



Original research article

Landscape conditions and elevation interact to influence the distribution and density of state-endangered Humboldt martens

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ARTICLE INFO

Keywords:

Endangered species
Forest heterogeneity
Non-invasive sampling
Martes
Pacific marten
Spatial capture-recapture
Threatened species

ABSTRACT

Estimating population demographic parameters and habitat relationships is central to recovery planning for imperiled species. These parameters and relationships are often unavailable for rare and elusive species but are necessary to inform their conservation and management. The Humboldt marten (*Martes caurina humboldtensis*) is a subspecies of the Pacific marten that was historically distributed in coastal forests in California and Oregon, was extirpated from more than 95 % of its historical distribution, and is listed as endangered in California and federally listed as threatened. To better understand their distribution, abundance, and habitat relationships in northwestern California, we non-invasively surveyed for Humboldt martens and fit an integrated spatial capture-recapture model to estimate their abundance and density, and a post-hoc generalized linear model to evaluate the influence of landscape and forest conditions within different elevation bands on marten density. We estimated a posterior median density (95 % credible interval) of 0.276 (CRI 0.183–0.364) martens per 1 km² and a posterior median abundance of 111 (CRI 73–146) martens within our 399 km² study area. Our results suggest that marten density was heterogeneous and influenced by topographic position, ladder fuel density, and diameter diversity index and these effects varied by elevation across a 399 km² portion of the 1580 km² North Coastal California Extant Population Area. Our estimates of marten density and abundance establish a baseline for this endangered population and will inform future monitoring to estimate apparent survival and recruitment, additional relationships to environmental conditions and change, and demographic trends over time.

1. Introduction

The recovery of imperiled populations often depends on conservation and management decisions informed by baseline demographic parameters (e.g., abundance, population density) and habitat relationships (Grace et al., 2021; Hoekstra et al., 2002; Lawler et al., 2002). Species of conservation concern often exist as imperiled populations of a widely-distributed species or as endemic species limited to small geographic areas (Margules and Pressey, 2000; Schwartz, 2008). Small, isolated populations are particularly

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vulnerable to extirpation due to stochastic shifts in environmental conditions, demographic parameters, and genetic degradation (Lande, 1993, Frankham, 2005). Therefore, recovery of imperiled populations is often directly linked to environmental conditions and the availability of resources (Kerr and Deguise, 2004). While not a perfect proxy for quality (Van Horne, 1983), population density is often related to environmental conditions and resource availability and is often interpreted as an indicator of population status (Santini et al., 2018). Thus, an examination of density-habitat relationships allows managers to interpret population-level responses to the environment and identify habitat conditions that support those populations (Matthiopoulos et al., 2015; Veloz et al., 2015). This information can then inform recovery strategies (e.g., habitat restoration, predator reduction, assisted dispersal) for species of conservation concern (Hoekstra et al., 2002).

Forest-dependent species rely on the spatial configuration (e.g., patch size, edge density) and structural components (e.g., cavities, large downed woody debris) of forests to acquire food, avoid antagonistic interactions, reproduce, and raise offspring (North et al., 2000; Martin et al., 2019; Jensen et al., 2023). Stochastic disturbance events (e.g., wildfire) and forest management practices (e.g., selective logging, clear cutting) alter forest conditions and the availability of resources while creating heterogeneity in the landscape (McRae et al., 2001; Venier et al., 2014). When forest conditions are altered, the response of forest-dependent wildlife populations varies depending on the severity of change. For example, high-severity wildfire and post-fire salvage logging can negatively affect population demographics of forest-dependent species (e.g., Rockweit et al., 2017; Green et al., 2022). Similarly, the abundance of many forest-dependent species is lower in fragmented forest patches compared to intact patches (Pfeifer et al., 2017). However, heterogeneous landscapes with moderate levels of disturbance can support relatively high densities of avian populations (Cushman and McGarigal, 2003; Taillie et al., 2018) and many carnivore species use mosaics of late seral, regenerating, and recently harvested forest patches (Scrafford et al., 2017; Holbrook et al., 2018; Parsons et al., 2019). Forested landscapes managed with harvest practices that mimic mixed-severity disturbance events tend to have greater prey abundance and availability compared to more homogenous forests,

