 2007 and 2008, and 10 detections in winter 2007–2008 were limited to higher elevations in the southwestern portion of SEF. No martens were detected in the lower elevations where most of the recent forest management activity occurred. We suggest that the marten population at SEF has been negatively affected by the loss and fragmentation of habitat. We recommend that future management of forests in the Sagehen basin focus on restoring and connecting residual marten habitat to improve habitat quality for martens.

KEY WORDS American marten, California, fragmentation, habitat loss, *Martes americana*, Sagehen Experimental Forest.

The distribution of American martens (*Martes americana*) in California has changed from being relatively continuous throughout the higher elevations of the Cascades and Sierra Nevada mountain ranges in the early 1900s to isolated and discontinuous populations today (Zielinski et al. 2005). The causes of these declines are poorly understood, and the phenomenon needs to be examined at a finer scale to evaluate potential mechanisms responsible for these changes. In the Sierra Nevada and Cascades mountains of California, martens reside primarily in high elevation forests and are associated with areas of dense canopy cover (Spencer et al. 1983). They often occupy areas where more than two-thirds of the landscape is covered by closed canopy forests that have complex structure, including multi-layered canopies and comparatively high amounts of dead trees, logs, and large trees (Chapin et al. 1998, Hargis et al. 1999, Fuller 2006). Martens may be associated with such forests because they can forage most effectively in dense forests with complex structure (Bissonette et al. 1997, Andruskiw et al. 2008), and because forests with complex structure and large trees and snags provide resting and denning sites (Spencer 1987, Slauson and Zielinski 2009), as well as escape and thermal cover (Strickland and Douglas 1987, Drew 1995).

The first quantitative studies of marten abundance in the Sierra Nevada were initiated in 1980 at what was known as the Sagehen Creek Field Station, largely corresponding to the watershed of Sagehen Creek on the eastern slope of the Sierra Nevada Mountains (Spencer 1981, Zielinski 1981). Sagehen Creek was an ideal location for these surveys as martens were abundant to the northwest (Simon 1980) and the area had earlier been described by trappers as a marten stronghold (Grinnell et al. 1937:189–190). Martin (1987) conducted a series of follow-up surveys in Sagehen Creek in 1983-1993 (S. K. Martin, Washington State University, unpublished data). These researchers conducted 9 systematic marten surveys at Sagehen, providing a time series of information on the occupancy and abundance of martens and a history of forest management on the study area that spanned 1980–1993.

In 2007, we initiated a new survey of martens in the same area, since renamed the Sagehen Experimental Forest (SEF), to determine if trends observed in the earlier surveys had continued, and to evaluate the possible influence of habitat change on the observed trends in marten distribution. Our

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objectives were to 1) resurvey SEF using methodology similar to previous studies to assess current marten occupancy; 2) evaluate changes in marten occupancy during the period 1980–2008; and 3) examine changes in marten occurence relative to changes in habitat and landscape metrics.

STUDY AREA

Our research was conducted at SEF, a 40 km^2 research forest in the Sagehen Creek watershed on the eastern slope of the Sierra Nevada Mountains approximately 12 km northwest of Truckee, California (Fig. 1). Sagehen Experimental Forest has been managed by the University of California, Berkeley since 1951 and was designated as California's 11th Experimental Forest in 2005. Elevations ranged from 1,862 m to 2,670 m. The climate was characterized by short dry summers and cold winters. In the period 1953–2006, the average low and high temperatures measured at 1,943 m were: 10° C and 4° C in January and 3° C and 26° C in July. Average annual precipitation was 88 cm, of which approximately 80% occurred as snow in winter. Annual cumulative snowfall averaged 515 cm (Western Regional Weather Center 1953–2006). In a typical year, snow was present from December to May.

Sagehen Experimental Forest contained both montane and subalpine flora (Barbour et al. 2007). Major vegetation cover types included a mixture of riparian corridors, fens, and wet meadows at lower elevations, and mixed-conifer forests throughout the study area (Savage 1973). Riparian and mesic areas at lower elevations were dominated by lodgepole pine (*Pinus contorta*) with a ground cover of sedges, forbs, and willows (*Salix* spp.). Xeric south-facing slopes were covered by Jeffrey pine (*P. jeffreyi*) or mixed stands of Jeffrey pine and white fir (*Abies concolor*). Above the Jeffrey pine zone, there were mixed stands of white and red fir (*A. magnifica*) with intermixed lodgepole stands. Red fir was dominant at high elevations and often associated with mountain hemlock (*Tsuga mertensiana*) and western white pine (*P. monticola*). Patches of mountain mahogany (*Cercocarpus montanus*) occurred at the highest elevations. Where trees were absent, vegetation was dominated by shrubs, including snowbrush (*Ceanothus velutinus*), gooseberries (*Ribes* spp.), and greenleaf manzanita (*Arctostaphylos patula*).

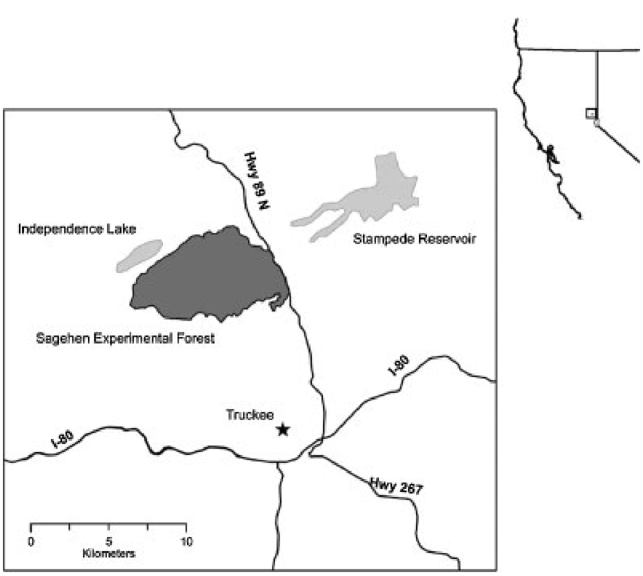

Figure 1. American marten (*Martes americana*) study area during 1980–2008. We surveyed within Sagehen Experimental Forest (SEF; shaded in gray) on the east slope of the Sierra Nevada Mountains, California.

During the 20th century, 4 large wildfires and periodic timber harvests occurred at SEF. The fires occurred from 1914 to 1960, all prior to the first marten surveys in 1980. Post-fire, the majority of the burned areas were replanted with monotypic stands of Jeffrey pine (West 1982), which are currently about 50-yr old, with understories dominated by shrubs. Based on unpublished records maintained by the Tahoe National Forest, we estimated that 72% of SEF was affected by some form of timber harvest during the 28 yr considered in our study. Of the area harvested, 4.3% was clear-cut, 12.0% was cut with shelterwood methods, 38.3% was thinned from either above or below, 41.4% was salvage-logged, and 4% was harvested with unknown methods. Shelterwood cuts were similar to clear-cuts except that a few mature trees were left standing. Salvage logging, which mostly occurred within 200 m of roads, typically targeted living or dead trees that were damaged or dying (Smith et al. 1997). Salvage logging was often designed to remove trees damaged by fir engraver beetles (*Scolytus ventralis*) or dwarf mistletoe (*Arceuthobium* sp). Although the wood volume removed was recorded for most harvests, the size, age, and status of trees removed during salvage logging was rarely described. Thinning projects typically retained an even distribution of trees and reduced the canopy cover to $\leq$40%. Approximately 77% of the logging at SEF occurred in late-seral stands of red fir or mixed conifer. The remaining logging occurred in Jeffrey or lodgepole pine stands. Approximately 16.3% of SEF had not been harvested or burned at the time of our study.

METHODS

Historical marten surveys at SEF were conducted within a semi-permanent rectangular grid established in 1980 by Spencer (1981) and Zielinski (1981). This grid included 336 stations spaced at 400 m $\times$ 600 m intervals and covered 65% of SEF. An average of 50 stations (range = 32–84) were surveyed during the 9 previous sampling periods using track plates (Ray and Zielinski 2008). Track plate protocols used by Spencer (1981), Zielinski (1981), and Martin (1987) included wooden enclosures mounted in trees (Barrett 1983). In summer 2007, we also used track plate methods to detect the presence of martens, but unlike previous studies we used corrugated plastic enclosures placed on the ground with a 63-mm wire mesh back, and aluminum plates coated with printer toner (Ray and Zielinski 2008). Martens forage in terrestrial and arboreal environments (Spencer et al. 1983) and previous uses of ground and tree-based detection devices do not suggest any difference in the probability of detection based on placement (Zielinski et al. 2008).

Some of the early marten surveys at SEF used a combination of non-invasive methods (track plates, snow-tracking) and live trapping to evaluate marten distribution (Spencer 1981, Martin 1987). Our analysis of these early studies was limited to the results from non-invasive methods, which were comparable to the methods that we used. We used data from theses (Spencer 1981, Zielinski 1981, Martin 1987), published reports (Spencer et al. 1983, Spencer 1987, Martin and Barrett 1991), and field notes (S. K. Martin, unpublished data) to estimate marten occurrence during each survey period. We summarized these records as binary (detection or non-detection) data.

The 9 marten surveys prior to our study were conducted on the same sampling grid. However, the number of stations surveyed and the number of survey days per station varied among studies, such that the percent of the study area sampled varied from 33% to 73% ($\bar{x} = 59\%$, SE $= 4\%$). Instead of using the same grid used in previous surveys, we used a new sampling grid that was established at SEF for interdisciplinary studies of fire behavior, vegetation, and wildlife (Vaillant 2008). This grid covered 32 km^2, with sampling stations at 500-m intervals. It covered the same area surveyed in the previous surveys, but also included more of SEF (80%) than the previous surveys. Any one of our sampling stations was within 726 m of a previously surveyed station ($\bar{x} = 276$ m, SE $= 27$). Opportunities for detection were similar across years because an average female home range of 4.0 km^2 (Powell 1994) would encompass 16.7 and 16.0 stations using the previous and current grid spacing, respectively.

