

DISTRIBUTION AND HABITAT USE OF A RECENTLY DISCOVERED
POPULATION OF HUMBOLDT MARTENS IN CALIFORNIA

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A Thesis Presented to

The Faculty of Humboldt State University

In Partial Fulfillment of the Requirements for the Degree

Master of Science in Natural Resources: Wildlife

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December 2019

ABSTRACT

DISTRIBUTION AND HABITAT USE OF A RECENTLY DISCOVERED POPULATION OF HUMBOLDT MARTENS IN CALIFORNIA

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The Humboldt marten (*Martes caurina humboldtensis*) has declined from over 95% of its historic range in California, with only two populations remaining. In response to the forthcoming listing of the Humboldt marten a conservation assessment and strategy was developed to address the most important conservation needs for this species. This assessment identified an area near the California – Oregon border as the second extant population area in California based on a small number of recent detections. However little else was known of this population, and this prompted my investigation to determine 1) the distribution and potential population size and 2) habitat use by Humboldt martens in this area. This study addresses a key information need identified in the conservation strategy. Between May – August of 2017 and 2018, I used a 2-km systematic grid to sample 51 sample units using baited remote cameras and track plates and detected martens at 20 (39.2 %) sample units. Using an occupancy modeling approach, I found that a combination of elevation and amount of forest habitat with large diameter trees (size class 5, ≥ 60.0 cm QMD) measured at the home range scale (1-km radius, 314 ha) influenced marten occupancy. Marten occupancy was highest in low elevation sample units (mean = 614.6 m, SE = 35.6 m) with an average of 65.3 ha (20.1% of 314 ha, SE =

12.0 ha) of forest habitat in the largest tree size class. The limited number of detections precluded evaluating models with > 3 habitat variables, as well as assessing finer scale habitat use; however, univariate results suggested stream density may also be influential at the home range scale. Consistent with results from the larger California population, managers interested in promoting marten conservation in the California – Oregon extant population area should maintain and increase large patches of forest habitat with large-diameter trees. A novel finding for this population was the importance of low-elevation forest habitat dominated by size class 4 (27.9 – 59.9 cm QMD), suggesting the combination of home-range sized areas with these two habitat compositions is capable of supporting marten occupancy in this region.

ACKNOWLEDGEMENTS

I would like to express my gratitude to all those who contributed and supported me through this project. I would like to especially thank the members of my committee, Dr. Micaela Gunther, Dr. Tim Bean, and Dr. Keith Slauson, for their time, patience, and guidance throughout each step of the project. With their help I was able to grow and progress as a scientist as I worked through the completion of this project. I would also like to thank Brenda Devlin and the U.S. Forest Service for their financial support and guidance, as well as the U.S. Fish and Wildlife Service for their financial support. I would also like to thank the members of my field crew, Sheri Hart, Alexander Benn, Karis Wright, and Rebecca Carniello, as well as the numerous volunteers who contributed their time and were willing to head into the forest with me. I would also like to thank my lab mates Andria Townsend, Jon Ewanyk, Rudy Mena, and Steffen Peterson for their support, guidance, and friendship. I would like to thank the faculty of the Humboldt State University Wildlife Department, with a special thank you to Dr. Dan Barton for his invaluable advice and assistance, and the Wildlife Graduate Student Society for their continued support and guidance throughout my time as both an undergraduate and graduate student. This community has been vital to my ability to develop into a wildlife biologist. Lastly, I would like to thank Alexander Davidson and Woodrow for their continued love and support, and all my friends and family who have been there along the way as I work toward completing my goals.

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INTRODUCTION

The Humboldt marten (*Martes caurina humboldtensis*) is a medium-sized forest carnivore that has declined in over 95% of its historic range in the coastal forests of northwestern California and Oregon (Slauson et al. 2018). Much of this decline can be attributed to the historical impacts of unregulated fur trapping that occurred during the 1800s, as well as extensive habitat loss due to unregulated timber harvesting (USFWS 2015; Slauson et al. 2018). Furthermore, populations of martens are naturally characterized by low densities, low reproductive rates, and large home range sizes with a limited tolerance to such habitat loss (Buskirk and Ruggiero 1994; USFWS 2015).

The Humboldt marten was believed to be extinct until 1996 when a single population was rediscovered on the Six Rivers National Forest in Del Norte County, California (USFWS 2015). In response to their conservation needs the Humboldt marten was listed as endangered under the California Endangered Species Act in 2018 (CBD 2018), and a petition to list the subspecies as threatened at the federal level is pending (83 FR 50574). Although little is known about the size and range of the extant populations of Humboldt marten, considerable survey effort has been made to determine this information (Moriarty et al. 2016). Two extant populations have been identified in California: one in northern coastal California (CA EPA, Figure 1), and another near the California – Oregon border (CA – OR EPA, Figure 1). These have been the only populations of Humboldt martens detected within its historic range in California despite extensive surveying efforts. In 2009, the CA EPA was estimated to contain fewer than

100 individuals (Slauson et al. 2009), but the distribution and population size in the CA – OR EPA remain unknown. One or two verifiable marten detections were also captured on remote cameras in Prairie Creek Redwoods State Park, but due to the low number of detections it is unknown whether these represent a viable extension of the two populations.

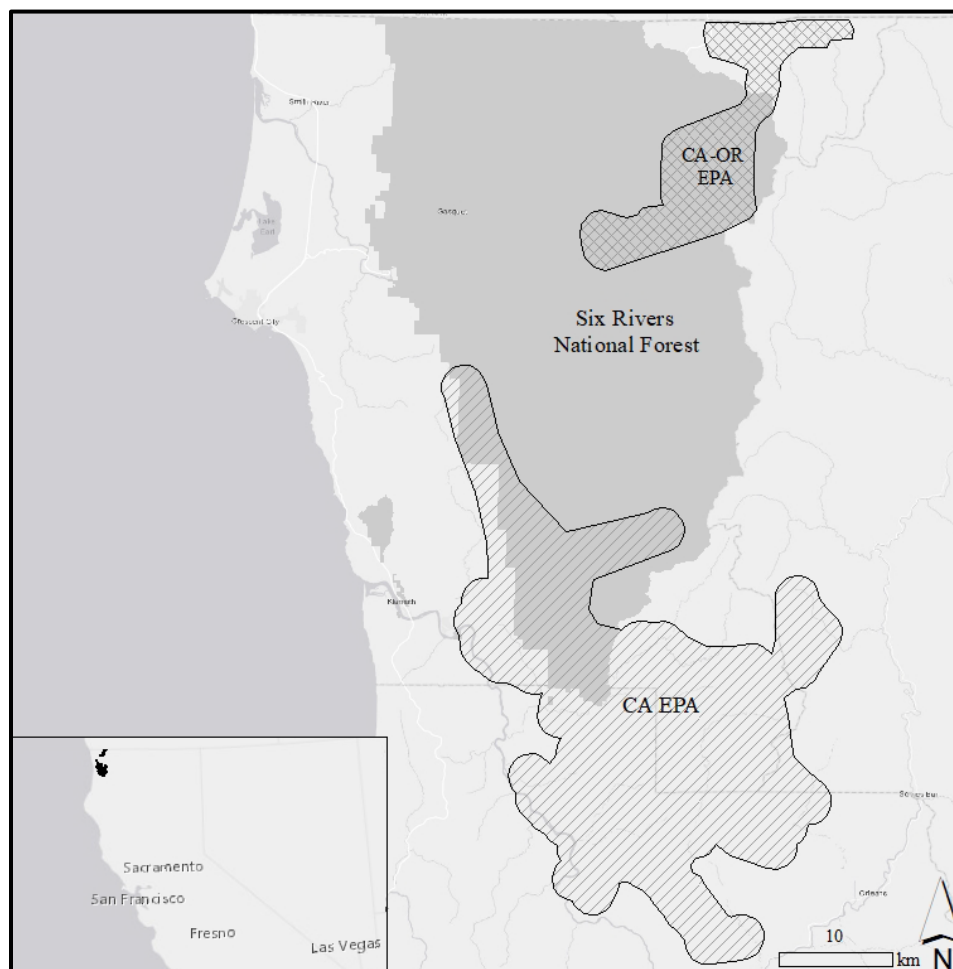


Figure 1. Locator map for the CA – OR Extant Population Area (EPA) in Del Norte County, northern California, USA, in relation to the California EPA.

With the Humboldt marten emerging from believed extinction and occupying less than 5% of its historic range, it is now critical to identify suitable areas of habitat within its historic range where additional populations may occur or return. A recent study summarized data on >1000 occupancy surveys to develop the first range-wide landscape habitat suitability models for the Humboldt marten throughout its historic range (Slauson et al. 2019), identifying the CA – OR EPA as containing highly suitable habitat. In addition to high suitability, Humboldt martens have been detected in this area in recent years. The first detection occurred in 2011, and survey efforts between 2012 – 2014 detected five additional martens in this area (Slauson et al. 2018).

With so little known about the CA – OR EPA, it has been recognized as one the most important information gaps identified in the Humboldt marten conservation strategy (Slauson et al. 2018). I investigated the area that included the CA – OR EPA 5 years after the initial detections using non-invasive survey techniques following the Humboldt marten population monitoring protocol (Slauson and Moriarty 2014) to determine the distribution of this population. Non-invasive survey techniques are one of the most effective methods for detecting carnivores, particularly due to their elusive behavior, territoriality, consistency with travel routes, and habit of marking items that enable researchers to successfully capture sign of these species (Long and Mackay 2012). Traditional capture-based methods of monitoring populations are difficult to implement with carnivores because they tend to have low-density populations and wide-ranging movement patterns, making obtaining sufficient sample sizes and high capture probability challenging and costly. Martens lend themselves readily to non-invasive

surveying techniques, as they are opportunistic hunters and are readily attracted to scent lures and baits (Zielinski and Kucera 1995). Furthermore, comparison of different surveying techniques has revealed that non-invasive techniques, such as remote cameras and track plates, are most effective at capturing marten presence (Gompper et al. 2006).