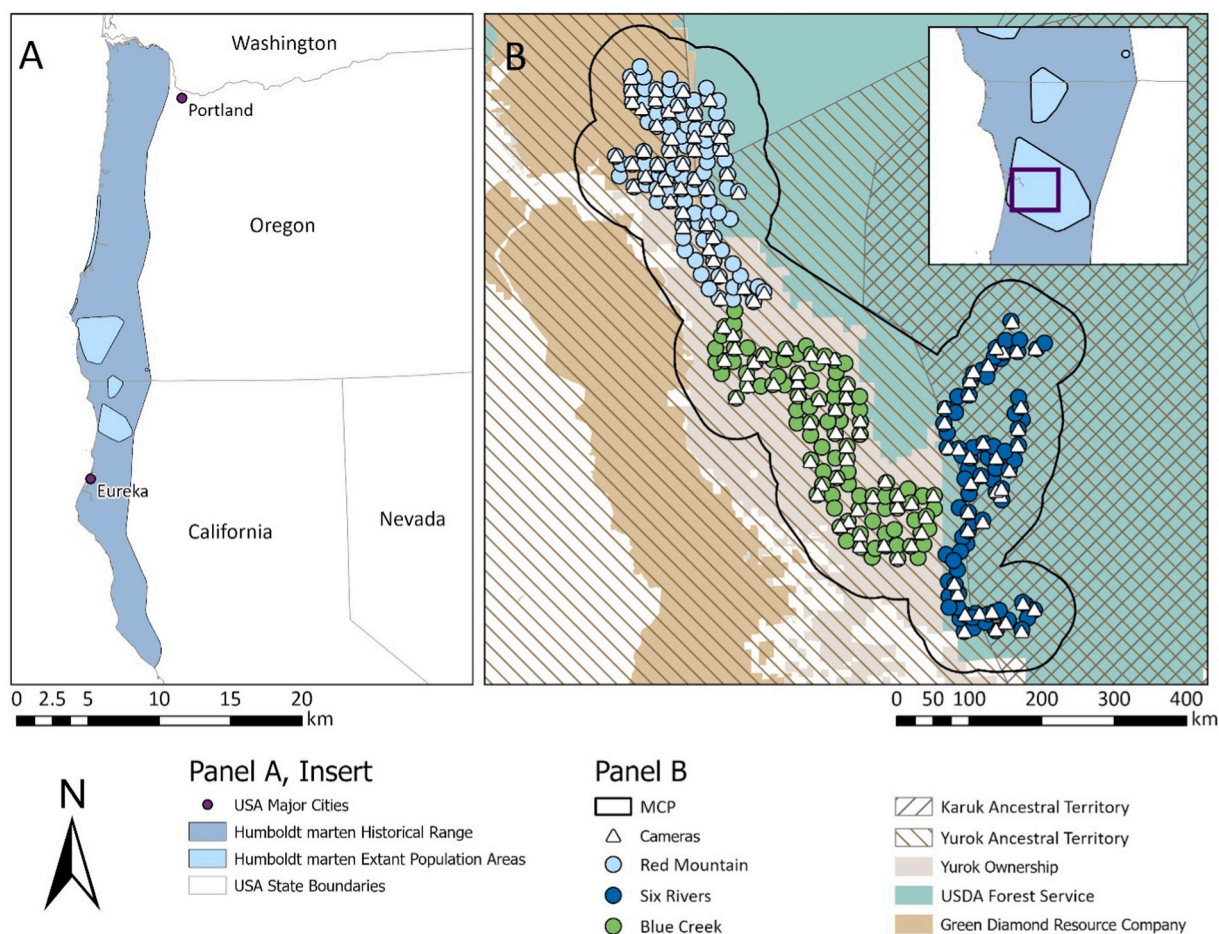


Fig. 1. (A) The historical distribution of Humboldt marten (dark blue) and the four Extant Population Areas (light blue) with North Coastal California being the most southern EPA. (B) The study area in northern California, USA and distribution of sampling sites across each land ownership within the sampling area. Circles represent hair snares (green = Blue Creek, dark blue = Six Rivers, light blue = Red Mountain), and white triangles represent remote cameras. The black solid line represents the MCP around sampling sites buffered by 2160 m in which the post-hoc GLM was performed.

thereby decreasing the energy expenditure needed for carnivores to acquire food and increase fitness (Holbrook et al., 2019; Zulla et al., 2023). These observations indicate that landscape heterogeneity provides a balance of resources (e.g., food, cover, rest sites) to support wildlife populations (Holbrook et al., 2019; Parsons et al., 2019). Given the varied effects of altered forest conditions on wildlife populations, identifying structural characteristics that support forest-dependent species of conservation concern across managed and heterogeneous landscapes is essential to promote population recovery.

Martens (*Martes* spp.) in North America are small-bodied and cryptic meso-carnivores often associated with late-successional forests and heterogeneous, structurally complex vegetation (Proulx et al., 2005). Martens generally select forest stands with greater than 50 % canopy cover and an abundance of large diameter trees, snags, and hollow logs which provide structure for resting and denning (Bull et al., 2005; Delheimer et al., 2023). Structural complexity with coarse woody debris improves hunting efficiency and success for martens (Bull et al., 2005; Andruskiw et al., 2008) and decreases mortality risk by providing escape cover from predators and competitors (M. Smith et al., 2022). In many areas, martens will preferentially use undisturbed and unharvested forest stands (Soutiere, 1979; Bull et al., 2005; Cushman et al., 2011; Moriarty et al., 2015). Martens often respond negatively to fragmented habitats and open areas (Hargis et al., 1999; Cushman et al., 2011). Snow cover, however, can facilitate movement through open areas and increase connectivity between forested areas by limiting the movement of larger carnivores and reducing intraguild competition and predation (Moriarty et al., 2015). Martens are territorial, typically exhibiting low tolerance of conspecifics outside of breeding and kit-rearing (e.g., Moriarty et al., 2017). However, marten abundance and density are highly variable among populations and are often linked to resource quality and forest conditions (e.g., Fryxell et al., 1999; Clare et al., 2019). Given their specific habitat requirements and sensitivity to disturbances, martens are often the subject of conservation concern in North America (Proulx et al., 2005).

The Humboldt marten (*M. caurina humboldtensis*) is a subspecies of the Pacific marten that was historically distributed in coastal forests from north coastal Oregon to the Sonoma Valley of northern California (Fig. 1; U.S. U.S. U.S. Fish Wildlife Service., 2019), Schwartz et al., (2020)). After decades of unsustainable fur trapping and habitat loss from commercial timber harvest (Grinnell and Dixon, 1926; Twining and Hensley, 1947), Humboldt martens were thought to be extirpated until they were detected during carnivore monitoring efforts in 1996 (Zielinski and Golightly, 1996; Zielinski et al., 2001). The Humboldt marten is listed as endangered by the state of California (California Fish and Game Commission, 2019) and the analogous “Coastal Distinct Population Segment” of Pacific martens is listed as federally threatened by the U.S. U.S. U.S. Fish Wildlife Service., 2019). As part of the listing process, the U.S. Fish and Wildlife Service identified four small and isolated Extant Population Areas (U.S. U.S. U.S. Fish Wildlife Service., 2019; Fig. 1). Humboldt martens continue to be threatened by the loss of structurally-complex, mature forests driven by commercial timber harvest, drought-induced tree mortality, insect outbreaks, and increasing wildfire frequency and severity (Slauson et al., 2019a, U.S. U.S. U.S. Fish Wildlife Service., 2019). Despite continued conservation concern over the last three decades, little is currently known about the distribution and demography of Humboldt martens and how forest conditions influence their distribution and density (Martin et al., 2022a). Understanding baseline population parameters and population-level responses to forest characteristics and management practices is necessary to support Humboldt marten conservation in an increasingly dynamic and heterogeneous landscape.

Our objectives herein were to 1) estimate the abundance and density of Humboldt martens in a portion of the 1580 km² North Coastal California Extant Population Area, and 2) evaluate the influence of landscape and forest conditions at two elevation bands on patterns of Humboldt marten (hereafter, “marten”) density. In structurally and topographically heterogeneous coastal forests, martens exhibit unique habitat relationships and often occur in low-elevation forests and riparian areas with structural complexity (Moriarty et al., 2021; Gamblin et al., 2025). We predicted marten density would be positively associated with structural heterogeneity (i.e., understory vegetation cover, tree size) and the relationship with local topography (e.g., prominent peaks, riparian drainages) would vary by elevation due to differences in vegetation structure and composition. We compared our estimates of Humboldt marten density and relationships to landscape conditions with those of other marten populations in North America and provide recommendations for future research to address persisting knowledge gaps in Humboldt marten ecology that can inform recovery and conservation efforts.