We conducted surveys during summer 2007 ($n = 104$ stations), winter 2007–2008 ($n = 94$ stations), and summer 2008 ($n = 10$ stations). We conducted surveys with enclosed track plates in summer 2007, cameras and snow-tracking in winter 2007–2008, and cameras in summer 2008. We monitored track plates for a minimum of 35 days at each of 104 stations during the first summer (Jun–Sep 2007). We baited enclosed track plates with chicken and a commercial scent lure (Gusto; Minnesota Trapline Products, Pennock, MN). We attempted to collect hair samples for genetic analyses by placing hair snare devices inside all track plate enclosures where martens were detected (Kendall and McKelvey 2008). Genetic analyses of hair and scat were conducted at the Rocky Mountain Research Station (Wildlife Genetics Laboratory, Missoula, MT). Sequencing of mitochondrial genes was used to determine if samples were from martens, and microsatellites were used to determine gender and individual identification (Riddle et al. 2003, Schwartz and Monfort 2008).

The 94 bait stations monitored during winter 2007–2008 included 69 snow-tracking stations and 25 camera stations. We used chicken and Gusto scent lure for bait. We alternated cameras and snow-tracking stations such that either a snow-tracking station or a camera station was placed every 500 m on the same grid as summer 2007, with the exception of 10 stations in avalanche zones. At stations where martens were detected with tracks or cameras, we placed a hair snare that consisted of gun cleaning brushes attached 10 cm apart on a corrugated plastic strip that was wrapped around the tree trunk so that the animal had to climb between the brushes to reach the bait (P. Figura, California Department of Fish and Game, unpublished report). We counted photographs, snow-tracks, or positively identified genetic samples (hair, scat) as verifiable detections. The number of snow-tracking visits ranged from 2 to 6 per station within 96 hr after a fresh snowfall, when snow-tracking conditions were appropriate (Halfpenny et al. 1995, Beauvais and Buskirk 1999). We assigned marten tracks that we detected while snow-tracking to the nearest station. We used the same remote cameras and surveyed a small number of stations in summer 2008 at stations where martens were detected in winter 2007–2008.

Imperfect detection and/or false absences will cause estimates of occupancy to be biased if not accounted for (Tyre et al. 2003, MacKenzie et al. 2006). We estimated the probability of detection ($\hat{p}$) at each station using data from 4 of the previous surveys that had complete detection histories at each station. We calculated the probability of detecting a marten at least once, if present, after K survey visits, as 1 minus the probability of not detecting the species in any of the K survey visits, or $1 - (1 - \hat{p})^K$ (MacKenzie et al. 2006). We estimated occupancy ($\hat{\psi}$), the probability that a randomly selected station was occupied by a marten at any sampling occasion, assuming a closed sampling period. We used program PRESENCE (available at http://www.mbr-pwrc.usgs.gov/software.html) to evaluate a suite of a priori models, including models that assumed constant occupancy throughout the survey period and models that allowed detection probabilities to vary among survey visits (Burnham and Anderson 2002). We evaluated the fit of each model to the data using Akaike's Information Criterion (AIC). We used paired t-tests to compare the naïve estimates of occupancy (the number of stations with marten detections divided by the total number of stations) with the occupancy estimates from our models created with program PRESENCE. If estimated occupancy significantly differed from the naïve estimate, then we adjusted occupancy estimates for all surveys, including those with incomplete detection histories, from the naïve estimates.

Although there may have been differences in detection probabilities based on different survey methods, we did not have enough detections to test for such differences. Therefore, we used a composite detection history from all methods combined to estimate occupancy (Long et al. 2007). Occupancy estimates are similar using multiple methods for most species when probability of detection is >15% (O'Connell et al. 2006). Zielinski et al. (2008) found that the probability of detecting martens was >94% after 4 visits at a study site approximately 60 km south of SEF, regardless of season or survey method (track station vs. camera). Thus, we believe that probabilities of detection of martens are similar using different detection methods and that our results are comparable to previous surveys.

To explain variation in habitat use by martens at SEF, previous researchers analyzed their data separately for 2 seasonal periods, which they referred to as the snow period (1 Dec–31 May) and snow-free period (1 Jun–30 Nov; Spencer 1981, Zielinski 1981, Martin 1987). We used the same seasonal periods in our analysis to account for potential seasonal differences in detection probabilities.

In their analyses, Spencer (1981) and Martin (1987) used the 2,050 m elevation contour to subdivide the study area into an upper and lower watershed. Vegetation in the upper and lower watersheds primarily consisted of forests dominated by true fir (*Abies* spp.) and mixed-conifer, respectively. We used the same elevation contour to compare marten detections in the upper and lower watershed in our analysis. We used a Fisher's exact test to determine if the odds ratio was equal to 1 (Ramsey and Schafer 2002) in order to compare the percent of marten detections between the upper and lower watersheds.

We used the percent of stations where martens were detected during each survey period to compare among seasons and studies. After adjusting for the probability of detection (if necessary), we used an arcsine square root transformation to normalize the percent of stations where martens were detected. We used a general linear model to evaluate the trend in transformed marten detections while accounting for survey duration (number of survey nights per station), number of stations, and time since the initial survey in 1980.

We used satellite imagery with supervised and unsupervised algorithms to transform spectral data into vegetation maps for 1978 and 2007, which corresponded to vegetation conditions during the earliest surveys at SEF and during our most recent survey. Both maps were created by the United States Department of Agriculture (USDA) Forest Service Region 5 Remote Sensing Laboratory (RSL). We resampled both the 1978 Multi-spectral scanner (MSS) Landsat-3 image and 2007 Thematic Mapper (TM) Landsat-5 image to a 57-m spatial resolution to enable execution of identical analysis procedures and grain size for both maps. Broad vegetation type classifications such as conifer, hardwood, mixed conifer, shrub, barren, and water were produced using program LIFEFORM, which uses an unsupervised procedure to classify spectrally similar pixels into vegetation categories (Brohman and Bryant 2005). We scanned, georeferenced, and transformed aerial photographs from 1977 into photo-mosaics (ERDAS, Inc., Norcross, GA). We overlaid a 100-m grid on the study area and chose 235 randomly selected reference sites. A remote sensing analyst and photo-interpreter confirmed or modified the 1977 LIFEFORM classifications using the photo-mosaic. Similarly, we checked the 2007 LIFEFORM site classifications against 2005 National Agriculture Imagery Program images at 1-m resolution at the same 235 reference sites.

To make our results comparable with other recent marten research in California, we transformed the LIFEFORM vegetation classes into a standardized vegetation classification system, CalVeg (Parker and Matayas 1979). Then, we used automated algorithms to reclassify the vegetation layer based on the California Wildlife Habitat Relationships (CWHR 2006) classification, which is a commonly used vegetation classification system for wildlife applications in California (Mayer and Laudenslayer 1988).

We transformed the vegetation type, tree size, and canopy density layers to create maps that predicted the distribution of high or low quality marten habitat for 1978 and 2007. We considered the predicted high-quality reproductive habitat (hereafter marten habitat) the limiting factor for martens and permitted the most strategic evaluation of change in habitat over time. We modified our habitat values from a pre-existing CWHR model (Table 1; Mayer and Laudenslayer 1988). We altered CWHR's definition of reproductive habitat to include changes made by Kirk and Zielinski (2009). This included the removal of the Douglas fir and montane hardwood-conifer types as marten reproductive habitat and the inclusion of the white fir type, provided that stands were of moderate to dense condition and composed of moderate to large diameter trees. We also followed recommendations to include dense canopy and large diameter stands within the Sierra mixed conifer type as marten habitat when they were classified as fir-dominated (mixed conifer-fir) in CalVeg (Green 2007). To ensure that our designation of marten habitat depicted potential areas used by martens, we compared previous marten locations (rest sites) with the polygons that were labeled as marten habitat. We found that 100% of previously known rest sites used by martens at the study area (Spencer 1981, Martin 1987) occurred in vegetation types we designated as high-quality marten habitat.

Table 1. Definitions of high-quality American marten (*Martes americana*) reproductive habitat based on forest types and metrics published by the California Department of Fish and Game (CWHR 2006) and modified metrics based on Spencer (1981), Martin (1987), Green (2007), and Kirk and Zielinski (2009).

	CWHR high-quality habitat		Modified high-quality habitat	
Forest type	**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
Montane riparian (MRI)	5, 6	M, D	4, 5, 6	M, D
Red fir (RFR)	4, 5	M, D	4, 5	M, D
Subalpine conifer (SCN)	4, 5	M, D	4, 5	M, D
Sierra mixed conifer (SMC)[c]			5, 6	M, D
White fir (WFR)			4, 5	M, D

[a] Diameter at breast height (DBH) class 4 = 28–60 cm, class 5 = >60 cm, class 6 = >60 cm with multi-layered canopy.
[b] M, moderate (40–60%); D, dense (>60%).
[c] Sierra mixed-conifer was split into mixed-conifer-fir and mixed-conifer-pine. We only considered mixed-conifer-fir reproductive habitat.

We were unable to create a map-specific accuracy assessment for our vegetation classifications during both time periods (1978 and 2007). However, the USDA Forest Service RSL estimated accuracy for similar remote sensing procedures, and for the same general area (Foody 2002, CalVeg 2004). The LIFEFORM accuracy estimate for conifers was 94% correct. Within the conifer classification, correct designation of lodgepole pine, red fir, white fir, and mixed conifer-fir were 100%, 53%, 80%, and 84%, respectively (CalVeg 2004). Overall correct classification for canopy cover and tree size was 91% and 78%, respectively (CalVeg 2004).