Martens, like many other species, are known to exhibit habitat selection at multiple spatial scales, with individuals making choices ranging from landscape level movement decisions to microscale selection of denning and foraging sites (Johnson 1980; Slauson et al. 2007; Kirk and Zielinski 2009; Thompson et al. 2012; Lipsey et al. 2017). Habitat selection at the home range scale (i.e., 2nd order: establishment of the home range) is particularly important for martens as it is most influential on individual fitness (Thompson et al. 2012), but few studies have been able to capture habitat selection at the finer stand-scale (i.e., 3rd order: within the home range) (Johnson 1980; Slauson et al. 2007; Baldwin and Bender 2008). Studies that produce detection/non-detection data have been used for *Martes* research for decades and allow for the comparison of key ecological differences at multiple spatial scales between sample units that are occupied to those that are unoccupied (Slauson et al. 2012).

Humboldt martens are associated with structurally complex, late-successional and old-growth coniferous forests (Zielinski et al. 2004). They utilize the structural complexity of older forests to meet many of their life history needs, including large downed woody debris, dense forest cover, understory shrub cover, and large, live trees and snags (Zielinski et al. 2004; Andruskiw et al. 2008). Dense shrub cover provides refuge and cover for prey (Slauson et al. 2007), while large diameter live trees, snags, and

logs provide locations for resting and denning (Payer and Harrison 2003; Kirk and Zielinski 2009).

In addition to late-successional and old growth forest habitat, Humboldt martens also occur in fog-influenced mixed conifer forests found on serpentine soils (Slauson et al. 2009), with patterns of use differing based on habitat type (Slauson et al. 2007). Serpentine soils are characterized by low nutrients, resulting in slower growth of trees and shrubs. It provides a harsh growing environment for plants, with vegetation features often sparse and stunted (Harrison et al. 2006). Occupied serpentine habitat may include any seral stage with tree canopy closures ranging from sparse to dense, but often retain key features known to be important to martens, such as dense shrub cover and rocky outcrops with interstitial spaces that martens use for resting (Slauson et al. 2018).

Previous habitat analyses for Humboldt martens have found that habitat variables measured at the stand (i.e., forest developmental stage, tree canopy cover, shrub cover) and home range scales (i.e., amount of late seral forest, percent area logged, riparian habitat, serpentine habitat) can be influential on occupancy (Slauson et al. 2007; Zielinski et al. 2015). Studies on martens have also used movement data from GPS collars to assess fine-scale habitat selection within the marten home range (Porter et al. 2005; Moriarty 2014; Tweedy 2018), and although these methods provide valuable insight, they also have significant logistical limitations (Caravaggi et al. 2017). Remote camera and track plate surveys provide a minimally invasive, cost effective method to survey carnivores, and this study aimed to address both large scale and finer stand-scale habitat

selection by implementing non-invasive techniques under a multi-scale occupancy framework (MacKenzie et al. 2002; Nichols et al. 2008).

The primary objective of this study was to conduct the first systematic survey of the CA – OR EPA to determine the distribution and size of the marten population, addressing one of the most important information gaps identified in the Humboldt marten conservation strategy. Understanding the habitat needs for a species of conservation concern is necessary for providing a sound basis for developing management and conservation actions. Therefore, a secondary objective was to conduct the first multi-scale occupancy analysis for this population to assess both stand and home range scale occupancy. It is unknown how Humboldt martens are using habitat in the CA – OR EPA, and if a viable population exists in this area it is critical to understand how this population is selecting habitat at multiple spatial scales.

MATERIALS AND METHODS

Study Area

The CA – OR EPA is located primarily in the Six Rivers National Forest (78.6%) and part of the Siskiyou National Forest (21.3%) just east of U.S. Highway 199 in Del Norte County, California near the California – Oregon border ($-123^{\circ} 42' 58''$ W, $41^{\circ} 53' 41''$ N; Figure 2). The study area encompasses approximately 247.9 km², with 90% of the land managed by the U.S. Forest Service. The area is characterized by warm, dry summers and cool, wet winters (3 – 30 °C; Jimerson 1989), and ranges in elevation from 265 – 1910 m. Average annual precipitation is 237 cm, with an average snowfall of 6 cm. The study area ranges from 27.3 to 47.5 km from the coastline. Wildfire is the main disturbance factor in the study region and 13 fires have occurred since 1960, affecting approximately 6.8% of the study area (Fire, Appendix A). Stand clearcutting, commercial thinning, and patch clearcutting are the most prominent treatment types conducted by the U.S. Forest Service in this area, with 7.45% of the study area having experienced clearcutting since 1960.

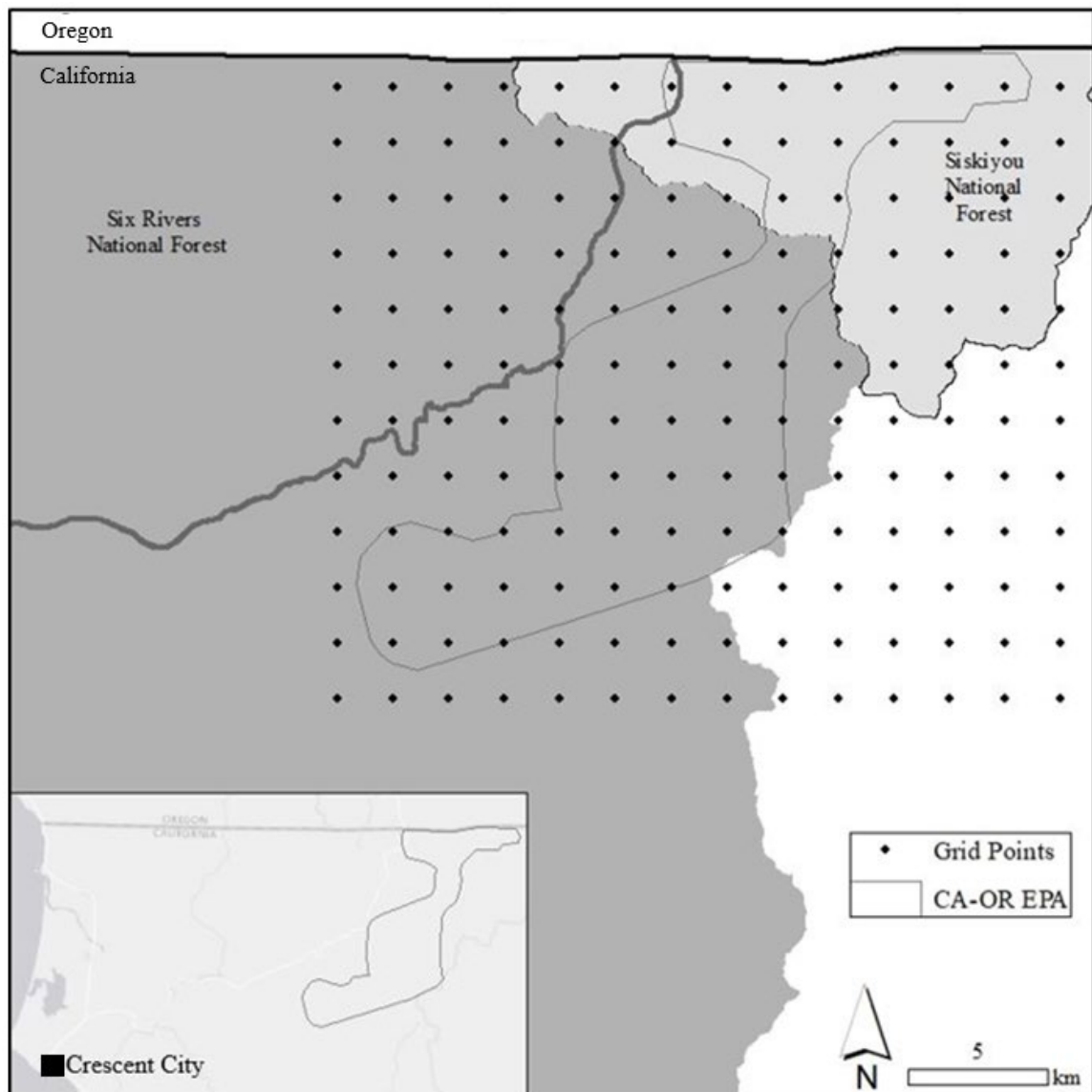


Figure 2. CA – OR Extant Population Area (EPA) in Del Norte County, northern California, USA, 2017 – 2018, depicting central grid points spaced 2-km apart.

The study region is composed of 81.3% non-serpentine soil habitat and 18.7% serpentine soil habitat. The dominant forest types found on serpentine soil within the study area were Jeffrey pine (*Pinus jeffreyi*), knobcone pine (*Pinus attenuata*), manzanita

(*Arctostaphylos spp.*), and some Douglas fir (*Pseudotsuga menziesii*) plant associations. The dominant shrub species on serpentine soil were huckleberry oak (*Quercus vacciniifolia*), manzanita, tanoak (*Lithocarpus densiflora*), and red huckleberry (*Vaccinium parvifolium*) (SERP_hr, Appendix A). The dominant forest types found on non-serpentine soil were primarily Douglas fir plant associations, as well as incense-cedar (*Calocedrus decurrens*), Port Orford-cedar (*Chamaecyparis lawsoniana*), red fir (*Abies magnifica*), and white fir (*Abies grandis*). Hardwoods, such as tanoak plant associations, madrone (*Arbutus menziesii*), and canyon live oak (*Quercus chrysolepsis*) can also be found in the overstory. Tanoak and ericaceous shrubs, such as evergreen huckleberry (*Vaccinium ovatum*) and salal (*Gaultheria shallon*), dominate the understory on non-serpentine soil.

The study area is also characterized by high canopy cover, with 78.8% of the area having canopy cover greater than 55% and 16.2% of the area covered by large trees (size class 5, ≥ 60.0 cm QMD; SC_aveg_5, Appendix A). Areas without trees, small seedling trees, or sapling trees compose 11.4% of the study area (size class 0 – 2, ≤ 14.9 cm QMD). Pole trees (size class 3, 15.0 – 27.8 cm QMD) compose 24.4 % of the study area, and small trees (size class 4, 27.9 – 59.9 cm QMD) compose 48.0% of the study area.