2. Materials & methods

2.1. Study area

Our surveys occurred across 399 km² of the North Coastal California Extant Population Area (hereafter, population area), designated by the U.S. Fish and Wildlife Service as one of four extant populations of coastal martens (U.S. Fish Wildlife Service, 2019, Fig. 1). The population area was located on ancestral lands of the Yurok and Karuk Tribes in Humboldt and Del Norte Counties. Elevations ranged from 30 to 1400 m.

The study area encompassed five level IV ecoregions (Griffith et al., 2016) representing a diversity of climatic conditions and vegetative communities. The Northern Franciscan Redwood Forest (<915 m) and Outer North Coast Range (<1065 m) experienced high rainfall and were dominated by fog-dependent coastal redwood (*Sequoia sempervirens*) and Douglas-fir (*Pseudotsuga menziesii*), and intermixed with hardwoods such as tanoak (*Notholithocarpus densiflorus*) and red alder (*Alnus rubra*). The Serpentine Siskiyou ecoregion was composed of nutrient-poor soils resulting in sparse vegetation communities comprised of specialist species (Alexander et al., 2007). Jeffrey pine (*Pinus jeffreyi*), endemic oak (*Quercus* spp.), Douglas-fir, western white pine (*Pinus monticola*), and *Ceanothus* species were common throughout. Western Klamath Low Elevation Forests and Western Klamath Montane Forests occurred at elevations < 1065 m and > 1065 m, respectively. Douglas-fir occurred throughout both ecoregions, while Port Orford cedar (*Chamaecyparis lawsoniana*), red and white alder (*Alnus rhombifolia*) occurred on lower slopes, and white-fir (*Abies concolor*) and red-fir (*Abies magnifica*) occurred at higher elevations (Griffith et al., 2016).

Contemporary land ownership and management objectives varied across the study area (Fig. 1). The U.S. Forest Service managed

189 km² (47.4 % of the study area) for habitat and watershed restoration, timber harvest, cattle grazing, and public recreation (U.S. Forest Service, 1995). The Yurok Tribe owned 135 km² (33.8 % of the study area), an area that was privately owned and managed for commercial timber production by Green Diamond Resource Company until a transfer of ownership that was finalized in 2019. The Yurok Tribe managed their land for multiple uses, including plant and wildlife habitat restoration, conservation of cultural resources, cottage industries and some timber harvest. Lastly, 75 km² (18.8 %) of our study area occurred on private timberlands owned by Green Diamond Resource Company and was managed for the commercial harvest of coastal redwood and Douglas-fir trees (Fig. 1).

2.2. Site selection

We identified three sampling areas within the North Coastal California Extant Population Area: 1) Blue Creek, located on Yurok Tribal land, 2) Six Rivers, located on Six Rivers National Forest, and 3) Red Mountain that was 54 % Green Diamond Resource Company land, 27 % Yurok Tribal land, and 19 % Six Rivers National Forest land (Fig. 1). We used the oSCR package (Sutherland et al., 2018) in R v. 4.1.2 (R Core Team, 2021) to generate an array of sampling locations within each of the three sampling areas following Sutherland et al. (2020). The systematic array maximized the survey area and the possibility of spatial recaptures in our three priority sampling areas. We used a mean female home range size of 2.4 km² (USDA Forest Service Pacific Southwest Research Station, 2019) to guide spacing of sampling devices so that any individual marten in our sampling area could access a minimum of two sampling locations. Given the extremely steep, rugged terrain and dense understory, we constrained sampling locations to be within 200 m of a road to ensure crew member safety and maximize the number of stations we could deploy and maintain. Roads were abundant throughout the study area and road density had no correlation with any of the covariates analyzed in this study.

2.3. Data collection

2.3.1. Non-invasive hair snares

We deployed non-invasive hair snares (one at each sampling location, $n = 285$ hair snares) in each sampling area for 21 days starting in Blue Creek (100 hair snares, 22 August to 16 September), then in Six Rivers (83 hair snares, 19 September to 14 October), and then in Red Mountain (102 hair snares, 17 October to 15 November 2022). We adapted the hair snare design used by Pauli et al. (2008) and constructed our hair snares out of 15.24 cm diameter polyvinyl chloride (PVC) pipe cut into a crescent shape approximately 46 cm long. One side of the hair snare was closed off with 1.27 cm galvanized hardware cloth and the entrance of the hair snare was fixed with a non-toxic glue strip attached to a wooden, half-round molding (8.64 cm diameter and 20.32 cm long) (Anderson, 2023). The hair snares were attached to a fallen log or live-standing tree with the entrance facing down. We baited the hair snares with a chicken drumstick that was tied to a screw with twine and fixed towards the back and inside of the hair snare. To maximize the probability of detecting a marten, we placed hair snares on large-diameter logs in the most-dense vegetative cover available within 100 m of each oSCR generated location. Hair snares were checked once every six to eight days to collect genetic samples and replace bait. Hair samples were handled with latex gloves to reduce contamination and were placed in a 50 ml centrifuge tube (EasyReader, FisherBrand, Ottawa, Ontario) with approximately 15 ml of desiccant.

2.3.2. Remote cameras

To survey for martens and co-occurring carnivores, we paired an unbaited remote camera at a random subset of hair snares ($n = 135$ cameras, 47 in Blue Creek, 39 in Six Rivers, and 49 in Red Mountain). Cameras were set 50–100 m away from hair snares and aimed at a wildlife trail, decommissioned road, or lightly travelled road without bait or scent lure, which allowed us to monitor the normal activity patterns of carnivores along movement corridors (Kolowski and Forrester, 2017; Stewart et al., 2019). Cameras were programmed to take a burst of three images when triggered with a three second delay before being triggered again. We included photos taken during our hair sampling efforts (22 August to 11 November 2022) in our integrated spatial capture-recapture model and stored and tagged photos in Wildlife Insights, an open-source platform where global wildlife data is aggregated, analyzed and shared, and allows users to tag images using standard taxonomic nomenclature (Ahumada et al., 2020).