We used program FRAGSTATs Version 3.3 (McGarigal et al. 2002) to assess changes in landscape composition and configuration during the 29 yr from 1978 to 2007. For these analyses, we examined habitat attributes within the entire SEF boundary and above and below the 2,050-m elevation contour separating the upper and lower watersheds. We also used the raster calculator tool in ArcMap (Spatial Analysis Toolbox; Environmental Systems Research Institute, Inc., Redlands, CA) to evaluate habitat change from 1978 to 2007. We created change maps, reflecting either habitat gain or habitat loss over the 29-yr period, by adding or subtracting pixels to the 1978 map, depending on whether or not the pixels were classified as marten habitat in 2007. Habitat gain pixels were composed of habitat that did not occur in 1978 but were designated as habitat in 2007. We presumed this change to occur with increased canopy cover or tree diameter growth within vegetation types suitable to martens. Conversely, habitat loss pixels were those labeled as habitat in 1978 and non-habitat in 2007. Loss occurred when areas had disturbance that decreased the canopy cover or tree diameter in vegetation types previously labeled as suitable for martens.

We used 5 class and 6 patch metrics to describe habitat configuration (McGarigal et al. 2002). Class metrics are those that aggregate properties of habitat patches, and patch metrics are computed for every patch in the landscape. Because Levene's test for equality of variances revealed divergences from normality in all patch metrics, we used 2-sided nonparametric Wilcoxon-rank sum tests to evaluate differences in patch metrics. Our selected class metrics were relatively robust to changing scales in respect to grain size and ability to detect differences between different spatial extents (Wu 2004). Class metrics used to assess change in habitat amount included the percent cover of marten habitat (PLAND), the number of patches of marten habitat (NP), the largest patch index (LPI), and the percent and number of core habitat patches (CPLAND, NDCA). Patch metrics included those that would reflect both the amount of habitat and core areas (AREA_MN, CORE_AM and DCORE_AM) as well as metrics that we used to assess patch connectivity using area-weighted gyration (GYRATE_AM) and fragmentation such as the mean proximity index (PROX_MN) and the Euclidean nearest neighbor distance (ENN; McGarigal et al. 2002, Leitão et al. 2006). We defined core area patches as those with an edge depth >100 m. This was probably a reasonable definition given that Heinemeyer (2002:101) found that, on average, marten foraging and subnivean locations were 213 m from forest edges in contiguous forests (<25% clear cut) and 85 m from edges in landscapes with >50% clear cut. The mean proximity index depicts the mean isolation of each habitat patch by accounting for the size and proximity of all patches and may serve as a more ecologically significant metric than nearest neighbor distances (Gustafson and Parker 1992). We used area-weighted indices for core area, distinct core area, and gyration to evaluate associations between marten detections and large patches of marten habitat (McGarigal et al. 2002). Many of these class and patch metrics have been used in previous marten research (Hargis et al. 1999, Kirk and Zielinski 2009). Habitat configuration was reported for the SEF at each point in time, for the habitat that was gained and lost, and for the upper and lower watersheds separately.

We used the Tahoe National Forest East Side Disturbance Layer (TNFESDL) to evaluate our predicted habitat loss metrics in relation to forest management history. The TNFESDL was created from a variety of sources including Stand Record System Cards, California Timber Harvest Plans, orthophotos, approved planned activities from National Environmental Policy Act maps, timber sale maps, and information from the USDA Forest Service Activity Tracking System. Where multiple disturbances occurred at the same location, we applied the action having the most relevant disturbance potential to the disturbance polygon. We recorded all disturbances that occurred in the previous 30 yr. We checked disturbance polygons in the TNFESDL against Landsat TM imagery (C. Ramirez, USDA Forest Service RSL, personal communication) and with aerial photographs to assure their accuracy. In addition to the TNFESDL, we examined timber sale reports and maps from 2 prominent harvests within SEF, the Golden Harvest, which occurred in 1988 and produced 13,450 m^3 of wood (West 1982), and a salvage harvest that took place in 1990 which affected as much as 26% (10.4 km^2) of SEF. Some polygons in the TNFESDL did not fully represent the extent of the 1988 Golden Harvest, so we modified this portion of the layer to reflect the actual boundaries of the harvest unit, which were documented in stand survey reports at the time of harvest. The 1990 salvage was not included in the TNFESDL layer, so we added polygons for the salvage event by hand tracing a boundary map of the sale unit (1:24,000 scale) that included contour lines. Because areas salvaged were primarily near roads, and the number of trees removed within these areas was unknown, we included these polygons in our analyses but mapped them separately from the TNFESDL layer. Although salvage harvests did not disturb the ground as much as the other harvest methods, we presumed they disproportionately affected marten resting habitat in that salvage typically removed the largest trees and those with defects, forest elements that are important to martens (Spencer et al. 1983, Slauson and Zielinski 2009).

RESULTS

The average per visit probability of detection ($\hat{p}$) based on surveys with complete detection history was 57.8%

Table 2. Results of Akaike's Information Criterion (AIC) model selection based on a priori models that included constant occupancy ($\psi(.)$) and detection probabilities that were either constant ($p(.)$) or variable ($p(t)$) among sampling visits during 4 studies of American martens (*Martes americana*) at Sagehen Experimental Forest, California during 1980–2008. We estimated the probability of detection per survey visit ($\hat{p}$) and for the entire survey period (detection probability) based on the formula $1 - (1 - p)K$ and the methods described by MacKenzie et al. (2006.)

Survey	Model	AIC	ΔAIC[a]	w[b]	Npar[c]	Naïve est.[d]	$\hat{\psi}$[e]	SE($\hat{\psi}$)	$\hat{p}$[f]	SE ($\hat{p}$)[g]	Detection probability
$1991_{\text{Snow-free}}$	$\psi(.)p(.)$	157.55	0.00	0.95	2	0.26	0.26	0.06	0.78	0.04	1.00
	$\psi(.)p(t)$	163.61	6.06	0.05	6		0.26	0.06			
1992_{Snow}	$\psi(.)p(.)$	115.06	0.00	0.87	2	0.15	0.15	0.05	0.45	28.0	0.95
	$\psi(.)p(t)$	119.40	4.32	0.10	6		0.17	0.05			
$1993_{\text{Snow-free}}$	$\psi(.)p(.)$	99.64	0.00	0.93	2	0.24	0.24	0.05	0.83	0.06	1.00
	$\psi(.)p(t)$	104.71	5.01	0.07	6		0.25	0.06			
2008_{Snow}	$\psi(.)p(.)$	139.00	0.00	0.99	2	0.10	0.13	0.04	0.24	0.06	0.75
	$\psi(.)p(t)$	142.29	10.29	0.01	9		0.12	0.06			

[a] The relative difference in AIC values compared to the top ranking model.
[b] Akaike weight, the probability of the model being correct in relation to candidate models given the data provided.
[c] Number of parameters.
[d] Number of stations with detections divided by the total number of stations (n).
[e] Estimated occupancy or the probability that a randomly selected station was occupied by a marten at any sampling occasion.
[f] Estimated probability of detection.
[g] The probability of detection is low and the standard error is high for the 1992 survey, mostly likely due to the fact that stations were removed immediately after the first marten detection.

(range = 24.0–83.3%), and the average detection probability per seasonal survey period was 92.5% (range = 75–100%). Because probability of detection was high, estimated site occupancy ($\hat{\psi}$) did not differ significantly from naïve occupancy for any of the surveys conducted in 1991–1993 or 2007–2008 ($t_3 = 1.17$, $P = 0.32$; Table 2). We assumed, therefore, that the naïve occupancy estimates for the surveys that were missing detection history data (1980–1983) were also no different than those adjusted for imperfect detection. Estimated site occupancy was higher for the snow-free period ($n = 2$) than for the snow period ($n = 2$; average $\hat{\psi} = 0.25$ and 0.14 respectively; Table 2).

The distribution of marten detections changed spatially from well-distributed in the 1980s, to detections that were clustered in the southwest corner of the upper watershed in the 1990s (Fig. 2). In the 4 surveys conducted in 1980–1983, the average percent of stations with marten detections was 65% (SE = 0.047, 95% CI = 49.7–79.7%; Table 3), and the average percent of stations with marten detections in the upper and lower watersheds was 77% and 43%, respectively.