Marten Survey Design

I used the 2-km systematic grid and sample unit design from the Humboldt marten population monitoring protocol (Slauson and Moriarty 2014) as the sampling frame (Figure 2). The distance between grid points is larger than the average diameter of male martens' home ranges elsewhere in California (Slauson et al. 2007), likely ensuring spatial independence from detecting the same individual at adjacent sample units. Sample units were surveyed from June – August during 2017 – 2018 to increase the likelihood of detecting resident adults rather than dispersing juveniles (Slauson and Moriarty 2014; Zielinski et al. 2015).

At each grid point, a two-station sample unit was established: one placed on the grid point (station A) and the second placed 500 m away in a random direction (station B) in an effort to place the stations in two different forest stands. At each station either one remote camera or one track plate was used. If a combination of a remote camera and a track plate was used within one sample unit, I randomly selected at which station each detection device would be used. Survey stations were deployed for a minimum of 21 days as recommended by the protocol (Slauson and Moriarty 2014), with station checks occurring every 3 – 4 days to replace bait, lure, SD cards and batteries for camera stations, and contact paper and toner for track plate stations. Batteries were replaced at camera stations when battery life dropped below 75%.

At stations with remote cameras I used passive infrared-triggered cameras (Command Ops Pro; Browning Trail Cameras, Morgan, Utah) loaded with 32 GB

memory cards programmed to record date, temperature, and time. Camera delays were set to take pictures every 5 seconds once the camera was triggered, with an 8-Shot Standard mode selected. Cameras were mounted to trees with straps and bolts and covered with a security box to prevent bear (*Ursus americanus*) damage. Bait was mounted opposite of the camera tree on a tree no further than 10 m away and less than 0.66 m from the ground. At stations with track plates, I used methods described by Slauson and Moriarty (2014) for placement and bait setup. Due to the challenge of finding two trees suitable for station placement or safety considerations (i.e., avoiding steep cliffs), I allowed for a distance ≤ 50 m from the grid point to find suitable station locations within the same stand.

At each station (camera and track plate) two chicken drumsticks and a commercial trapping lure (Gusto; Minnesota Trapline Products, Pennock, MN) were used to attract local martens (Baldwin and Bender 2008; Moriarty et al. 2018). Hair snares were used at both camera and track plate stations. During 2017, camera hair snares consisted of a strip of 3 gun brushes wrapped with glue (Catchmaster Mouse/Insect Glue Boards 72MB; Catchmaster, Brooklyn, NY) placed approximately 24 cm below the bait on a coroplast collar. During 2018, I added a triangular shaped funnel above the bait with 2 additional gun brushes placed at the entrance of the funnel to increase likelihood of capturing hair at camera stations (Figure 3). At track plate stations, a triangular hair snare was placed inside the box with 3 hair snares (Slauson and Moriarty 2014). All survey methods were approved by the Humboldt State University Institutional Animal Care and Use Committee (protocol 16/17.W.05-A).



Figure 3. Example of a baited remote camera with the funnel hair snare design implemented during the summer field season in northern California, USA, 2018. During 2017 only the strip of 3 gun brushes placed below the bait was deployed.

Occupancy Analysis

I used occupancy modeling to account for imperfect detection and model the influences of habitat characteristics on marten occurrence (MacKenzie et al. 2002). Non-detection of a species in a sample unit does not always indicate that it is unoccupied, only that during the survey period the animal was not detected. Due to the possibility of imperfect detection, occupancy modeling can be used to estimate site occupancy when detection probability is imperfect using the parameter ψ , the probability of site occupancy (MacKenzie et al. 2002).

Due to the fact that habitat selection can occur at multiple spatial scales, I used a multi-scale occupancy analysis to evaluate the influence of habitat characteristics at the stand and home range scale (Nichols et al. 2008). The home range scale was defined as the area within 1 km from the center grid point of each sample unit (314 ha), an area similar to the average home range size of martens elsewhere in California (Slauson et al. 2018). The stand scale was defined as the area of the stand in which the individual station was deployed within each sample unit. A stand refers to a community of trees that can be distinguished from surrounding communities based on uniformity in tree or site characteristics, such as tree age, structure, or species composition (USFS 2016). Stands in the study area ranged in size from 2 – 360 ha.

The robust design multi-scale occupancy framework is an expansion of the single-scale occupancy modeling framework, where the sampling design contains nested primary and secondary surveys to represent multiple spatial scales (Nichols et al. 2008; Mordecai et al. 2011; Pavlacky et al. 2012; Hagen et al. 2016). Two key single-scale occupancy model assumptions are violated under this framework: 1) each site's occupancy status is constant throughout the survey and closed to changes, and 2) detection at each site is independent of the others (Slauson et al. 2012). Nichols et al. (2008) developed a method to account for the closure and non-independence of detection assumptions between scales by introducing the parameter θ , the probability the species is present at the secondary station given occupancy at the primary sample unit. This approach allows for the assessment of occupancy at two spatial scales simultaneously: the larger, primary sample unit (Ψ) and the smaller secondary stations (θ) deployed within

the sample unit (Mordecai et al. 2011). Multi-scale occupancy involves 3 model parameters: the probability of detecting an individual given that the sample unit is occupied and the species is present at the station (p), probability of occupancy at the secondary station (stand) scale given occupancy at the sample unit scale (θ), and probability of occupancy at the primary sample unit (home range) scale (ψ).

A standard encounter history to describe detection/non-detection data is expressed by a series of dummy variables (0 and 1), where 0 indicates non-detection and 1 indicates detection (Cooch and White 2001). For example, the encounter history 010 indicates that an animal was detected at the second survey event but not detected at the first or third. Because there are multiple stations within a sample unit, the encounter history under a multi-scale framework for the sample unit must incorporate the $L = 5$ replicate surveys at $K = 2$ survey stations for a total of 10 dummy variables (Nichols et al. 2008). Survey events were grouped by each of the 3 – 4 day checks, for a total of 5 survey events (L) for each station (K). A sample unit was classified as occupied if a marten detection occurred at one or both stations within a sample unit. An example encounter history for one of the sample units in my study would be written as 00011 10010 under this framework, indicating that a detection occurred at station A on the fourth and fifth survey and on the first and fourth survey at station B.

Previous studies have cautioned against application of occupancy models to sparse data, as it results in poor estimates of occupancy and detection probability (Nichols et al. 2008). Therefore, provided that the data could support a multi-scale occupancy framework, I used a hierarchical modeling approach by first modeling the

detection process (p), followed by the primary home range spatial scale of interest (Ψ), and lastly the secondary stand scale of interest (θ). Due to the limited number of data points available for comparison at the stand scale ($n = 16$), if the data could not support a multi-scale framework, models would be created to address the primary question of what factors most influence marten occupancy at the home range scale under a single scale, single-season occupancy framework. Under this framework, only 2 model parameters are estimated: detection probability (p) and probability of occupancy at the home range scale (Ψ). Comparisons at the stand level (θ) are excluded, and the encounter history for a sample unit is truncated to reflect detections at the home range scale only. For instance, if a sample unit had a detection history of 00011 for station A and 10010 for station B, the encounter history for the entire sample unit is coded with 5 dummy variables as 10011 because detections occurred at station B at event 1, both stations at event 4, and station A at event 5. Assessing habitat use at the home range scale was the primary objective, as this level of selection is particularly important for martens: it provides the resources needed to support year-round life history requirements and is most influential on individual fitness (Thompson et al. 2012; Slauson et al. 2018).

Occupancy modeling allows researchers to model variation in species occurrence and detection simultaneously while exploring hypotheses about site-specific variables (i.e., habitat, environmental factors), as well as survey-specific variables that may influence detection (i.e., bait type used, survey effort) (Cooch and White 2001). To identify candidate variables, I reviewed variables determined to be important based on marten ecology from previous literature (Slauson et al. 2007; Kirk and Zielinski 2009),

expert opinion, and those I hypothesized may be unique to my study area (Appendix A). I used an information-theoretic approach to develop a candidate model set (Burnham and Anderson 2002) by first developing a set of a priori models representing alternative hypotheses of the most influential site-specific and survey-specific variables on marten occurrence and/or detection.

A summary list of variables was considered for inclusion in the models to address my hypotheses, resulting in 52 candidate variables (Table 1, Appendix A). Thirty-five candidate variables were excluded from the candidate set because they were not applicable to my study area, they were highly correlated with other variables, or there were not comparable spatial datasets available for my study area. I conducted a correlation analysis to identify highly correlated variables. Variable pairs with a correlation coefficient $|r| > 0.6$ had the variable with the lower significance at the univariate level (P value) removed from the candidate set. The variables excluded based on correlation included canopy cover, various combinations of patch size, and various combinations of size classes of trees. Land ownership, edge habitat, fire history, and management history were not applicable to the study area as so little of the study area was effected by these factors in the past 60 years. Variables describing seral stage were excluded from the candidate set due to the spatial dataset lacking coverage of the entire study area (SERAL; Appendix A). The final candidate set of variables included 7 variables for detection probability (p), 5 for stand scale occupancy (θ), and 5 for home range scale occupancy (Ψ) (Table 2).

Table 1. List of variables and their associated predictions evaluated during the exploratory analysis for predicting single- and multi-scale occupancy for Humboldt martens in northern California, USA, 2017 – 2018.