2.4. Analyses

2.4.1. Genetic identification

All hair samples were processed at the USDA National Genomics Center for Wildlife and Fish Conservation (Missoula, MT, USA). We extracted DNA from hair samples using the QIAGEN Dneasy Blood and Tissue kit (Qiagen, Valencia, CA, USA) according to manufacturer's instructions for tissue and using modifications for hair samples from Mills et al. (2000) in a dedicated lab for low-quality DNA from non-invasive samples. To identify species, we amplified and sequenced about 360 base pairs (bp) of the 16S rRNA region of mitochondrial DNA using primers 16SL: TTAAACGGCCGCGGTATCC and 16SR: GAATTACGCTGTTATCCCT adapted from universal primers (Hoelzel and Green, 1992). The quality and quantity of template DNA were determined by 1.6 % agarose gel electrophoresis. PCR products were purified using ExoSap-IT (Affymetrix-USB Corporation, OH, USA) according to manufacturer's instructions. Reactions were sequenced at Eurofins Genomics (Louisville, KY, USA) using standard Sanger sequencing protocols and the same primers. DNA sequence data were viewed and aligned with Sequencher (Gene Codes Corp. MI, USA), and sequences were compared to reference sequences from known species.

Confirmed marten samples were genotyped using 13 microsatellite loci used previously on marten: (Ma1, Ma2, Ma3, Ma8, Ma18, Ma19, Ggu234, Lut604, Mp197, Ggu216, Mer041, Gg3, Gg7) (Dallas and Piernney, 1998; Davis and Strobeck, 1998; Duffy et al., 1998;

Fleming et al., 1999; Jordan et al., 2007). Amplification and error checking procedures were performed as described in Schwartz et al. (2020) and Chmura et al. (2024). DNA sex identification was determined using the dbxy-215 primers and digest (Sekiguchi et al., 2010). Data were error checked using programs Dropout (McKelvey and Schwartz, 2005) and GenAIEx (Peakall and Smouse, 2006, 2012), and we used Dropout to calculate probability of identity (PI; Paetkau and Strobeck, 1994) and probability that siblings were identical (Pisib; Evett and Weir, 1998), which were 4.90×10^{-7} and 4.69×10^{-5} , respectively.

2.4.2. Modelling framework

We estimated the density, abundance, and distribution of Humboldt martens in our study area using an integrated spatial capture-recapture model (*sensu* Jiménez et al., 2022). This approach incorporates occupancy data with detection histories for known individuals to improve the precision of spatial capture-recapture parameter estimates. We included detection histories for known individuals from our genotyped marten hair samples and detection-non-detection data of unknown martens from remote camera data. Additionally, we incorporated 8 incidental locations of 4 known martens that were detected during concurrent survey efforts by the Yurok Tribe (S. Demers, pers. comm.).

We assumed a population of N individuals were sampled and that each individual had an activity center, s_i , expressed by its XY coordinates. In the integrated spatial capture-recapture model, the spatial capture-recapture (hereafter, SCR) and occupancy submodels share the same underlying point process in which we assumed that each of the N activity centers were uniformly distributed over the state space S such that $s_i \sim \text{Uniform}(S)$. In SCR models, S must be large enough to accommodate any individual that could have been detected at the hair snares, including those whose activity center occurred outside the bounds of our sampling area. Thus, we defined S as the bounding box of the sampling area encompassing hair snare stations buffered by three times the mean radius of a male marten home range ($1160 \text{ m} * 3 = 3480 \text{ m}$; K. Moriarty, pers. comm.). We modelled the encounter rate λ_{ij} as a function of the baseline detection rate at hair snares ($p0_j^{np}$), and the distance between the hair snare location and the individual's activity center:

$$\lambda_{ij} = p0_j^{np} * \exp\left(-\frac{d_{ij}^2}{2\sigma^2}\right)$$

where d_{ij} is the Euclidean distance between hair snare j and the latent activity center of individual i , and σ is the spatial scale parameter of the half-normal detection function that describes animal movement.

To account for differences in the timing of hair snare deployment, we included a season-specific effect on the baseline detection rate at hair snares to determine whether the time period in which each hair snare was deployed affected detection probability:

$$\text{logit}(p0_j^{np}) = \alpha 0 + \alpha 1 * \text{season}_j$$

In the SCR submodel, we modelled individual encounter histories for individual i , at hair snare j , in week k as a Bernoulli-distributed random variable:

$$Y_{ijk} \sim \text{Bernoulli}(p_{ij} * \text{deployed}_{jk} * z_i)$$

where the observed data Y_{ijk} is the realization of a Bernoulli process with probability p_{ij} , which represents the detection probability of individual i , at hair snare j , and where deployed_{jk} is a binary variable for whether hair snare j was deployed and functioning during week k . Detection probability (p_{ij}) is defined by a log-log link function that relates it to the encounter rate λ_{ij} as:

$$p_{ij}^{scr} = 1 - \exp(-\lambda_{ij})$$

We fit the SCR model by augmenting the observed dataset with a sufficiently large number of all zero encounter histories, M , such that if n is the number of observed individuals, then $M+n$ is the number of potential individuals in the population N . We introduced a partially latent binary variable z_i which represents the probability that an augmented individual is a real and undetected member of the population N . We set z_i to 1 for individuals that were sampled and assumed $z_i \sim \text{Bernoulli}(\varphi)$ for all augmented individuals M such that the number of individuals in the state space is:

$$N = \sum_{i=1}^M z_i$$

The occupancy submodel states that a detection occurs at camera j during week k if at least one unknown (or unidentified) individual is detected. Thus, the model for the detection data Occ_{jk} was defined as:

$$\text{Occ}_{jk} \sim \text{Bernoulli}\left(1 - \prod_{i=1}^M (1 - p_{ijk}^{occ} * z_i)\right)$$

Where p_{ijk}^{occ} is analogous to p_{ij}^{scr} but with latent identities and differing baseline detection rates (e.g., $p0_j^{np}$ vs $p0_j^{cam}$) between the two methods. By truncating weekly counts to binary observations (0/1) and using a Bernoulli model in the SCR and occupancy submodels, we can avoid violating the independence assumption because counts at camera traps are usually unrelated to the fundamental space use process that underlies SCR data (Jiménez et al., 2022).

Survey effort can influence detection probability for carnivores (Long et al., 2007). To control for variation in survey effort among cameras, we included the number of camera days that each camera was deployed and functioning as a covariate for baseline detection

rate at cameras in the occupancy submodel:

$$\text{logit}(p0_j^{cam}) = \beta_0 + \beta_1 * \text{camera.days}_j$$

Finally, we added the incidental locations of known individuals to increase precision of SCR parameters and coded these locations as thinned outcomes of a movement model with a stationary bivariate normal utilization distribution (*sensu* Jiménez et al., 2022).