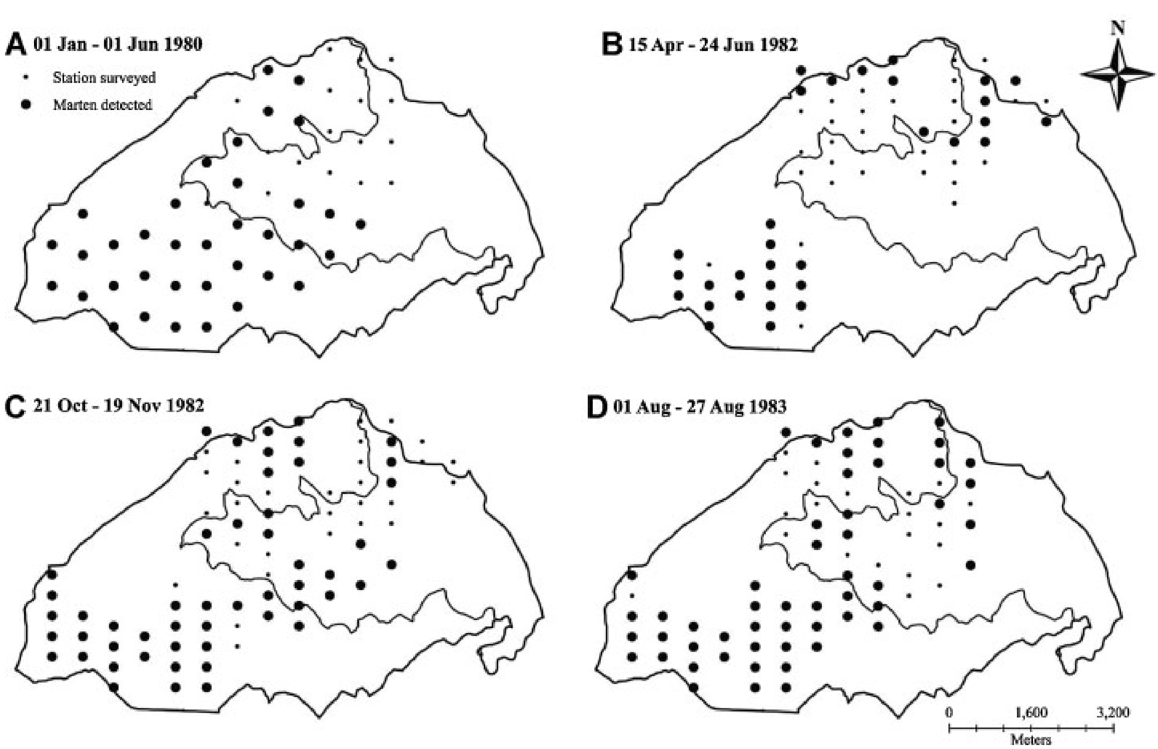

Figure 2. American marten (*Martes americana*) detections in, and immediately north of, the Sagehen Experimental Forest, California during 9 previous surveys 1980–1993 (Spencer 1981; Zielinski 1981; Martin 1987, 1995) and during our 3 surveys in 2007–2008. Stations with and without marten detections are indicated by large and small solid circles, respectively. The upper watershed is west of the 2,050 m contour line within the study area outline.

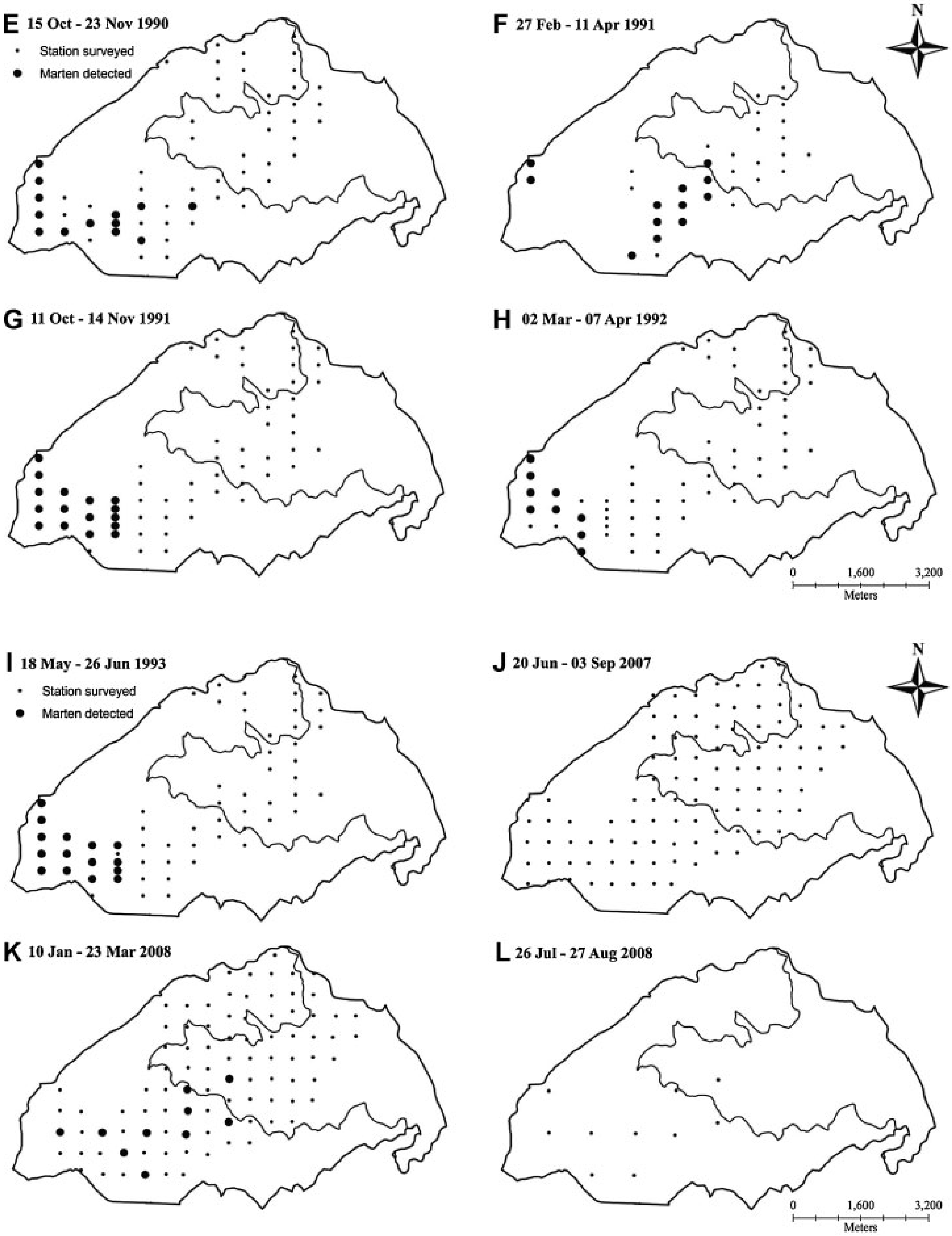

Figure 2. (Continued).

In 1980–1983, it was 4 times more likely to detect a marten in the upper watershed than the lower watershed (odds ratio $= 4.21$, $P < 0.001$).

In the 5 surveys completed in 1990–1993, the overall average percent of stations with martens detected was 25% (SE $= 0.034$, 95% CI $= 15.4$–34.9%; Table 3). The average percent of stations with detections in the upper and lower watersheds was 36% and 2%, respectively, and it was 650 times more likely to detect a marten in the upper than in the lower watershed (odds ratio $= 650.01$, $P < 0.001$).

We detected no martens in summers of 2007 or 2008 despite the fact that the 2007 summer survey effort (3,640 survey days) exceeded the effort in all previous surveys conducted during the snow-free period (Table 3). In winter

Table 3. Timing, duration, sample size, and number of American marten (*Martes americana*) detections in marten surveys at Sagehen Experimental Forest, California during 1980–2008. We subdivided surveys based on whether they occurred in the snow season (1 Dec–31 May) or snow-free season (1 Jun–30 Nov).

Surveyor	Date begin	Date end	Time after 1980 (yr)	Season	Duration (days)	No. stations (*N*)	No. survey visits (*K*)[a]	Survey effort (days $\times$ *N*)	No. detections	% of stations with detections
Spencer (1981) and Zielinski (1981)	1 Jan 80	1 Jun 80	0.0	Snow	180	53		9,540	38	0.72
Martin (1987)	15 Apr 82	24 Jun 82	1.9	Snow	69	60		4,140	31	0.52
Martin (1987)	21 Oct 82	19 Nov 82	2.4	Snow-free	27	80		2,160	51	0.64
Martin (1987)	1 Aug 83	27 Aug 83	3.2	Snow-free	25	74		1,850	53	0.72
Martin[b]	15 Oct 90	23 Nov 90	10.4	Snow-free	38	59		2,242	13	0.22
Martin[b]	27 Feb 91	11 Apr 91	10.8	Snow	41	32		1,312	12	0.38
Martin[b]	11 Oct 91	14 Nov 91	11.4	Snow-free	22	62	5	1,364	16	0.26
Martin[b]	2 Mar 92	7 Apr 92	11.8	Snow	40	62	5	2,480	9	0.15
Martin[b]	18 May 93	25 Jun 93	13.0	Snow-free	38	62	5	2,356	15	0.24
This study	20 Jun 07	13 Aug 07	27.1	Snow-free	35	104	5	3,640	0	0.00
This study	10 Jan 08	23 Mar 08	27.6	Snow	40	94	7	3,760	10	0.11
This study	26 Jul 08	27 Aug 08	28.2	Snow-free	35	10	5	350	0	0.00
Snow-free combined ($n = 7$)					220	451		13,962	148	0.33
Snow combined ($n = 5$)					370	301		21,232	100	0.33

[a] Number of survey visits unknown 1980–Spring 1991.
[b] S. K. Martin, Washington State University, unpublished data.

2007–2008, we detected martens at 10 stations. The average percent of stations with $\geq$1 marten detection among our 3 surveys was 4% (SE = 0.061, 95% CI = 16.0–23.0%; Table 3). Because of the low percent of stations with marten detections in both the upper and lower watersheds, the difference between the 2 areas (8% vs. 1%) was less dramatic than in earlier surveys. However, it was still 9 times more likely to detect a marten in the upper watershed than in the lower watershed (odds ratio = 8.82, $P = 0.019$).

The 10 marten detections in winter 2007–2008 were all in the southwest portion of the upper watershed, and included 8 camera detections (6 with tracks), 1 snow-track only, and 1 genetic hair sample only. Hair snare devices deployed for >1 week at each of the 10 stations where martens were detected produced 12 marten hair samples. Of these, 5 were from 3 individuals (2 F and 1 M) and 7 did not have enough DNA to document individual identity.

After accounting for survey duration, number of stations, and time since survey, there was strong evidence that marten detections declined significantly at SEF from 1980 to 2008 (Fig. 3). Marten detections were predicted by a negative relationship with time since the 1980 survey, a positive relationship with survey duration, and a positive relationship with number of stations surveyed: [(ArcSineSqrt (Detections) = 0.83 − 0.03(Time) + 0.0005(Duration) + 0.0014(Number stations)]; $R^2 = 0.88$, $F_{3,11} = 19.2$, $P < 0.01$). Time (years) since the 1980 survey was the only significant explanatory variable in the model (Parameter estimate [β] = −0.03, SE = 0.006, $P = 0.003$). The average percent of stations with marten detections declined from 65% in the 1980s to 4% in our contemporary surveys.