Variable	Reference	Ecology	Prediction
Canopy Cover	Slauson et al. 2007; Thompson et al. 2012; Moriarty et al. 2016	Foraging/Cover	Select for high canopy cover
Habitat Type	Slauson et al. 2007; Slauson et al. 2009; Kirk and Zielinski 2009; Zielinski 2014; Moriarty et al. 2016	Resting/Denning/Foraging	Select for late-seral, old growth
Course Woody Debris	Slauson et al. 2007; Andruskiw et al. 2008; Kirk and Zielinski 2009; Thompson et al. 2012; Zielinski 2014	Resting/Denning/Foraging	Select for high density of course woody debris (i.e., logs)
Snags	Payer and Harrison 2003; Thompson et al. 2012	Resting/Denning	Select for high density of snags, > 10 m ³ /ha
Elevation	Kirk and Zielinski 2009; Slauson et al. 2009; Zielinski 2014; Zielinski et al. 2017	Competitive Exclusion/Prey Availability	Select for high elevation ($\geq 1,350$ m)
Patch Size	Slauson et al. 2009; Zielinski et al. 2015	Connectivity	Select for larger patch size
Land Ownership	Kirk and Zielinski 2009	Habitat/Fragmentation	Select for public land
Shrub Cover	Slauson et al. 2007; Slauson et al. 2009; Payer and Harrison 2003	Cover/Foraging/Resting	Select for high shrub cover
Road	Slauson et al. 2009; Zielinski 2014	Fragmentation/Direct Mortality/Predators/Competitors	Select against high road density
Edge	Kirk and Zielinski 2009; Slauson et al. 2009; Moriarty et al. 2016	Fragmentation	Select against increased amount of edge habitat
Fire History	Zielinski 2014	Habitat Alteration	Select against areas with burned sites
Management History	Zielinski 2014	Habitat Alteration	Select against areas recently altered (clear cut, thinned)
Basal Area	Payer and Harrison 2003; Thompson et al. 2012	Habitat/Denning/Resting	Select for large basal area (≥ 60.0 cm QMD)
Mean Tree Height	Payer and Harrison 2003	Cover	Select for tree height > 9 m

Table 2. Final set of candidate variables included in each level of analysis in modeling detection probability p ($n = 7$), stand scale occupancy θ ($n = 5$), and home range scale occupancy Ψ ($n = 5$) for Humboldt martens in northern California, USA, 2017 – 2018.

Scale	Variable	Description	Prediction	Source
p	Session_B	Survey session (Jun or July+Aug)	p decreases later in season	Raw data
	Duration	Number of days station was out	p increases for longer survey duration	Raw data
	sc_everg_5	Stand was classified as size class 5 (Yes or No)	p increases in habitat with large trees	SRNF GIS Database
	stream_s	Distance to nearest stream (m)	p increases closer to streams	U.S. Census Bureau
	shrub	Average % shrub cover	p increases with higher shrub cover	Raw data
	road_s	Distance to nearest road (m)	p increases further from roads	U.S. Census Bureau
	log_snag	Density of snags & logs ≥ 60 cm diameter and 2 m height/unit area	p increases with higher density of snags & logs	Raw data
θ	stream_s	Distance to nearest stream (m)	θ increases closer to streams	U.S. Census Bureau
	road_s	Distance to nearest road (m)	θ increases further from roads	U.S. Census Bureau
	shrub	Average % shrub cover	θ increases with higher shrub cover	Raw data
	sc_everg_5	Stand was classified as size class 5 (Yes or No)	θ increases in habitat with large trees	SRNF GIS Database
	log_snag	Density of snags & logs ≥ 60 cm diameter and 2 m height/unit area	θ increases with higher density of snags & logs	Raw data
Ψ	elev_ave	Average elevation (m) per 1 km buffer, standardized using z-scores	Ψ increases at higher elevation	SRNF GIS Database
	slope	Average slope (%) across 1 km buffer	Ψ increases with lower slope	SRNF GIS Database
	SC_everg_5	Proportion of size class 5 per 1 km buffer	Ψ increases with greater proportion of large trees	SRNF GIS Database
	STREAM_hr	Stream density (km/km ²)	Ψ increases with greater stream density	U.S. Census Bureau
	ROAD_hr	Road density (km/km ²)	Ψ increases with lower road density	U.S. Census Bureau

To generate site-specific habitat variables used in the candidate set of models, I used a combination of available geographic information system (GIS) layers and vegetation data I collected in the field. At the stand scale and detection level, GIS layers were used to calculate the distance to roads (m), distance to streams (m), and the size class (1 – 5) of the stand each station was placed in (Appendix A). I also measured variables in the field representing elements of forest structural complexity known or hypothesized to be important for martens at the stand level, but that are not typically available from remotely sensed GIS vegetation layers (i.e., density of logs, snags, and percent shrub cover). Survey-specific variables, such as the duration and month stations were active, were recorded and used to model the detection process. I hypothesized that site-specific habitat variables may influence both the detection process (i.e., whether martens are more frequently detected within more productive stands), as well as occurrence at the stand level (i.e., whether martens are more likely to occupy more productive stands).

To measure stand structural elements, I used variable-width belt transects to assess the density of snags, coarse woody debris (i.e., downed logs), and cut stumps (Bate et al. 1999). At each station, two 100 m transects were established using a random azimuth to determine the direction of the first. The second transect was placed perpendicular to the first with their crossing point centered on the station location. Transect width varied between 5 – 40 m along each transect based on the maximum distance to which the observer could reliably see snags and downed logs. For each snag and downed log counted, I measured DBH (cm), height (m), and decay using the decay

classification system of Thomas et al. (1979). I only recorded snags that were taller than 2 m and wider than 60 cm in diameter, and downed logs that had a maximum diameter \geq 60 cm. The density of logs and snags was calculated by dividing the number of snags and logs recorded per transect by the total area of the transect (transect length x belt width). Average stand densities of snags and downed logs were used as covariates in the multi-scale occupancy analysis (log_snags, Table 2) and for univariate comparison between stations where martens were and were not detected.

To characterize the shrub layer in each stand, I estimated the total percent shrub cover and rank-order shrub species dominance using a 1x1 m quadrant placed at each 5 m interval along each variable-width belt transect. To estimate shrub cover, I visually estimated the percentage of the quadrant covered by shrubs less than 2 m in height to exclude small hardwood trees. Next, I determined the most dominant plant species within each quadrant. By assigning rank-dominance values from 1 – 5, with 5 given to the most dominant species and 1 to the least dominant, this allowed me to generate a total rank-sum estimate for all shrub species at each station (i.e., stand). Estimates of total shrub cover were used as covariates for multi-scale occupancy analysis (shrub, Table 2) and for univariate comparison between stations where martens were and were not detected. Shrub species rank-sums were only used for univariate comparison between stations with and without marten detections.

At the home range level, GIS layers were used to calculate the average elevation (m), percent slope, stream density (km/km²), and road density (km/km²) within each 1 km radius sample unit (Appendix A). The California Wildlife Habitat Relationships (CWHR)

system was used to classify trees in the study area and estimate the percent of large diameter trees (size class 5 trees ≥ 60.0 cm QMD) present in each 1 km radius sample unit. The CWHR variable ‘size class 5’ (SC_aveg_5; Table 2) was used to identify vegetation types associated with forest compositional features most important for martens’ life history requirements (i.e., reproduction), as large diameter trees are closely associated with dense, late-seral forest types and females are highly selective for reproductive habitat features associated with these trees (Kirk and Zielinski 2009). Variables with widely differing ranges from others, such as elevation (444 m – 1,528 m) compared to percent large diameter trees (0 – 100 %), were standardized around a mean of zero by subtracting each value by the mean and dividing by the standard deviation, where a one-unit change reflects a change of one standard deviation away from the mean of the original variable (Kéry and Royle 2016).

I limited the total number of variables per occupancy model to include a minimum of 10 observations per variable, resulting in all models with ≤ 4 variables. Using this approach, 18 candidate models were developed to model detection probability, then 23 models were developed to model occupancy at the home range scale, and 11 models were developed at the stand scale. Program PRESENCE (MacKenzie and Hines 2006) and MARK (White 2001) were used to fit occupancy models to the data.

I used Akaike’s Information Criterion adjusted for small sample size (AIC_c) to evaluate alternative models for detection probability and occupancy. To evaluate the relative strength of each variable I calculated adjusted variable importance weights (Burnham and Anderson 2002). I calculated a 95% confidence set of models by summing

the Akaike weights of the top models until they reached 0.95 (Burnham and Anderson 2002). Individual model fit was evaluated in program PRESENCE (MacKenzie and Hines 2006) using a parametric bootstrap goodness of fit test with 10,000 simulations. The goodness of fit test was used to generate an overdispersion parameter, \hat{c} , to evaluate whether the top model adequately fit the data set. The general approach for this method is to run the test on the most global model; however, when the number of parameters in the global model is large then poor precision of \hat{c} can make it difficult to detect lack-of-fit. In such cases it is recommended to perform the test on a more parsimonious model (MacKenzie and Bailey 2004), and the resulting \hat{c} was used to adjust the model set if warranted.

Univariate Analysis

I conducted univariate analyses of covariates at both the stand and home range scales during the preliminary stages of the analysis to identify variables that were significantly different between sample units and stations that had or had not detected martens. At the stand scale, paired t-tests were performed on the sample units with detections at one station but not the other to assess variables that may be important at the stand scale within known occupied home ranges. Two-sample t-tests were performed on all stations with detections compared to non-detections regardless of sample unit level occupancy to further assess the variables that may be significant at the stand scale. Furthermore, descriptive statistics for the vegetation sampling were generated, including

box and whisker plots and the mean density of logs, snags, and percent shrub cover. Two-sample t-tests were also performed at both stand and home range scales to assess differences between detections and non-detections at stations/sample units placed on serpentine soil, as well as between serpentine detection stations/sample units and non-serpentine detection stations/sample units.

RESULTS

Marten Surveys

I surveyed for martens at 51 sample units from June – August in 2017 and 2018. Martens were detected at 20 of 51 sample units (Figure 4), resulting in an unadjusted naïve occupancy of 0.39. Of the 102 stations surveyed (2 per sample unit), martens were detected at 24 stations. Four sample units had marten detections at both stations, and 16 sample units had detections at only one station. Two sample units detected multiple individuals (apparent family groups) in the same image, suggesting reproducing females were detected at these sample units (Figure 4, Appendix B). Nine sample units were dominated by serpentine habitat and martens were detected at four (44.4%) of these. Forty-two sample units were dominated by more productive, non-serpentine forest habitat and martens were detected at 16 (38.1%) of these.