2.4.3. Influence of forest conditions on marten density

We examined the relationship between marten density and four covariates with a generalized linear model (Table 1). First, we created a marten density surface for the state space using the posterior marten activity centers from our integrated spatial capture-recapture model. To achieve this, we discretized our state space into 1000 m grid cells and assigned all posterior activity center estimates to the nearest grid cell. Next, we cropped the state space to a minimum concave polygon around our sampling sites and buffered the polygon by three times the mean radius of a marten home range (male and female combined; $3 * 870 = 2610$ m; K. Moriarty, pers. comm), resulting in a 399 km² marten density surface. We related marten density to four spatial covariates: 1) elevation, extracted from the elevatr (Hollister et al., 2023) package using the get_elev_raster function 2) diameter diversity index (DDI), a measure of the structural diversity of a forest stand based on tree densities in different size (i.e., diameter at breast height [DBH]) classes (Ohmann and Gregory, 2002), 3) ladder fuel density which we used as a proxy for understory vegetation cover and downed woody debris because it represents the proportion of surface fuels (i.e. woody material, shrubs, low-hanging branches) in the understory (California Forest Observatory, 2020), and 4) topographic position index (TPI), a measure of how prominent (positive TPI; e. g., prominent peaks) or recessed (negative TPI; e.g., riparian drainage) a location is, calculated from the elevation raster using the tpi function in the terra package (De Reu et al., 2014). We resampled covariates to the resolution of the marten density surface and calculated the average values for each grid cell using the exactextractr package (Baston, 2024). Finally, we standardized covariates to have a mean of 0 and standard deviation of 1 and all covariates exhibited Pearson's correlation < 0.55.

We modeled marten density as a linear function of DDI, ladder fuel density, and TPI and allowed the slopes for each covariate to vary by two discrete elevational bands (low [≤ 700 m], high [> 700 m] [e.g., Kramer et al., 2021]). Density was log-transformed prior to analysis to achieve normality. Elevation bands were chosen based on the distribution elevation values in the state space so that we had a similar sized sample for each band. We modelled density as a normally-distributed variable such that:

$$\text{Density} \sim \text{normal}(\mu_i, T)$$

$$T = 1/\sigma^2$$

$$\mu_i = \alpha_0 + \alpha_{1\text{Elevation}} * \text{DDI} + \alpha_{2\text{Elevation}} * \text{LadderFuel} + \alpha_{3\text{Elevation}} * \text{TPI}$$

Where mean density μ in each grid cell i was modeled to vary as a function of an intercept (α_0) and the elevation-specific effects of diameter diversity index, ladder fuel density, and topographic position index (α_1 , α_2 , and α_3 , respectively).

2.4.4. Model fitting and assessment

We fit our spatial capture-recapture model and post-hoc generalized linear model using Markov Chain Monte Carlo (MCMC) methods in nimble (de Valpine et al., 2022) in R v. 4.1.2 (R Core Team, 2021). For the SCR model, we used weakly informative priors for all estimated parameters with the exception of sigma, where we used an informative prior based on home range estimates for collared martens in the study area (K. Moriarty, pers. comm.). Priors were specified as $\psi \sim \text{uniform}(0, 1)$, $p0^{hp} \sim \text{uniform}(0, 1)$; i.e., baseline detection rate at hair snares, $p0^{cam} \sim \text{uniform}(0, 5)$; i.e., baseline detection rate at cameras, and $\sigma \sim \text{uniform}(500, 1600)$. Parameter estimates were calculated from 49,998 MCMC samples, taken from three chains run for 100,000 iterations, thinned by three, and following a burn-in of 50,000.

For the post-hoc GLM, we used weakly informative priors for all estimated parameters, specifically, $\text{normal}(0, 0.001)$ for α_0 , α_1 , α_2 , α_3 and $\text{uniform}(0, 1000)$ for dispersion (tau) where $\tau = 1/\text{sd}^2$ (Kéry, Royle, 2016). Parameter estimates were calculated from 7500 MCMC samples, taken from three chains run for 10,000 iterations, thinned by two, and following a burn-in of 5000. We assessed model convergence by examining trace plots and $\hat{R}$ values for all parameter estimates (Gelman and Hill, 2007; Gelman et al. 2013).

Table 1

Covariates, including units, description, and native resolution, included in the generalized linear model to explain variation in Humboldt marten density in northern California, USA.

Covariate	Description	Unit of measure	Range of values	Native Resolution
Elevation	Elevation	Meters	36.00–1412.93	30 m
Topographic Position Index (TPI)	Difference between the elevation at a cell and the average elevation of surrounding cells	Meters	-61.79 – 80.02	30 m
Diameter diversity index (DDI)	A measure of structural diversity based on tree densities in different DBH class	None	75.14 – 827.93	30 m
Ladder fuel density	Proportion of surface fuels in the understory	Percent (%)	5.90–48.14 %	10 m

3. Results

3.1. Non-invasive hair snares

We deployed 285 hair snares from 22 August to 15 November 2022 across the three sampling areas. Hair snares were deployed for a mean 20.56 days (SD 1.71 days) for a total of 5838 survey nights. One hundred hair snares were deployed in the Blue Creek sampling area, 83 in Six Rivers, and 102 in Red Mountain. Of 420 total hair samples collected throughout the sampling season, 71 were genetically identified as marten, and 58 marten samples (82 %) were successfully genotyped for individual identification. We detected martens at 56 out of 285 hair snare stations (20 %) and individually identified martens were detected at 45 stations (16 %) including 16 in Blue Creek, 17 in Six Rivers, and 12 in Red Mountain. We identified 46 individuals with 28 males and 18 females. On average, individual martens were detected 1.21 (range 1–3) times at 1.07 (range 1–2) stations.

3.2. Camera surveys

We deployed 135 remote cameras across the three sampling areas. Forty-seven cameras were deployed in Blue Creek, 39 in Six Rivers, and 49 in Red Mountain. Of the 135 cameras deployed, 133 were included in analyses due to malfunctions from two cameras. From the remaining 133 functional camera stations, we collected a total of 56,915 photos over 7053 trap nights. Each camera was deployed for an average of 53.03 ± 28.86 days. Martens were detected 86 times at 20 out of 133 (15 %) camera stations. Seven cameras detected marten in Blue Creek, 6 in Six Rivers, and 7 in Red Mountain.

3.3. Marten abundance, density, and distribution

We estimated a posterior median of 111 (CRI 73–146) martens within the 399 km² study area (Table 2). We estimated a posterior median density of 0.276 (CRI 0.183–0.364) martens per 1 km² (Table 2). Marten density varied spatially across the study area with the highest densities observed in the northern portion of Red Mountain, the northeastern portion of Blue Creek, and heterogeneously throughout Six Rivers (Fig. 2). Detection probability of martens was slightly higher at hair snares (0.017 [CRI 0.004–0.026]) than at cameras (0.009 [(CRI 0.005–0.026); Table 2). We found no strong effect of season or the number of camera days on detection probability at either sampling device (Table 2).