During the period 1978–2007, all metrics describing patches of marten habitat within SEF changed in ways that we predicted would negatively affect martens (Tables 4 and 5). Several metrics indicated a reduction in the amount of marten habitat in the landscape and an increase in the distance between patches (Table 4). The percent cover of marten habitat (PLAND) declined by 25.4%, from 1,073 ha in 1978 to 800 ha in 2007. The total amount of marten habitat decreased by 628 ha, a 58.5% loss from 1978 to 2007 (Fig. 4C). Approximately 360 ha (9% of the total area) changed to high-quality marten habitat from 1978 to 2007 (Table 4, Fig. 4D). A portion of this habitat gain (52%) was in riparian zones and not in the upland conifer types that characterize typical marten reproductive habitat. Positive changes in habitat quality for martens from 1978 to 2007 were substantially less than the negative changes in terms of the total amount of habitat, number of habitat patches, core area, proximity mean index, and patch quality (area-weighted gyration; Table 4, Fig. 4). Increases in core area index

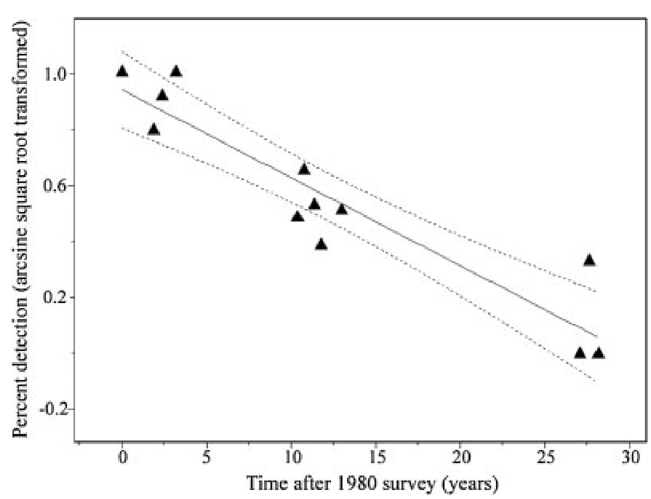

Figure 3. Relationship between time after the first survey of American martens (*Martes americana*) in Sagehen Experimental Forest, California in 1980 and arcsine square root transformed occupancy rates reported in 11 subsequent studies ending in 2008. Line of fit and 95% confidence interval shown and represented by the model: ArcSineSqrt(Detections) = 0.83 − 0.03(Time) + 0.0005(Duration) + 0.0014(Number of stations).

Table 4. Estimated amount and configuration of high-quality American marten (*Martes americana*) habitat in 1978 and 2007 at Sagehen Experimental Forest, California. We defined habitat gain as areas of habitat that did not occur in 1978 but were designated as habitat in 2007 (gain). Conversely, we defined habitat loss as areas labeled as habitat in 1978 and non-habitat in 2007 (loss). Standard errors for patch metrics are in parentheses.

Variable name	1978	2007	Gain	Loss
Percentage of landscape (PLAND)	27.0	20.1	8.9	15.8
Number of patches (NP)	19	18	29	46
Largest patch index (LPI)	17.8	8.2	1.83	6.8
Percent cover of core areas (CPLAND)	9.1	4.9	0.9	4
Number of distinct core areas (NDCA)	25	24	12	19
Mean patch area (AREA_MN), ha	56.5 (36.5)	44.5 (19.2)	12.3 (3.0)	13.7 (6.6)
Area weighted core area (CORE_AM), ha	190.1 (9.8)	60.1 (2.6)	4.1 (0.5)	50.0 (2.3)
Area weighted distinct core area (DCORE_AM), ha	96.0 (0.2)	34.5(0.2)	6.8 (1.4)	43.4 (1.5)
Proximity mean index (PROX_MN)	283.2* (95.7)	83.5* (29.4)	11.1 (4.2)	46.3 (14.6)
Area weighted gyration (GYRATE_AM)	1045.7 (49.5)	746.6 (23.2)	308.9 (12.4)	635.6 (18.3)
Mean nearest neighbor distance (ENN)	194.4 (68.3)	240.5 (71.5)	302.4* (59.0)	221.2* (34.5)

* Statistically significant with $P \leq 0.05$.

because of forest growth were less than decreases in this index due to harvest, fire, and insect mortality (4.1 vs. 50.0, respectively, $Z = -1.28$, $P = 0.09$). Similarly, both the proximity mean index and mean nearest neighbor distance indicated that patches gained were further apart than patches lost ($Z = 1.48$, $P = 0.13$; $Z = -1.92$, $P = 0.05$).

Mean patch area, core area, and gyration increased in the lower watershed and declined in the upper watershed from 1978 to 2007 (Table 5). The largest habitat patch in the lower watershed increased 24% (from 96.5 ha to 127.2 ha) while the largest patch in the upper watershed decreased by 41% (from 559.0 ha to 329.3 ha). The upper watershed also had a 41% reduction in the total percent cover of core area of marten habitat (CPLAND), a 48% reduction in area-weighted core area, an increase of 64 m average patch distance, and a 72% increase in mean proximity index (Table 5). Area-weighted measurements exhibited large variation due to patch size differences. There were several small and a few disproportionately large patches of habitat in each portion of the watershed.

Of the 72% of SEF that was affected by some form of timber harvest from 1978 to 2007, 39% was harvested between the first (1980s) and second (1990s) series of marten surveys, when marten occupancy rates decreased the most (Fig. 5A). Approximately 70% of the predicted marten habitat loss during the study period occurred within the boundaries of timber harvest units (Fig. 5B).

DISCUSSION

The average percent of survey stations with marten detections in our recent surveys (4%) was markedly lower than in surveys conducted in the 1980s (65%). This suggests a substantial decline in the number of martens at SEF in the span of 28 yr. Similar declines in marten populations have been inferred from reduced geographic distributions at other locations in the Sierra Nevada and Cascade mountain ranges of California (Zielinski et al. 2005, Kirk and Zielinski 2009). The apparent decline of martens at SEF is of particular concern considering that this area was historically considered a marten stronghold by trappers (Grinnell et al. 1937) and was chosen as a study site for several early research projects because of the high density of martens (Spencer 1981, Zielinski 1981, Martin 1987). There are a number of possible explanations for this decline, including habitat loss, increased habitat fragmentation, and synergistic effects related to habitat change as discussed below.

The most noticeable decline in marten detections at SEF occurred between 1983 and 1990. During that period, 39% of the forested habitat in SEF experienced some form of timber harvest, including 11% harvested with clear-cut or shelter-

Table 5. Estimated amount and configuration of high-quality American marten (*Martes americana*) habitat in 1978 and 2007 at Sagehen Experimental Forest, California. We presented data separately for the lower and upper watersheds (below and above the 2,050 m elevation contour). Standard errors for patch metrics are in parentheses.

	Lower watershed		Upper watershed	
Variable name	1978	2007	1978	2007
Percentage of landscape (PLAND)	16.8	15.2	32.9	23.1
Number of patches (NP)	15	9	17	15
Largest patch index (LPI)	6.6	8.7	22.58	13.3
Percent cover of core areas (CPLAND)	3.6	2.53	10.51	6.22
Number of distinct core areas (NDCA)	9	9	24	15
Mean patch area (AREA_MN), ha	16.5 (3.0)	24.7 (6.3)	48.7 (32.6)	38.1 (23.5)
Area weighted core area (CORE_AM), ha	15.7 (13.9)	18.8 (17.5)	146.3 (143.7)	76.7 (66.3)
Area weighted distinct core area (DCORE_AM), ha	22.3 (14.1)	18.2 (13.2)	62.1 (58.1)	39.5 (36.4)
Proximity mean index (PROX_MN)	42.2 (27.6)	20.3 (7.8)	326.1* (101.6)	92.6* (35.2)
Area weighted gyration (GYRATE_AM)	348.4 (23.4)	614.5 (31.7)	932.0 (70.4)	785.9 (45.8)
Mean nearest neighbor distance (ENN)	254.7 (84.1)	236.5 (82.2)	144.7 (21.4)	208.8 (78.1)

* Statistically significant with $P \leq 0.05$.