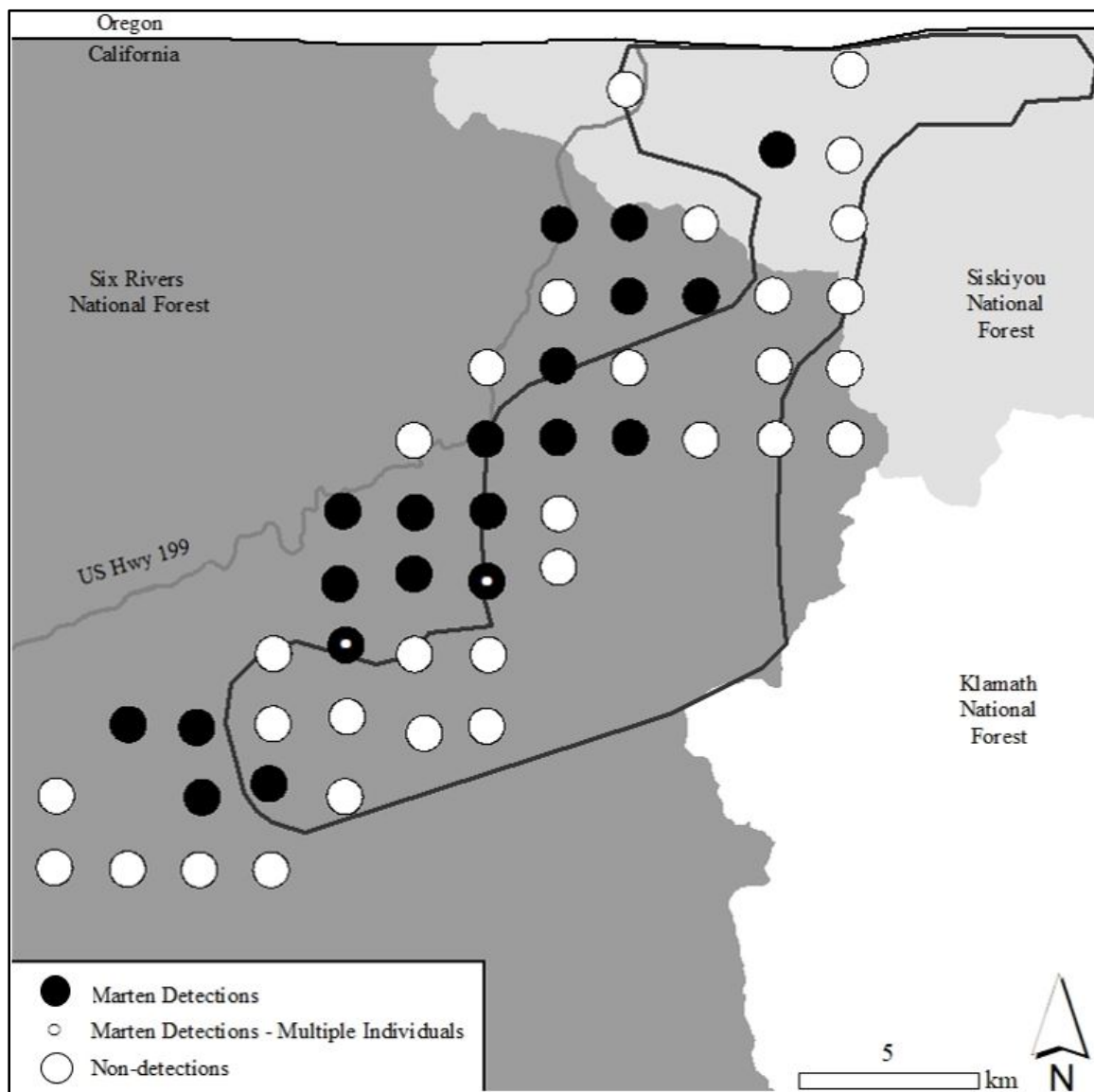


Figure 4. Locations of 51 sample units surveyed from 2017 – 2018 in the CA – OR Extant Population Area (EPA) in Del Norte County, northern California, USA, depicting sample units with Humboldt marten detections ($n = 20$; closed circles), no detections ($n = 31$; open circles), and where females with kits were detected ($n = 2$).

I surveyed 21 sample units in 2017 and 30 sample units in 2018 over two 1-month sessions each year (Table 3). Limited road access and hazardous terrain in some portions

of the study area limited my ability to survey all of the sample units in the CA – OR EPA. Survey stations were deployed for 14 – 28 days (mean = 20 days). Due to a fire near the end of session 4 and camera malfunctions, some stations were surveyed for fewer than the average number of survey days. A few sites with greater than the average number of survey days were left out longer to capture hair samples. I captured 14 hair samples that will be used in a future study to identify individuals, contributing to a population estimate and to understand their genetic relationship to other known populations. Track plate stations were inoperable on 29% of station checks due to bear damage. Inoperable station checks were coded as ‘missing data,’ and due to low detection probabilities from the track plate stations in 2017 (Figure 5) they were excluded from use during 2018, and two camera stations were deployed within each sample unit in the same layout as secondary stations were placed in 2017.

Table 3. Deployment dates for the four sessions of sample units established during the field seasons of 2017 ($n = 21$) and 2018 ($n = 30$) in northern California, USA, 2017 – 2018.

Session	No. sample units	Survey dates	Year
1	10	29 Jun – 22 Jul	2017
2	11	23 Jul – 9 Aug	2017
3	15	4 Jun – 27 Jun	2018
4	15	2 Jul – 23 Jul	2018

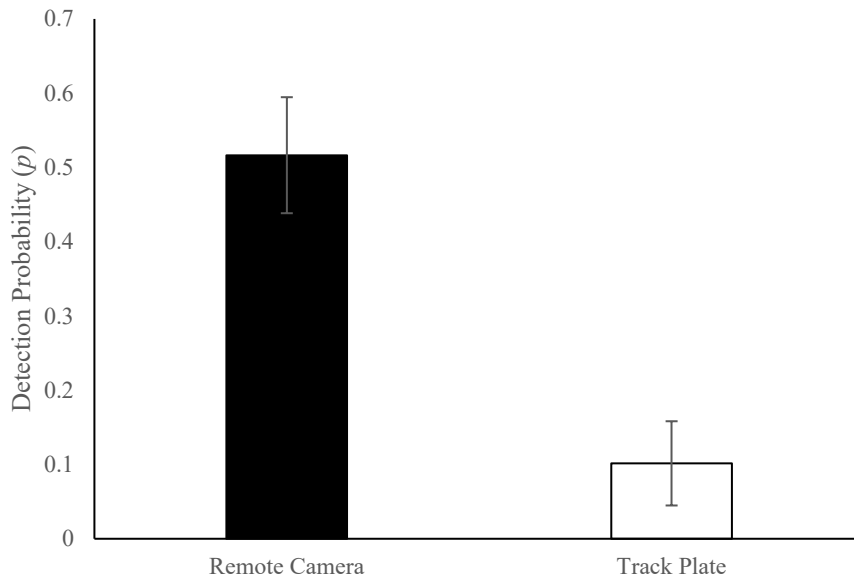


Figure 5. Detection probability per check interval (3 – 4 days) and standard error for remote camera stations ($n = 21$) and track plate stations ($n = 21$) deployed in northern California, USA, 2017.

Remote camera stations were active for a total of 1670 camera nights during 2017 – 2018. Marten detection events ($n = 68$) were primarily diurnal ($n = 44/68$), defined as 30 minutes after sunrise to 30 minutes before sunset. Fifty-three percent of marten detections ($n = 36/68$) occurred between 0530 – 0900. Latency to first detection at camera stations ranged from 2 – 13 days (mean = 6.6 days). At stations where martens were detected ($n = 24$), repeat detections occurred at 15 stations ($n = 14$ cameras and 1 track plate) and single detections occurred at 9 stations ($n = 7$ cameras and 2 track plates). The number of repeat detections at each camera station ranged from 2 – 13 detections (mean = 3.6 detections).

Occupancy Analysis

Detection Probability

Of the 18 candidate models estimating detection probability, nine models occurred in the 95% confidence set (Table 4). The top model for marten detection probability included the variables session (temporal period stations were active) and duration (length of time the station was surveyed) (Table 4; see Appendix C for complete model set). The top 3 models with session and/or duration held 73% of the total AIC_c weight, and the top model was 8.80 times more likely than model 4 based on relative weights (Table 4). Session and duration also had the highest variable importance weights (Table 5). The top model was used in all subsequent candidate models for estimating occupancy.

Based on the top model, odds of detecting a marten in July/August were 3.37 times greater than in June (Odds Ratio [OR] = 3.37, 95% CI = 1.25 – 9.10), after adjusting for the effects of duration (Figure 6a). Detection probability (p) for each check interval was 0.24 in June (95% CI = 0.13 – 0.40) and 0.52 in July/August (95% CI = 0.35 – 0.68), and the overall survey detection probability was 0.75 in June and 0.98 in July/August after five check intervals. For every 1 check interval increase in the duration that stations were active, the odds of detection were 11% greater (OR = 1.11, 95% CI = 1.00 – 1.22), after adjusting for the effects of survey session (Figure 6b).

Table 4. Detection probability models included in the 95% confidence set for Humboldt martens studied in northern California, USA, 2017 – 2018, ranked using $\Delta AICc$ values.

Model	Session	Duration	Stream	Road	Logs & Snags	K	$\Delta AICc$	Weight	Relative Weight
1	X	X				4	0.00	0.48	1
2	X					3	2.67	0.13	3.80
3		X				3	2.70	0.12	3.86
4			X	X		4	4.37	0.05	8.80
5					X	3	5.12	0.04	12.84
6			X		X	4	5.27	0.03	13.97
7				X	X	4	5.54	0.03	15.83
8			X			3	5.79	0.03	18.27
9				X		3	6.12	0.02	21.59
Null						1	6.99	0.01	33.93

X = variable was used in the model

K = number of parameters in the model

$\Delta AICc$ = difference in the Akaike's Information Criterion score (adjusted for small sample size) relative to the top model

Weights = Akaike weight (adjusted for small sample size)

Relative weight = likelihood of the top model relative to the other models

Table 5. Individual variable importance weights for detection probability variables, where n represents the number of times a variable occurred in the candidate model set.