3.4. Influence of forest conditions on marten density

Marten density varied with forest conditions, and these relationships varied by elevation (Table 3, Figs. 3 and 4). Marten density was negatively correlated with diameter diversity index at lower elevation sites (≤ 700 m; -0.015 [CRI -0.067 – 0.038]) and was positively correlated with diameter diversity index at higher elevation sites (> 700 m; 0.035 [CRI -0.013 – 0.084]) but both relationships had 95 % credible intervals that overlapped 0 (Table 3, Figs. 3 and 4). Marten density was negatively correlated with ladder fuel density at all elevational gradients. The negative relationship between marten density and ladder fuel density was stronger at higher elevation sites (> 700 m; -0.039 [CRI -0.089 – 0.012]) than at lower elevation sites (≤ 700 m; -0.008 [CRI -0.058 – 0.042]), though 95 % credible intervals overlapped 0 for both elevation bins (Table 3, Figs. 3 and 4). Finally, marten density was negatively correlated with topographic position at lower elevation sites (≤ 700 m; -0.057 [CRI -0.108 – -0.007]) and positively correlated with topographic position at higher elevation sites (> 700 m; 0.041 [CRI -0.010 – 0.090]), though the 95 % credible interval overlapped 0 for higher elevation sites (Table 3, Figs. 3 and 4).

Table 2

Parameter estimates from the integrated spatial capture-recapture model used to estimate Humboldt marten abundance in northern California, USA, including posterior mean, standard deviation (SD), median (50 %) and 95 % credible interval (2.5 % and 97.5 %) for the number of individuals in the 1082 km² state space ($N_{\text{Statespace}}$), number of individuals within our 399 km² sampling area ($N_{\text{StudyArea}}$), density (martens/1 km²), σ (movement parameter), and mean baseline detection probability at hair snares (Mean $p0^{\text{trap}}$) and cameras (Mean $p0^{\text{cam}}$). Detection intercepts are depicted by $\alpha 0$ and $\beta 0$ detection intercepts, and $\alpha 1_{\text{season}}$ and $\beta 1_{\text{camera days}}$ represent the effect of season and number of camera days on detection probability at hair snares and cameras, respectively. The probability that augmented individuals were real, undetected members of the population is depicted by ψ .

Parameter	Mean	SD	2.5 %	50 %	97.5 %
$N_{\text{Statespace}}$	298	53.238	198	297	394
$N_{\text{StudyArea}}$	111	19.588	73	110	146
Density	0.276	0.049	0.183	0.275	0.364
σ	1585.168	14.010	1548.036	1589.303	1599.621
Mean $p0^{\text{trap}}$	0.017	0.004	0.011	0.016	0.026
Mean $p0^{\text{cam}}$	0.009	0.002	0.005	0.008	0.026
$\alpha 0$	-4.090	0.236	-4.536	-4.093	-3.616
$\alpha 1_{\text{season}}$	-0.020	0.169	-0.352	-0.020	0.305
$\beta 0$	-4.770	0.276	-5.303	-4.771	-4.222
$\beta 1_{\text{camera days}}$	-0.191	0.201	-0.581	-0.194	0.206
ψ	0.745	0.134	0.491	0.743	0.983

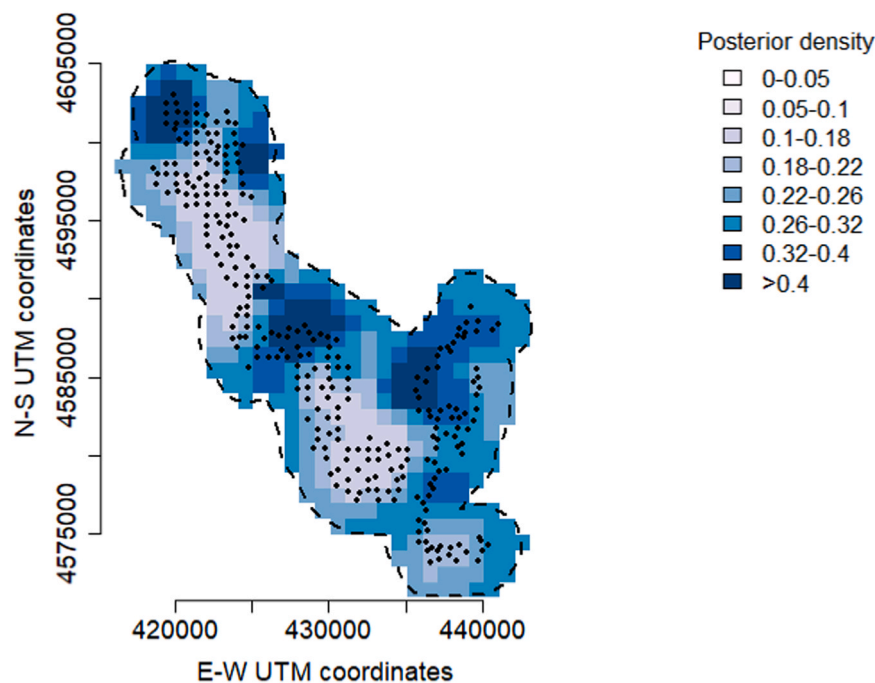


Fig. 2. Humboldt marten density surface over 399 km² in our sampling area in northern California, USA. Density is depicted as the number of posterior marten activity centers per 1 km², where darker pixels represent higher density of activity centers and lighter pixels represent lower density of activity centers. Black dots represent hair sampling devices.

Table 3

Results from the post-hoc generalized linear model assessing the relationships between Humboldt marten density and forest conditions in northern California, USA., including posterior mean, standard deviation (SD), median (50 %) and 95 % credible interval (2.50 % and 97.50 %), and the proportion of posterior samples with the same sign as the mean ($p(\pm/-)$). Covariates in bold indicate the 95 % credible interval had no overlap with 0.