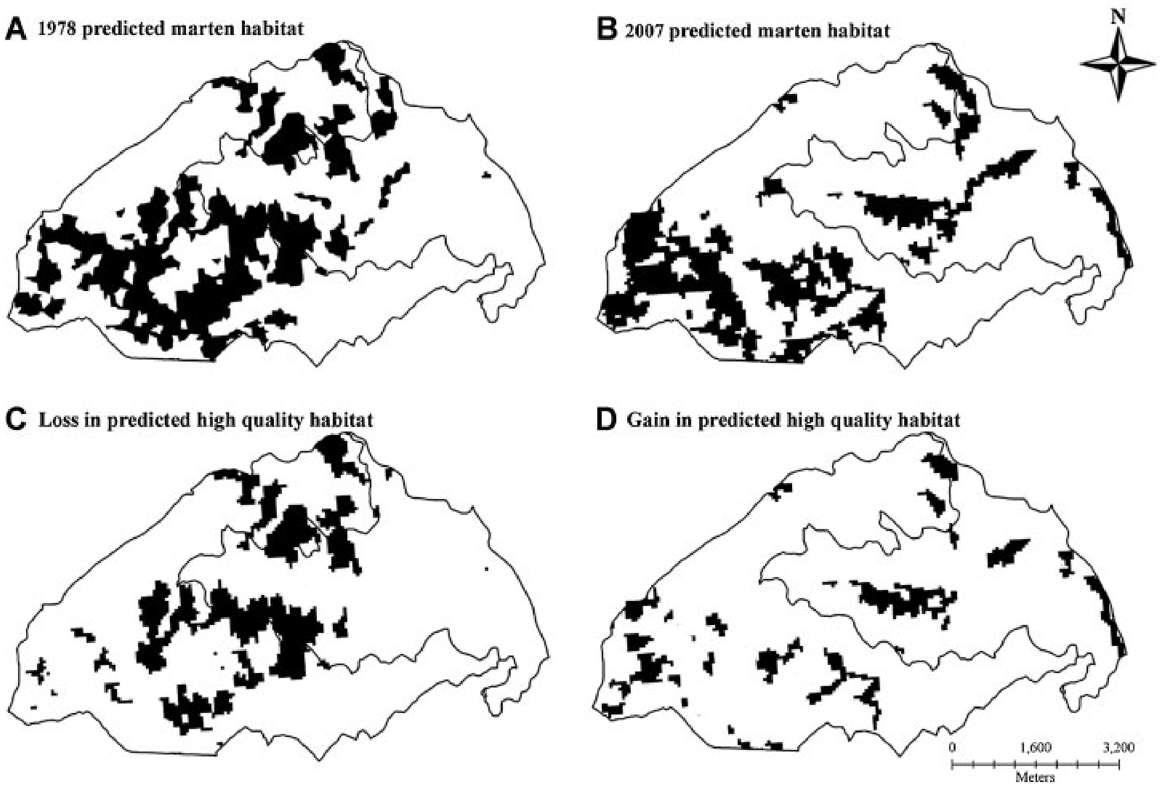

Figure 4. Predicted high-quality American marten (*Martes americana*) reproductive habitat at Sagehen Experimental Forest, California in 1978 (A) and 2007 (B). The loss of predicted habitat (C) and the gain of predicted habitat (D) are changes that occurred during 1978–2007. Predicted habitat was based on modified habitat definitions in the California Wildlife Habitat Relationship model (2006). The upper watershed is west of the 2,050 m contour line within the study area outline.

wood methods and 28% harvested with salvage sales (Fig. 5). As a result, we estimated that the percent cover of high-quality marten habitat in SEF declined from approximately 27% in 1978 to 15% by 1990. A number of other studies suggest that martens tend to disappear from an area after the percent of total forest cover is reduced below 45–75% (Hargis et al. 1999, Potvin et al. 2000, Fuller 2006, Webb and Boyce 2009). Sagehen Experimental Forest currently falls within this range as 42% of the marten habitat in SEF changed from a suitable to unsuitable class from 1978 to 2007. However, this estimate of the amount of habitat available to martens at SEF may be more conservative than in previous studies because we evaluated the change in high-quality reproductive habitat rather than the change in total forest cover.

Because martens avoid openings and are less abundant in landscapes with $\leq$65% forest cover (Hargis et al. 1999, Potvin et al. 2000), we predicted that loss of high-quality habitat in SEF would negatively affect marten occupancy. The total amount of habitat may not be the most important variable affecting the occurrence of martens. Instead, landscape attributes such as the size of patch core areas, distance between patches, spatial configuration of patches, and microhabitat features within patches may be more important (Hargis et al. 1999, Minta et al. 1999).

Our habitat configuration metrics were similar in the lower watershed in both 1978 and 2007 so it is surprising that we detected few martens there in the 2007–2008 surveys. Surveys in the lower watershed in the 1980s indicated that martens primarily selected for vegetation with high ground cover by downed wood and high basal area, especially in lodgepole pine stand (Martin 1987). Our habitat maps did not include ground cover by downed wood, so we could not evaluate this variable in our analysis.

In the upper watershed at SEF, significant reductions in marten habitat occurred between 1983 and 1990, and habitat loss caused by forest cutting has continued since then, albeit at a lower annual rate. Insofar as this management creates openings and reduces the amount of marten habitat, even small openings >50 m will likely negatively affect the use of the area by martens (Hargis and McCullough 1984, Payer and Harrison 1999, Heinemeyer 2002). In SEF, the loss of high-quality marten habitat in the upper watersheds, especially to the north and south of the lower watershed, may explain the loss of detections in the lower watershed both by reducing the total amount of available marten habitat and by increasing the distance between patches. In forests fragmented by clear cuts, martens tend to have larger home ranges and the amount of overlap between male and female home ranges is reduced, possibly limiting breeding opportunities (Payer et al. 2004). We suspect that the reduction of core habitat and the increase of patch distance at SEF may have exceeded the threshold for martens to persist year round.

We detected martens in winter 2007–2008 but not in summer of 2007 or during our limited surveys in the summer of 2008. Although our surveys and recent studies suggest that

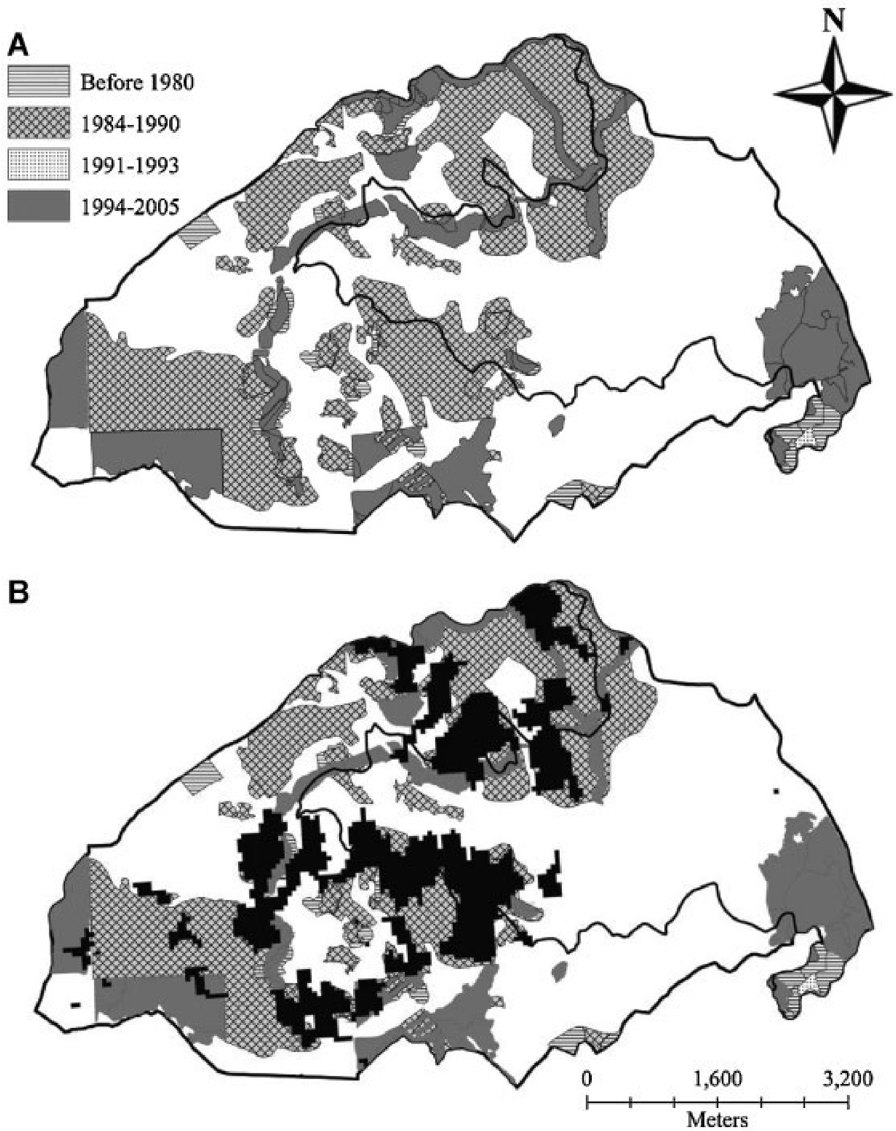

Figure 5. Locations of previous timber harvest activities (A) and the amount of predicted American marten (*Martes americana*) habitat loss, as shown in black, (B) in Sagehen Experimental Forest and vicinity, California in the interval from 1978 to 2007. Harvest information only included activities from 1972 to 2005. Geographic Information System (GIS) data were from the Tahoe National Forest Fire History Layer and East Side Disturbance Layer. The upper watershed is west of the 2,050 m contour line within the study area outline.

detection probabilities of martens may be highest during winter (W. J. Zielinski, USDA Forest Service, unpublished report), data from previous surveys at SEF are inconsistent in this regard. For example, there were fewer detections per unit effort in the snow seasons in 1992 and 2008 than in the snow-free seasons of 1991 and 1993, the only years for which detection histories were available (Table 2). The detection probability during the snow-free season in 1991 and 1993 was 100% and the per-visit probability of detection ranged from 78% to 83%. We expected more detections during our recent survey in the winter months due to juvenile dispersal (Broquet et al. 2006) and higher energetic requirements (hence more movement) in the fall and winter (Gilbert et al. 2009). However, we were not able to assess seasonal differences in the probability of detection because we did not detect any martens during the snow-free period in either 2007 or 2008. The lack of marten detections during summer in our contemporary surveys may be because martens detected in winter were dispersing individuals and not residents (Bull and Heater 2001, Broquet et al. 2006). If the detected individuals in winter were dispersing juveniles, we suspect they either did not reside in SEF during the snow-free months or may not have survived the winter. The influence of winter mortality and seasonal differences in detectability of martens need to be investigated with radio-collared animals to better understand why we detected martens in winter but not in summer.