Variable	Weights	n
Session	0.601	2
Duration	0.598	2
Stream	0.132	5
Logs/Snags	0.123	5
Road	0.119	5
Size Class 5	0.032	5
Shrub	0.029	4

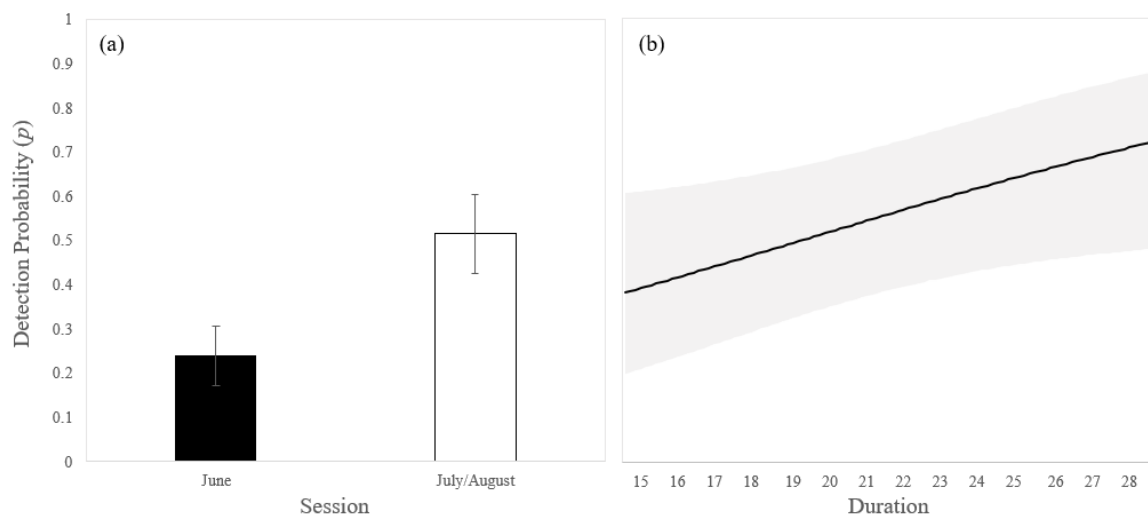


Figure 6. Probability of detecting a marten per check interval (3 – 4 days), along with associated 95% confidence intervals, as influenced by (a) survey session during June (0) and July/August (1), and (b) the duration of days the sample unit was deployed in northern California, USA, 2017 – 2018.

Stand Scale

There were only 16 paired stations (i.e., marten detections at one station but no detection at the second station within the same sample unit) available to draw inferences about θ , the probability of occupancy at the stand level, given occupancy at the home range level (Ψ). I attempted to fit models under the multi-scale occupancy framework, but models with this level of complexity could not be supported. Due to the sparseness of the dataset, extrinsic non-identifiability prohibited the estimation of parameters in the model. In the case of extrinsic non-identifiability, there is insufficient information in the dataset for a given parameter and thus it is difficult to draw conclusions from the data (Cooch and White 2001). After determining the multi-scale models could not be supported, I proceeded with a single-scale occupancy analysis at the home range scale and evaluated stand scale habitat relationships in a separate univariate analysis. Due to the differences between sample units dominated by serpentine habitat and those dominated by non-serpentine habitat, differences between sample units in these habitat types were analyzed separately. Due to the limited number of sample units dominated by serpentine habitat, I only included non-serpentine dominated sample units in the occupancy analysis.

Home Range Scale

Of the 23 candidate models for estimating marten occupancy at the home range scale, only 4 were included in the 95% confidence set (Table 6). The top model influencing marten occupancy at the home range scale included the variables elevation, amount of CWHR size class 5 forest habitat (% SC5), and an interaction between these

two variables (Table 6; see Appendix D for complete model set). The next most competitive model included only elevation, but the top model was 4.06 times more likely than this model based on its relative weight (Table 6). Elevation and amount of CWHR size class 5 forest habitat available had the highest variable weights (Table 7). Based on the top model, the adjusted occupancy estimate was 0.41 (95% CI 0.37 – 0.44), only slightly higher than the naïve estimate (0.39).

Table 6. Table of occupancy models included in the 95% confidence set for Humboldt martens studied in northern California, USA, 2017 – 2018, ranked using $\Delta AICc$ values.

Model	Elevation	% Size Class 5	Elevation * % Size Class 5	Stream	K	$\Delta AICc$	Weight	Relative Weight
1	X	X	X		7	0	0.67	1
2	X				5	2.8	0.17	4.06
3	X			X	6	4.89	0.06	11.51
4	X	X			6	5.39	0.05	14.84
Null					1	21.38	0.00	> 100

X = variable was used in the model

K = number of parameters in the model

$\Delta AICc$ = difference in the Akaike's Information Criterion score (adjusted for small sample size) relative to the top model

Weights = Akaike weight (adjusted for small sample size)

Relative weight = likelihood of the top model relative to the other models

Table 7. Variable weights for home range scale variables based on Akaike weight, where n represents the number of times the variable occurred in the candidate model set.

Variable	Weight	n
Elevation	0.992	8
% Size Class 5	0.770	13
Stream Density	0.080	10
Slope	0.030	9
Road Density	0.015	9

The top model for Humboldt marten occupancy contained an interaction between elevation and amount of CWHR size class 5 forest habitat (% SC5). To understand this interaction, the effects of elevation on occupancy were modeled against values selected to represent low (4.1%) and high (30.3%) values of % SC5. Similarly, the effects of % SC5 on occupancy were modeled against values selected to represent low (503 m) and high (913 m) elevation. High and low values for % SC5 and elevation were selected by using the values associated with one standard deviation below and above the mean for each variable. However, because the value for high elevation using one standard deviation above the mean of elevation (1,112 m) was beyond the range of the data available for accurate interpretation (Figure 7), the maximum elevation value where martens were detected (913 m) was used to model the effects of % SC5 at high elevation.

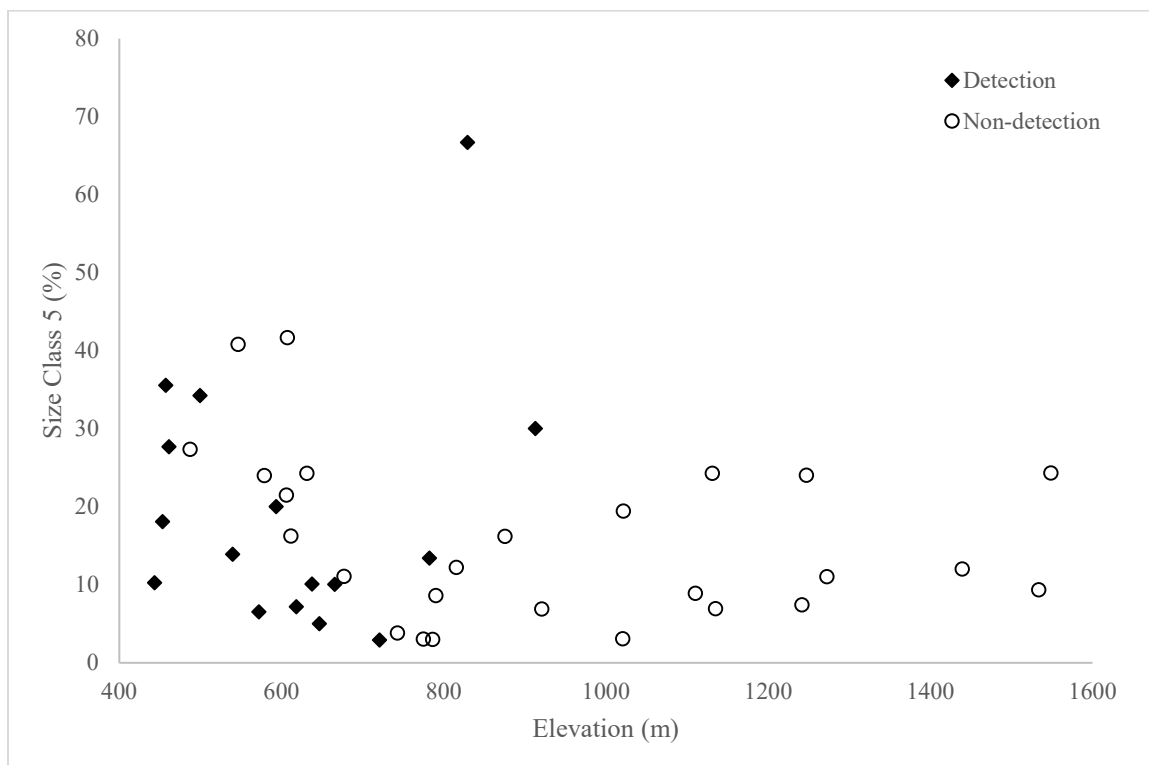


Figure 7. Relationship between elevation and % size class 5 between sample units (non-serpentine, $n = 42$) where martens were detected (closed) and not detected (open) in northern California, USA, 2017 – 2018.

Elevation ranged from 444 – 1,548 m (mean = 809.2 m, SE = 46.9 m) across all sample units, with most marten detections occurring in non-serpentine habitats between 444 – 913 m (Figure 8). Two detections occurred at higher elevations (1,068 and 1,117 m) with small amounts of % SC5 (<2%) but were excluded from the model due to the confounding nature of the serpentine habitat type on which they occurred. As elevation increased, probability of occupancy decreased in units of both low and high % SC5, but this decrease was more pronounced when there was low % SC5 (Table 8, Figure 9). A 100 m increase in elevation at low % SC5 was associated with an 88.7% decrease in odds

of occurrence (OR = 0.113, 95% CI = 0.054 – 0.235, Figure 9a), after adjusting for the effects of % SC5 and the interaction. A 100 m increase in elevation at high % SC5 was associated with an 11.5% decrease in odds of occurrence (OR = 0.885, 95% CI = 0.181 – 4.33, Figure 9b), after adjusting for the effects of % SC5 and the interaction.