Covariate	Mean	SD	2.5 %	50 %	97.5 %	$p(\pm/-)$
DDI (Elevation ≤ 700 m)	-0.015	0.027	-0.067	-0.015	0.038	0.71
DDI (Elevation > 700 m)	0.035	0.025	-0.013	0.035	0.084	0.92
Ladder Fuel Density (Elevation ≤ 700 m)	-0.008	0.026	-0.058	-0.009	0.042	0.63
Ladder Fuel Density (Elevation > 700 m)	-0.039	0.026	-0.089	-0.039	0.012	0.94
TPI (Elevation ≤ 700 m)	-0.057	0.026	-0.108	-0.056	-0.007	0.99
TPI (Elevation > 700 m)	0.041	0.025	-0.010	0.041	0.090	0.94

4. Discussion

This study provides the first robust estimate of Humboldt marten abundance and density in northern California, which addresses key demographic information gaps needed for the conservation and management of the species. Marten density occurred heterogeneously across our study landscape. Although effect sizes were small, we found that marten density was correlated with landscape conditions but that the effects of landscape conditions varied by elevation. This site-specific context effectively represents the conditions associated with the diverse array of ecotypes, ownerships, and management legacies that influence marten density across this heterogeneous landscape. Considering these findings and the diversity of landscape conditions in which Humboldt martens occur throughout their range, collaborative conservation among federal, state, private, and Tribal entities is essential to their persistence and recovery. Quantifying these relationships was an important first step towards understanding the conditions in which Humboldt martens may persist.

Marten density varies geographically and is often influenced by biotic and abiotic factors. In North America, marten density is often highest in coastal and island populations that typically exhibit densely aggregated resources, limited competitive pressure, and milder abiotic conditions (e.g., Oregon dunes 1.13/km² [Linnell et al., 2018], Apostle Islands 0.42–1.46/km² [Smith et al., 2021]). Conversely, martens in montane and boreal areas often occur at lower densities, likely due to pronounced seasonality and harsh winter conditions, seasonally limited resources, and greater inter- and intraspecific competition (e.g., Sierra Nevada 0.17–0.19/km² [Slauson et al., 2017], British Columbia 0.33/km² [Mowat and Paetkau, 2002], New Hampshire 0.45–0.60/km² [Sirén et al., 2016]). In some cases, lower density may be the result of a loss in forest structure from natural or anthropogenic disturbances, as is the case with a declining population in Maine (0.18/km²; Clare et al., 2019). Despite the proximity of our study area to the coast, our estimates of

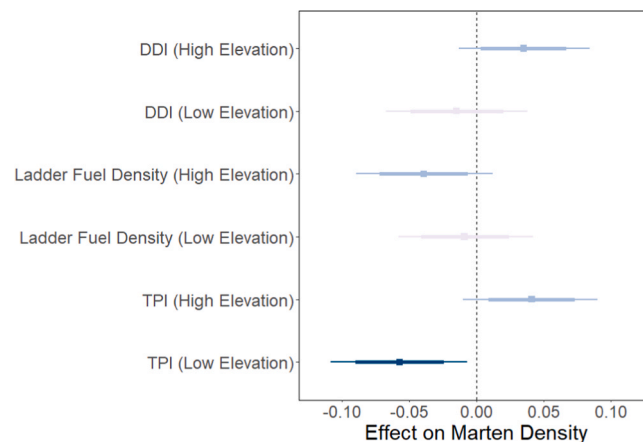


Fig. 3. Relationships between Humboldt marten density and landscape covariates (DDI = diameter diversity index, TPI = topographic position index) at high elevation (> 700 m) and low elevation (≤ 700 m) derived from a post-hoc linear model. Posterior median covariate effect is denoted by the square, and 80 % and 95 % credible intervals are depicted by thick and thin error bars, respectively. Covariate effects with 95 % credible intervals that did not overlap 0 are depicted in dark blue, 80 % credible intervals that did not overlap 0 are in light blue, and 95 % credible intervals that overlap 0 are in the light purple.

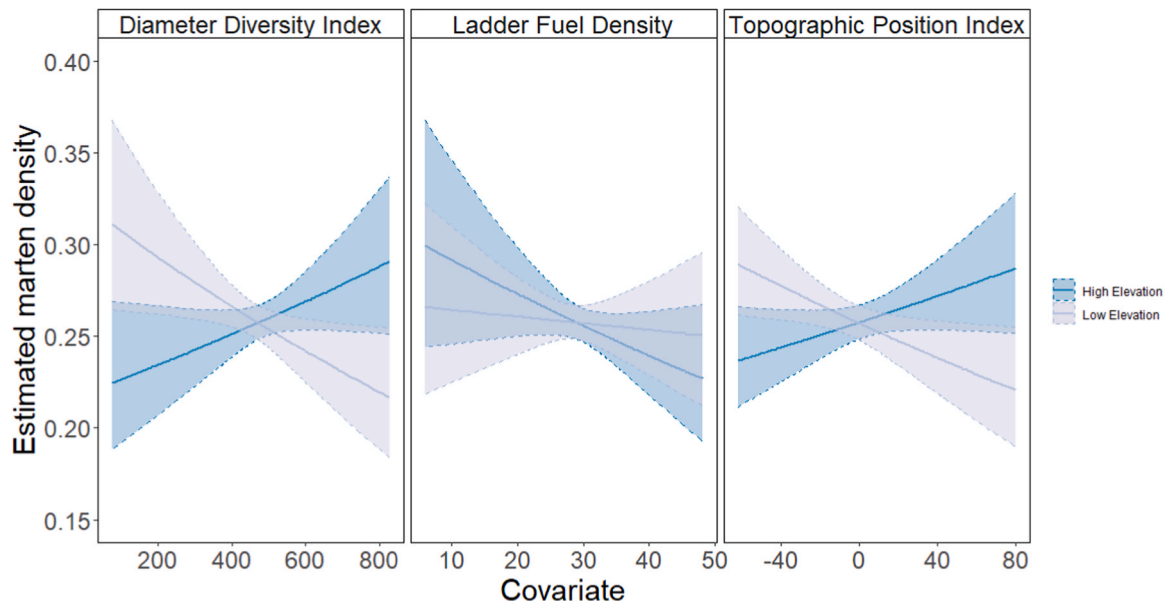


Fig. 4. Relationships between Humboldt marten density and landscape covariates derived from a post-hoc linear model. Covariate effects at effects at high elevations (> 700 m) are presented in dark blue and low elevations (≤ 700 m) are presented in light purple.

Humboldt marten density ($0.28 [0.18 - 0.36]/\text{km}^2$) are more similar to estimates from montane and northerly ecosystems, likely due to forest and landscape structure, variable forest management and fire histories (Knight et al., 2022), and a diverse community of co-occurring carnivores (i.e., fishers [*Pekania pennanti*], bobcats [*Lynx rufus*], gray foxes [*Urocyon cinereoargenteus*]) that can compete with or predate martens (Green et al., 2018; Furnas et al., 2022; Martin et al., 2022b).