Although it is unclear why martens are less common in SEF then they were in the 1980s, our findings are consistent with other large-scale contemporary surveys conducted throughout the Cascades and Sierra Nevada mountain ranges that suggest declining marten populations (Zielinski et al. 2005). There are a number of possible contributing factors; one of which is the amount of timber harvest in SEF. Areas with the greatest habitat loss, and the most resulting fragmentation were also areas affected by ≥ 1 forms of timber harvest. Clear cut and shelterwood harvests remove the most habitat, but selection and salvage logging of dead and dying trees can disproportionately reduce the availability of denning and resting structures (Martin 1987, Spencer 1987). Timber harvests that removed woody material and reduced understory complexity may affect habitat for marten prey and reduce the ability of martens to forage effectively (Sherburne and Bissonette 1994, Andruskiw et al. 2008). Sherburne and Bissonette (1994) reported martens foraged in areas with an average of 25% coarse woody material. Similarly, Andruskiw et al. (2008) concluded that martens are less likely to effectively encounter, attack, and kill prey in regenerating stands than in older uncut stands. Forest practices that decrease escape cover or increase the visibility of martens could also increase the risk of predation on marten (Hargis and McCullough 1984, Drew 1995). The combination of direct effects of forest fragmentation on habitat use by martens and indirect effects of harvest and thinning on resting sites, prey availability, and predator avoidance are the most likely cause for the reduction in occupancy of martens that occurred at SEF from 1978 to 2008.

We considered the possibility that climate change may have played a role in the decline of martens at SEF. Recent studies indicate that the climate is changing at a faster rate than previously expected (Cole 2010, Lawler et al. 2010), and SEF is located on the relatively xeric east side of the Sierra where vegetation may be disproportionately affected by change in climate (vanMatgem et al. 2009). In this region, martens reside primarily at high elevations where other species associated with boreal forests, such as the American pika (*Ochotona princeps*), also appear to be declining (Moritz et al. 2008, Beever et al. 2010). However, we believe that it is unlikely that climate change significantly affected vegetation or marten numbers during the 8-yr period (1983–1990) when we documented the period of most substantial change in marten occupancy. The decline in marten detections occurred over a relatively short period, too quickly to have been affected by the effect of climate on vegetation characteristics that are important to martens. Furthermore, the period between 1961 and 1990, encompassing the period when marten occupancy changed the most, is considered a reference period with normal climate variability (Hayhoe et al. 2004, Lawler et al. 2009).

Our study included some methodological issues that need to be considered in evaluating the results. First, we could not evaluate the accuracy of our vegetation maps in respect to all vegetation attributes used to characterize marten habitat. Based on related work, we expected 78–94% correct classification for tree size, canopy cover, and stand type. Most of the error was attributable to automatic assignment of stand type. Because we applied the same classification algorithms to both datasets (1978 and 2007), we do not believe that the accuracy issue affected our conclusions. We also used a slightly different grid to sample martens than in previous studies on SEF. However, both grids sampled the same area, and the difference in distance between stations was small relative to the typical home range size of martens. Thus, we do not think differences in spacing of sampling stations in our grid and the previous grid should have influenced our results. Lastly, we combined detection histories for all survey methods in winter 2007–2008, which meant that we could not estimate the probability of detection for snow-tracking. Probability of detection is similar between track plates, remote cameras, and hair snares (O'Connell et al. 2006). Snow-tracking within 24–96 hr after a snowstorm is an effective survey method for martens (Robitaille and Aubry 2000, Forsey and Baggs 2001, Mowat 2006) and undoubtedly increased our likelihood of detecting martens if they were present. Survey duration, number of stations sampled, and number of station days sampled in our study was as high or higher, than in previous surveys at SEF (Table 3). Therefore, despite the variation in station spacing and multiple methods, we believe that our ability to detect martens that were present was equal to or higher than in previous studies.

MANAGEMENT IMPLICATIONS

Our results and the results of several previous studies of martens suggest that marten detections may be positively associated with contiguous patches of late-seral and dense forest. We documented a substantial reduction in marten detections and suitable marten habitat on SEF. Future management plans for SEF include the removal of forest fuels in the form of systematically placed area treatments (SPLATs; Finney 1999). Although this strategy, if applied properly, may protect remaining fragments of marten habitat from loss due to fire, these treatments can also reduce canopy cover and ground cover by dead wood, and potentially increase fragmentation of residual habitat even further. Thus, although we agree that fuels treatments may be necessary to reduce the risk or severity of wildfire, we also believe that the retention of habitat for sensitive species such as martens should be a high priority (Forman and Collinge 1996, North et al. 2009). We suggest 3 strategies that may increase the likelihood of marten persistence in SEF. First, managers should consider retaining the remaining contiguous large patches of predicted marten reproductive habitat, both in the lower watershed near riparian corridors and in the true fir-dominated stands in the upper watershed. Second, corridors of dense, late-seral forest should be retained among thinned areas to reduce distances between patches of closed canopy forest and facilitate movement of martens and other cover-dependent species among patches. Lastly we suggest that managers strive for a silvicultural paradigm that retains large snags, diverse tree structure, large downed woody material, and patches of decadent trees as potential resting and denning habitat for martens, as suggested by most previous researchers who have studied martens in California (Spencer 1987, Martin and Barrett 1991, Slauson and Zielinski 2009).

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LITERATURE CITED

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

Barbour, M. G., T. Keeler-Wolf, A. A. Schoenherr, editors. 2007. Terrestrial vegetation of California. University of California Press, Berkeley, USA.

Barrett, R. H. 1983. Smoked aluminum track plots for determining furbearer distribution and relative abundance. California Fish and Game 69:188–190.

Beauvais, G. P., and S. W. Buskirk. 1999. An improved estimate of trail detectability for snow-trail surveys. Wildlife Society Bulletin 27:32–38.

Beever, E. A., C. Ray, P. W. Mote, and J. L. Wilkening. 2010. Testing alternative models of climate-mediated extirpations. Ecological Applications 20:164–178.

Bissonette, J. A., D. J. Harrison, C. D. Hargis, and T. G. Chapin. 1997. The influence of spatial scale and scale-sensitive properties on habitat selection by American marten. Pages 368–385 *in* J. A. Bissonette, editor. Wildlife and landscape ecology: effects of pattern and scale. Springer-Verlag, New York, New York, USA.

Brohman, R. J., and L. D. Bryant. 2005. Existing vegetation classification and mapping technical guide. USDA Forest Service, General Technical Report WO-97, Albany, California, USA.

Broquet, T., N. Ray, E. Petit, J. M. Fryxell, and F. Burel. 2006. Genetic isolation by distance and landscape connectivity in the American marten (*Martes americana*). Landscape Ecology 21:877–889.

Bull, E. L., and T. W. Heater. 2001. Home range and dispersal of the American marten in northeastern Oregon. Northwestern Naturalist 82:7–11.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and inference: a practical information–theoretic approach. Springer-Verlage, New York, New York, USA.

CalVeg [ESRI personal geodatabase]. 2004. CALVEG accuracy tables for Tahoe National Forest. <http://www.fs.fed.us/r5/rsl/projects/mapping/accuracies/aa-tnf.html>. Accessed 19 Oct 2010.

Chapin, T. G., D. J. Harrison, and D. D. Katnik. 1998. Influence of landscape pattern on habitat use by American marten in an industrial forest. Conservation Biology 12:1327–1337.

Cole, K. L. 2010. Vegetation response to early holocene warming as an analog for current and future changes. Conservation Biology 24:29–37.

California Wildlife Habitat Relationships (CWHR). 2006. California Wildlife Habitat Relationships 8.1. California Department of Fish and Game, Sacramento, USA.

Drew, G. S. 1995. Winter habitat selection by American marten (*Martes americana*) in Newfoundland: why old growth? Dissertation, Utah State University, Logan, USA.

Finney, M. A. 1999. Mechanistic modeling of landscape fire patterns. Pages 186–209 *in* D. J. Mlandenoff and W. L. Baker, editors. Spatial modeling of forest landscapes: approaches and applications. Cambridge University Press, Cambridge, United Kingdom.

Foody, G. M. 2002. Status of land cover classification accuracy assessment. Remote Sensing of Environment 80:185–201.

Forman, R. T., and S. K. Collinge. 1996. The spatial solution to conserving biodiversity in landscapes and regions. Pages 537–568 *in* R. M. DeGraff and R. I. Miller, editors. Conservation of faunal diversity in forested landscapes. Chapman and Hall, London, UK.

Forsey, E. S., and E. M. Baggs. 2001. Winter activity of mammals in riparian zones and adjacent forests prior to and following clear-cutting at Copper Lake, Newfoundland, Canada. Forest Ecology and Management 145: 163–171.

Fuller, A. K. 2006. Multi-scalar responses of forest carnivores to habitat and spatial pattern: case studies with Canada lynx and American martens. Dissertation, University of Maine, Orono, USA.

Gilbert, J. H., P. A. Zollner, A. K. Green, J. L. Wright, and W. H. Karasov. 2009. Seasonal field metabolic rates of American martens in Wisconsin. American Midland Naturalist 162:327–334.

Green, R. E. 2007. Distribution and habitat associations of forest carnivores and an evaluation of the California Wildlife Habitat Relationships model for American marten in Sequoia and Kings Canyon National Parks. Thesis, Humboldt State University, Arcata, California, USA.

Grinnell, J., J. S. Dixon, and J. M. Linsdale. 1937. Fur-bearing mammals of California. University of California Press, Berkeley, USA.

Gustafson, E. J., and G. R. Parker. 1992. Relationships between landcover proportion and indicies of landscape spatial pattern. Landscape Ecology 7:101–110.

Halfpenny, J. C., R. W. Thompson, S. C. Morse, T. Holden, and P. Rezendes. 1995. Snowtracking. Pages 91–124 *in* W. J. Zielinski and T. E. Kucera, editors. American marten, fisher, lynx and wolverine: survey methods for their detection. USDA Forest Service, General Technical Report, PSW-GTR-157, Albany, California, USA.