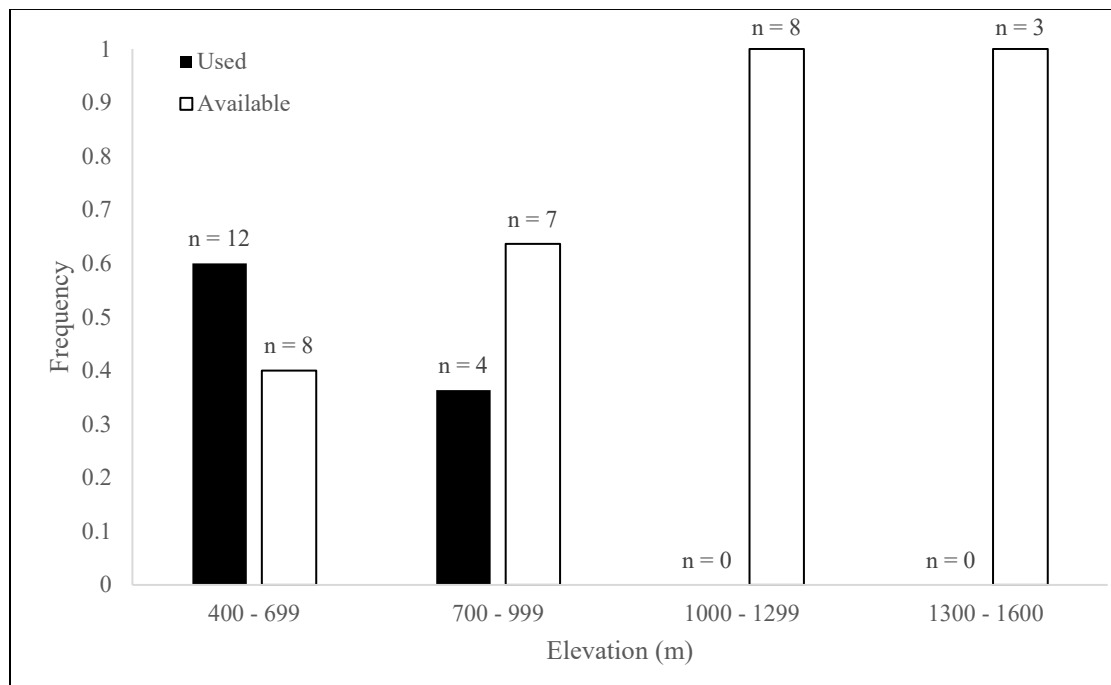


Figure 8. Proportion of used vs. available non-serpentine sample units within each range of elevation for Humboldt martens in northern California, USA, 2017 – 2018.

Table 8. Change in probability of occupancy (Ψ), with associated 95% confidence intervals, as percent size class 5 (% SC5) is held constant and elevation (Elev) changes for the population of Humboldt martens studied in northern California, USA, 2017 – 2018.

Elev (m)	% SC5	Ψ	LCI	UCI
506	4.1	0.988	0.707	1.000
809	4.1	0.099	0.012	0.498
913	4.1	0.011	0.000	0.303
506	30.3	0.57	0.230	0.855
809	30.3	0.477	0.120	0.859
913	30.3	0.446	0.063	0.906

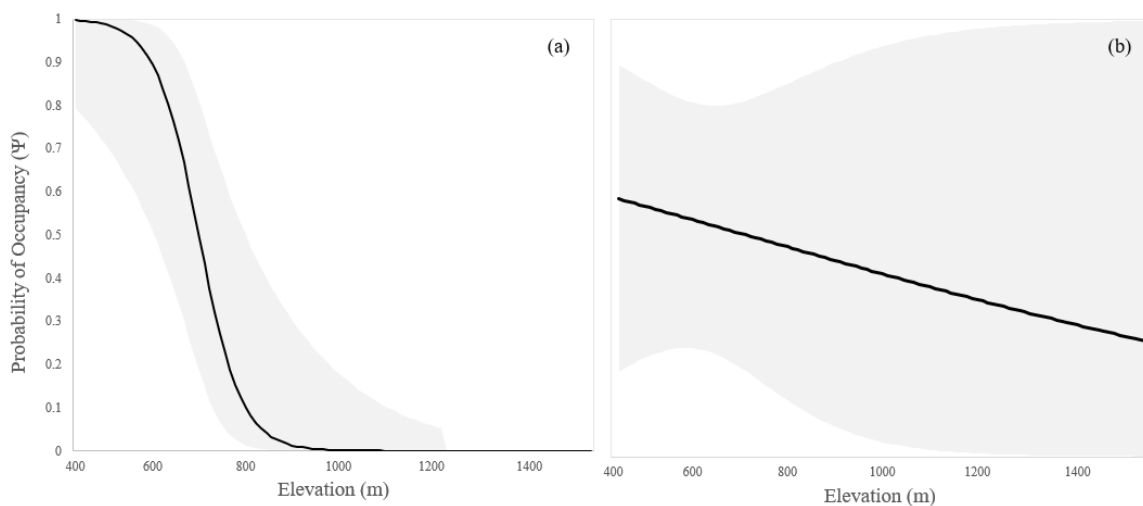


Figure 9. Probability of marten occupancy, along with associated 95% confidence intervals, as influenced by (a) elevation at low percent size class 5 (4.1%) and (b) elevation at high percent size class 5 (30.3%) in northern California, USA, 2017 – 2018.

Percent of CWHR size class 5 forest habitat measured at the home range scale

(314.1 ha) ranged from 0 – 66.7% (mean = 17.2% [54.1 ha], SE = 2.0% [6.4 ha]) across

all sample units. Marten detections primarily occurred in non-serpentine sample units containing between 2.9 – 41.7% (mean = 15.8% [49.7 ha], SE = 3.7% [11.5 ha]) with a disproportionate selection for sample units that fell within the % SC5 range of 30.0 – 42.0% (Figure 10). At the two sample units females with kits were detected, % SC5 was 13.9% (43.7 ha) and 27.7% (87.0 ha). Overall, occupancy decreased with increasing % SC5 at low elevation, whereas occupancy increased with increasing % SC5 at high elevations (Table 9). For every 5% increase in SC5 at low elevations, odds of occurrence decreased by 54.4% (OR = 0.456, 95% CI = 0.097 – 2.14, Figure 11a), after adjusting for the effects of elevation and the interaction. For every 5% increase in SC5 at high elevations, odds of occurrence was 2.25 times greater (OR = 2.25, 95% CI = 1.52 – 3.33, Figure 11b), after adjusting for the effects of elevation and the interaction.

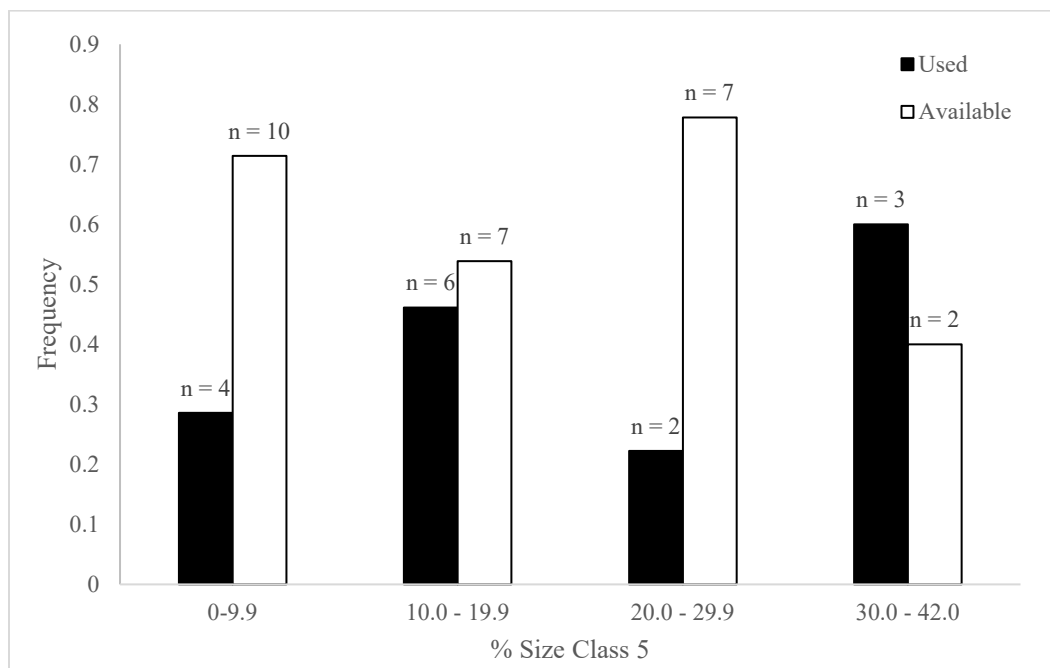


Figure 10. Proportion of used vs. available non-serpentine sample units within each range of percent size class 5 for Humboldt martens in northern California, USA, 2017 – 2018.

Table 9. Change in probability of occupancy (Ψ), with associated 95% confidence intervals, as elevation (Elev) is held constant and percent size class 5 (% SC5) changes for the population of Humboldt martens studied in northern California, USA, 2017 – 2018.

Elev (m)	% SC5	Ψ	LCI	UCI
506	4.1	0.988	0.715	1.000
506	17.2	0.912	0.603	0.986
506	30.3	0.57	0.229	0.858
913	4.1	0.011	0.000	0.295
913	17.2	0.088	0.013	0.429
913	30.3	0.446	0.060	0.908

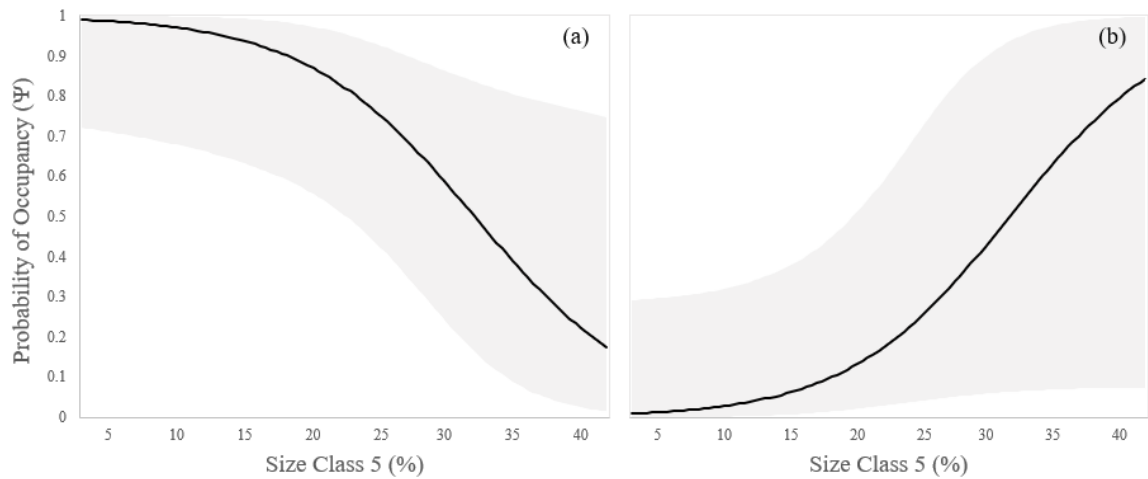


Figure 11. Probability of marten occupancy, along with associated 95% confidence intervals, as influenced by (a) percent size class 5 at low elevation (506 m), and (b) percent size class 5 at high elevation (913 m) in northern California, USA, 2017 – 2018.