Marten density was variable throughout our study area and, similar to other species of conservation concern (Kramer et al., 2021), exhibited context-specific relationships with topography and vegetation structure. Marten density was positively correlated with TPI at higher elevations, indicating marten density was greater in areas with high-elevation ridges and hilltops that exhibit consistent winter snowpack (Erickson et al., 2005) and dominated by late seral stands of red and white fir, which can provide refugia from competitive pressure and physiological stress and structure for resting and denning (Raphael and Jones 1997; Pauli et al., 2022). Conversely, marten density was negatively correlated with TPI at lower elevations, with marten density highest in areas overlapping ravines and drainages in lowland, coastal forests. These areas exhibit cooler microclimates, dense understory vegetation (Raphael and Jones 1997), and complex, late-seral structure due to nutrient and water flow into the drainage bottoms (Shirk et al., 2014). Additionally, challenges

with access for removing timber and more recent protections from timber harvest around riparian areas have allowed these areas to retain late-seral structure (California Department of Forestry and Fire Protection, 2022). These findings agree with Shirk et al. (2014), which found similar patterns in marten resource selection at fine spatial scales.

Although understory shrub cover and structural heterogeneity is important to marten ecology (Janssen et al., 2007; Eriksson et al., 2019; Slauson et al., 2019b; Moriarty et al., 2021), marten density was negatively correlated with ladder fuel density, a covariate we used as a proxy for understory cover, and weakly correlated with diameter diversity index, a covariate representing diversity in tree size class. We acknowledge that these metrics may not be effective proxies for understory structure important to martens in our study area (e.g., salal, huckleberry, rhododendron (*Rhododendron macrophyllum*), shrub form tan oak (*Lithocarpus densiflora*), Slauson et al., 2007, 2019; Moriarty et al., 2021) and may not capture the importance of structural diversity at the coarser spatial scale of our analysis. Future efforts to understand the relationship between marten density, vegetation complexity, and varying climate conditions would benefit from measurements that directly and more accurately quantify shrub communities and understory vegetation structure (e.g., terrestrial LiDAR: Batchelor et al., 2023) and provide context about the importance of topographic and structural heterogeneity and shifting conditions for marten persistence (Lawler et al., 2002; Suffice et al., 2017; Pauli et al., 2022).

Though marten density was weakly correlated with the forest structure covariates we used, structural diversity has been shown to be an important landscape component for martens here and throughout their range (e.g., M. Smith et al., 2022; A. Smith et al., 2022). Structural diversity, or heterogeneity, can provide a variety of resources to a single individual or a population, and many species benefit from structural heterogeneity at multiple spatial and ecological scales (Boyce et al., 2003; Parsons et al., 2019; Kuntze et al., 2023). Late-seral forest stands and legacy structures retained on the landscape provide cavities or platforms for resting, denning, or roosting for species such as fisher and spotted owls (*Strix occidentalis*), while early-seral stands often support greater prey abundances and efficient foraging opportunities (Thome et al., 1999; Parsons et al., 2019; Zulla et al., 2022, 2023; Kuntze et al., 2023). Landscape heterogeneity can also facilitate coexistence among sympatric carnivores by allowing different species to partition space, time, and resources among distinct portions of the landscape (Zielinski et al., 2017; Manlick et al., 2020). In areas that are highly fragmented or receive relatively little snow, structural diversity may be a key component allowing martens to successfully forage and avoid predators and competitors (Andruskiw et al., 2008; Kautz et al., 2021). Cumulatively, these findings suggest promoting and retaining structural heterogeneity should be a priority for land managers to support the persistence of Humboldt martens and other imperiled species.

Despite the conservation status of Humboldt martens, there have been few evaluations of their demographics (e.g., abundance, density) prior to our work (see Slauson et al., 2009, Slauson et al., 2019a; Delheimer et al., 2021; Martin et al., 2022a) and no robust baselines for their abundance and density outside of the Oregon Dunes (Linnell et al., 2018). Previously, the best estimate for Humboldt marten abundance was that no more than 100 individuals existed in the North Coastal California Extant Population Area (Slauson et al., 2009). However, the precision of this estimate was limited due to few recaptures and poor DNA quality, resulting in an inability to incorporate data into spatial capture-recapture estimates, and the survey area was limited to a portion of the EPA that did not entirely overlap our subsequent surveys. Using spatial capture-recapture, our estimates establish a baseline estimate of abundance and density for 25 % of the 1580 km² North Coastal California Extant Population Area, representing a portion of the Extant Population Area where martens have been consistently detected since their re-discovery in 1996. Despite addressing this knowledge gap, apparent survival and recruitment of Humboldt martens, and the relationship between forest conditions and survival, remain as major knowledge gaps for wildlife and land managers in this region. Additionally, we were unable to fit a sex-specific model due to the low number of spatial re-captures limiting the model's ability to estimate sex-specific sigma. While this study shows that marten populations can exist at relatively high densities in a variety of habitat conditions and management histories, understanding the effects of forest and landscape structure on survival and recruitment are necessary to inform our understanding of marten persistence and adaptive capacity. We encourage future research to focus on multi-year monitoring to capture trends in Humboldt marten abundance, density, and apparent survival and recruitment in this population.

CRediT authorship contribution statement

Marie E. Martin: Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization. **Erika L. Anderson:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis. **Kristine L. Pilgrim:** Writing – review & editing, Formal analysis. **Gunther Micaela:** Writing – review & editing, Supervision. **Sean M. Matthews:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization. **Scott A. Demers:** Writing – review & editing, Methodology.

Funding

This project was funded by a Traditional Section 6 Grant (F21AP00465) provided by the U.S. Fish and Wildlife Service and administered by the California Department of Fish and Wildlife. Additional funding was provided by The Volgenau Foundation. In-kind support was provided by Green Diamond Resource Company, Cal Poly Humboldt, and the University of Wisconsin, Madison.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

The authors express their sincere gratitude to K. Barnes, J. Bettaso, D. Early, S. Fresz, K. Hamm, J. Hutchinson, E. Tripp, and T. Williams-Clauson for their contributions to the project. This work would not be possible without the support from numerous wildlife field technicians; we thank M. Cameron, S. Daniel, D. Fehring, T. Hannon, J. Lucchesi, T. McLeod, K. Parker, A. Roos, L. Salas, and A. Schwecke. Locations of previous marten detections were provided by the U.S. Fish and Wildlife Service, National Council for Air and Stream Improvement, Green Diamond Resource Company, and the Yurok Tribe.

Data availability

Data will be made available on request.

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