Hargis, C. D., J. A. Bissonette, and D. L. Turner. 1999. The influence of forest fragmentation and landscape pattern on American martens. Journal of Applied Ecology 36:157–172.

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

Hayhoe, K., D. Cayan, C. B. Field, P. C. Frumhoff, E. P. Maurer, N. L. Miller, S. C. Moser, S. H. Schneider, K. N. Cahill, E. E. Cleland, L. Dale, R. Drapek, S. C. Sheridan, and J. H. Verville. 2004. Emission pathways, climate change, and impacts on California. Proceedings of the National Academy Sciences of the United States of America 101:12422–12427.

Heinemeyer, K. S. 2002. Translating individual movements into population patterns: American marten in fragmented forested landscapes. Dissertation, University of California, Santa Cruz, USA.

Kendall, K. C., and K. S. McKelvey. 2008. Hair collection. Pages 135–176 *in* R. A. Long, P. MacKay, J. C. Ray, and W. J. Zielinski, editors. Noninvasive survey methods for North American carnivores. Island Press, Washington, D.C., USA.

Kirk, T. A., and W. J. Zielinski. 2009. Developing and testing a landscape habitat suitability model for the American marten (*Martes americana*) in the Cascades mountains of California. Landscape Ecology 24:759–773.

Lawler, J. J., S. L. Shafer, B. A. Bancroft, and A. R. Blaustein. 2010. Projected climate impacts for amphibians of the western hemisphere. Conservation Biology 24:38–50.

Lawler, J. J., S. L. Shafer, D. White, P. M. Kareiva, E. P. Maurer, A. R. Blaustein, and P. J. Bartlein. 2009. Projected climate-induced faunal change in the Western Hemisphere. Ecology 90:588–597.

Leitão, A. B., J. Miller, J. Ahern, and K. McGarigal. 2006. Measuring landscapes: a planner's handbook. Island Press, Washington, D.C., USA.

Long, R. A., T. M. Donovan, P. MacKay, W. J. Zielinski, and J. S. Buzas. 2007. Comparing scat detection dogs, cameras, and hair snares for surveying carnivores. Journal of Wildlife Management 71:2018–2025.

MacKenzie, D. I., H. T. Nichols, J. A. Royal, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Elsevier, Boston, Massachusetts, USA.

Martin, S. K. 1987. Ecology of the pine marten (*Martes americana*) at Sagehen Creek, California. Dissertation, University of California, Berkeley, USA.

Martin, S. K., and R. H. Barrett. 1991. Resting site selection by marten at Sagehen Creek, California. Northwestern Naturalist 72:37–42.

Mayer, K. E., and W. F. Laudenslayer. 1988. A guide to the wildlife habitats of California. California Department of Forestry and Fire Protection, Sacramento, California, USA.

McGarigal, K., S. A. Cushman, M. C. Neel, and E. Ene. 2002. FRAGSTATS: spatial pattern analysis program for categorical maps. University of Massachusetts, Amherst, USA.

Minta, S. C., P. M. Kareiva, and A. P. Curlee. 1999. Carnivore research and conservation: learning from history and theory. Pages 323–404 *in* T. W. Clark, A. P. Curlee, S. C. Minta, and P. M. Kareiva, editors. Carnivores in ecosystems: the Yellowstone experience. Yale University Press, London, UK.

Moritz, C., J. L. Patton, C. J. Conroy, J. L. Parra, G. C. White, and S. R. Beissinger. 2008. Impacts of a century of climate change on small-mammal communities in Yosemite National Park, USA. Science 322:261–264.

Mowat, G. 2006. Winter habitat associations of American martens *Martes americana* in interior wet-belt forests. Wildlife Biology 12:515–561.

North, M., P. Stine, K. O'Hara, W. J. Zielinski, and S. Stephens. 2009. An ecosystem management strategy for Sierran mixed conifer forests. USDA Forest Service, General Technical Report, PSW-GTR-220, Albany, California, USA.

O'Connell, A. F., N. W. Talancy, L. L. Bailey, J. R. Sauer, R. Cook, and A. T. Gilbert. 2006. Estimating site occupancy and detection probability parameters for meso- and large mammals in a coastal ecosystem. Journal of Wildlife Management 70:1625–1633.

Parker, I., and W. Matayas. 1979. CALVEG: a classification of California vegetation. USDA Forest Service, San Francisco, California, USA.

Payer, D. C., and D. J. Harrison. 1999. Influence of timber harvesting and trapping on habitat selection and demographic characteristics of marten. Final contract report to Maine Department of Inland Fisheries and Wildlife. University of Maine, Orono, USA. <http://library.umaine.edu/cfru/pubs/CFRU281.pdf>. Accessed 17 Feb 2011.

Payer, D. C., D. J. Harrison, and D. M. Phillips. 2004. Territoriality and home-range fidelity of American martens in relation to timber harvesting and trapping. Pages 99–114 *in* D. J. Harrison, A. K. Fuller, and G. Proulx, editors. Martens and fishers (*Martes*) in human-altered environments: an international perspective. Springer Science, New York, New York, USA.

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

Powell, R. A. 1994. Structure and spacing of Martes populations. Pages 101–121 *in* S. W. Buskirk, A. S. Harestad, M. G. Raphael, and R. A. Powell, editors. Martens, sables, and fishers: biology and conservation. Cornell University Press, Ithaca, New York, USA.

Ramsey, F. L., and D. W. Schafer. 2002. The statistical sleuth: a course in the methods of data analysis. Second edition. Duxbury, Pacific Grove, California, USA.

Ray, J. C., and W. J. Zielinski. 2008. Track stations. Pages 45–109 *in* R. A. Long, P. MacKay, W. J. Zielinski, and J. C. Ray, editors. Noninvasive survey methods for carnivores. Island Press, Washington, D.C., USA.

Riddle, A. E., K. L. Pilgrim, L. S. Mills, K. S. McKelvey, and L. F. Ruggiero. 2003. Identification of mustelids using mitochondrial DNA and non-invasive sampling. Conservation Genetics 4:241–243.

Robitaille, J. F., and K. Aubry. 2000. Occurrence and activity of American martens *Martes americana* in relation to roads and other routes. Acta Theriologica 45:137–143.

Savage, W. 1973. Annotated check list of vascular plants of Sagehen Creek drainage basin, Nevada County, California. Madrono 22:115–139.

Schwartz, M. K., and S. L. Monfort. 2008. Genetic and endocrine tools for carnivore surveys. Pages 238–262 *in* R. A. Long, P. MacKay, W. J. Zielinski, and J. C. Ray, editors. Noninvasive survey methods for carnivores. Island Press, Washington, D.C., USA.

Sherburne, S. S., and J. A. Bissonette. 1994. Marten subnivean access point use: response to subnivean prey levels. Journal of Wildlife Management 58:400–405.

Simon, T. L. 1980. Ecological study of the marten in the Tahoe National Forest, California. Thesis, California State University, Sacramento, USA.

Slauson, K. M., and W. J. Zielinski. 2009. Characteristics of summer and fall diurnal resting habitat used by American martens in coastal northwestern California. Northwest Science 83:35–45.

Smith, D. M., B. C. Larson, M. J. Kelty, and P. M. Ashton. 1997. The practice of silviculture: applied forest ecology. Ninth edition. John Wiley and Sons, Inc., New York, New York, USA.

Spencer, W. D. 1981. Pine marten habitat preferences at Sagehen Creek, California. Thesis, University of California, Berkeley, USA.

Spencer, W. D. 1987. Seasonal rest-site preferences of pine martens in the northern Sierra Nevada. Journal of Wildlife Management 51:616–621.

Spencer, W. D., R. H. Barrett, and W. J. Zielinski. 1983. Marten habitat preferences in the northern Sierra Nevada. Journal of Wildlife Management 47:1182–1186.

Strickland, M. A., and R. J. Douglas. 1987. Marten. Pages 530–547 *in* M. Novak, J. A. Baker, M. E. Obbard, and B. Malloch, editors. Wild furbearers management and conservation in North America. Ontario Ministry of Natural Resources, Toronto, Canada.

Tyre, A. J., B. Tenhumberg, S. A. Field, D. Niejalke, K. Parris, and H. P. Possingham. 2003. Improving precision and reducing bias in biological surveys: estimating false-negative error rates. Ecological Applications 13:1790–1801.

Vaillant, N. M. 2008. Sagehen Experimental Forest past, present, and future: an evaluation of the finished assessment process. Dissertation, University of California, Berkeley, USA.

vanMatgem, P. J., N. L. Stephenson, J. C. Byrne, L. D. Daniels, J. F. Franklin, P. Z. Fule, M. E. Harmon, A. J. Larson, J. M. Smith, A. H. Taylor, and T. T. Veblen. 2009. Widespread increase of tree mortality rates in the western United States. Science 323:521–524.

Webb, S. M., and M. S. Boyce. 2009. Marten fur harvests and landscape change in West-Central Alberta. Journal of Wildlife Management 73: 894–903.

West, C. I. 1982. Management options for the Sagehen Creek Basin. Thesis, University of California, Berkeley, USA.

Wu, J. 2004. Effects of changing scale on landscape pattern analysis: scaling relations. Landscape Ecology 19:125–138.

Zielinski, W. J. 1981. Food habits, activity patterns and ectoparasites of the pine marten at Sagehen Creek, California. Thesis, University of California, Berkeley, USA.

Zielinski, W. J., K. M. Slauson, and A. E. Bowles. 2008. Effects of off-highway vehicle use on the American marten. Journal of Wildlife Management 72:1558–1571.

Zielinski, W. J., R. L. Truex, F. V. Schlexer, L. A. Campbell, and C. Carroll. 2005. Historical and contemporary distributions of carnivores in forests of the Sierra Nevada, California, USA. Journal of Biogeography 32:1385–1407.

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