Stream density was the third variable to occur in the 95% confidence set (Table 6) and was the third most important variable based on variable importance weights (Table 7). Stream density per sample unit ranged from 0.11 – 2.41 km/km² (mean = 1.29 km/km², SE = 0.07), with marten detections occurring between 0.64 – 2.41 km/km² (mean = 1.44 km/km², SE = 0.11) (Figure 12). Average stream density for sample units ≤ 800 m elevation was 1.43 km/km², whereas average stream density for sample units > 800 m elevation was 1.08 km/km².

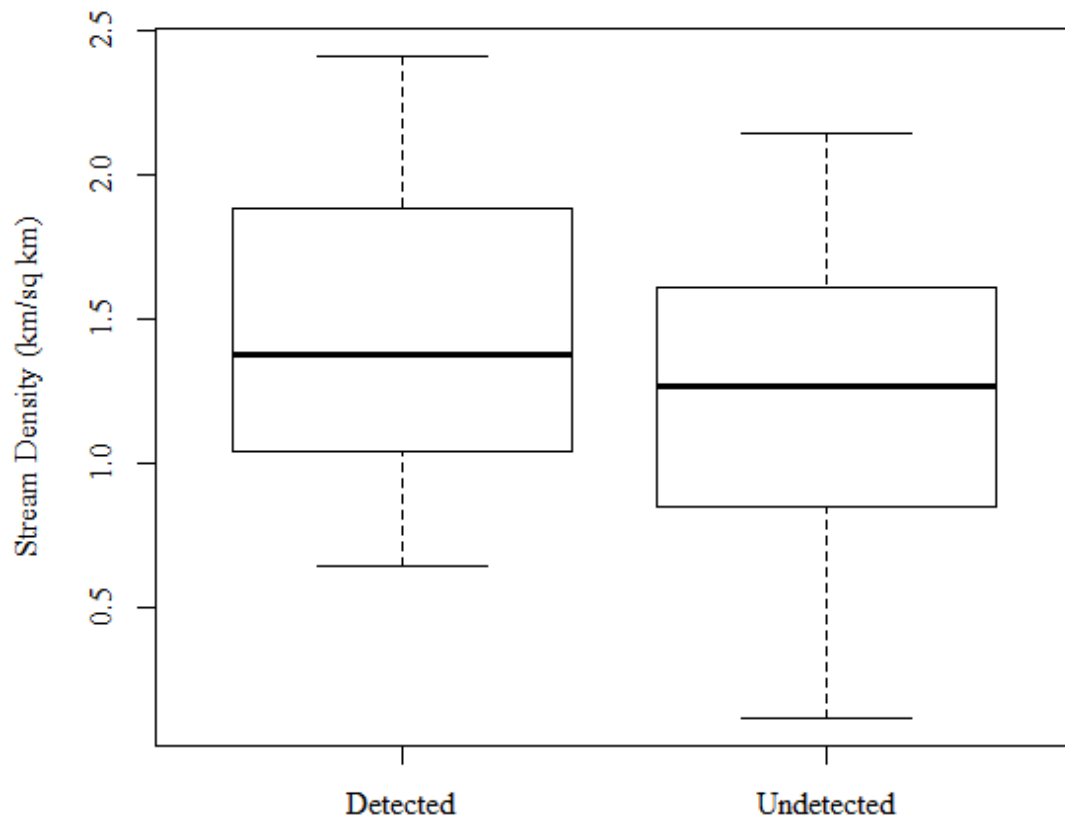


Figure 12. Box and whisker plot for stream density at sample units where martens were detected ($n = 20$) and not detected ($n = 31$) in northern California, USA, 2017 – 2018. The box depicts the interquartile range (middle 50%), and the whiskers depict the minimum/maximum values of each field.

Univariate Analysis

A total of 204 vegetation transects were completed to estimate stand scale structural conditions. The most dominant shrub species present in all stands surveyed, as well as stands where martens were detected, were evergreen huckleberry, salal, and tanoak (Table 10). There was no significant difference between percent shrub cover, proportion of logs, snags, or cut stumps at detection and non-detection stations (Table 11). Seventy-five percent of the data fell between 19.3 – 65.3% shrub cover at detection sites, and 14.6 – 72.4% at non-detection sites (Figure 13). Seventy five percent of the data fell between 0 – 19.7 logs and snags per hectare at detection sites, and 0 – 8.3 logs and snags per hectare at non-detection sites (Figure 14).

Table 10. Top-ranking dominant shrub species present in all vegetation transects conducted (detection and non-detection stations), as well as for transects conducted where martens were detected. Rank estimates were taken from rank-order transect sampling from 2017 – 2018 in northern California, USA.

Shrub species (All transects, $n = 204$)	% Rank Total	Shrub species (Martens detected, $n = 48$)	% Rank Total
Tanoak (<i>Notholithocarpus densiflorus</i>)	25.5	Evergreen huckleberry (<i>Vaccinium ovatum</i>)	24.6
Evergreen huckleberry (<i>Vaccinium ovatum</i>)	14.2	Tanoak (<i>Notholithocarpus densiflorus</i>)	22.8
Salal (<i>Gaultheria shallon</i>)	10.7	Salal (<i>Gaultheria shallon</i>)	10.7
Huckleberry oak (<i>Quercus vacciniifolia</i>)	10.5	Sword fern (<i>Polystichum munitum</i>)	8.8
Manzanita (<i>Arctostaphylos</i> spp.)	8.9	Manzanita (<i>Arctostaphylos</i> spp.)	7.7
Sword fern (<i>Polystichum munitum</i>)	6.6	Oregon grape (<i>Mahonia aquifolium</i>)	6.3
Oregon grape (<i>Mahonia aquifolium</i>)	5.9	Other	< 5%
Other	< 5%		

Table 11. Mean density of snags, logs, and cut stumps calculated from all vegetation transects (detection, $n = 48$, and non-detection stations, $n = 156$) conducted in northern California, USA, 2017 – 2018. Standard error is in parentheses.

Variable	Detection	Non-detection	<i>P</i>
Shrub Cover (%)	33 (4)	29.5 (2)	0.36
Snags (#/ha)	2.74 (1.07)	1.51 (0.29)	0.12
Logs (#/ha)	7.57 (1.59)	5.39 (0.90)	0.29
Logs & Snags (#/ha)	10.31 (2.12)	6.91 (0.98)	0.14
Cut stumps (#/ha)	6.26 (1.34)	6.28 (1.49)	0.99

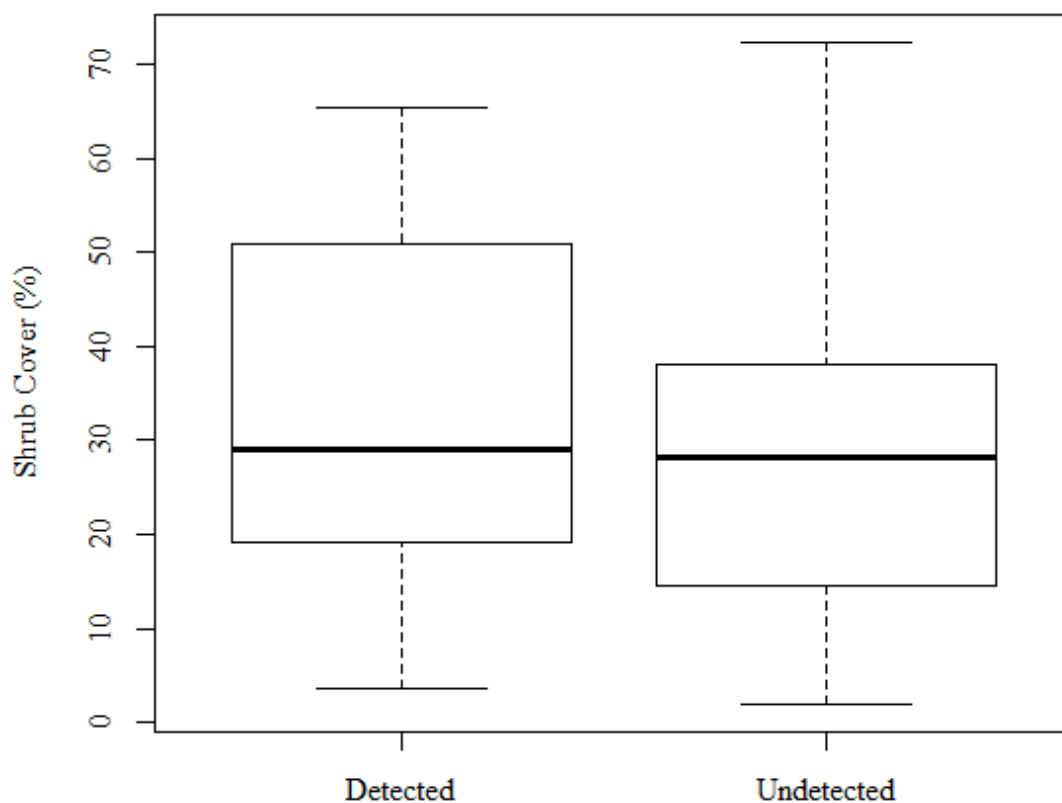


Figure 13. Box and whisker plot for mean percent shrub cover at stations where martens were detected ($n = 24$) and not detected ($n = 78$) in northern California, USA, 2017 – 2018. The box depicts the interquartile range (middle 50%), and the whiskers depict the minimum/maximum values of each field.

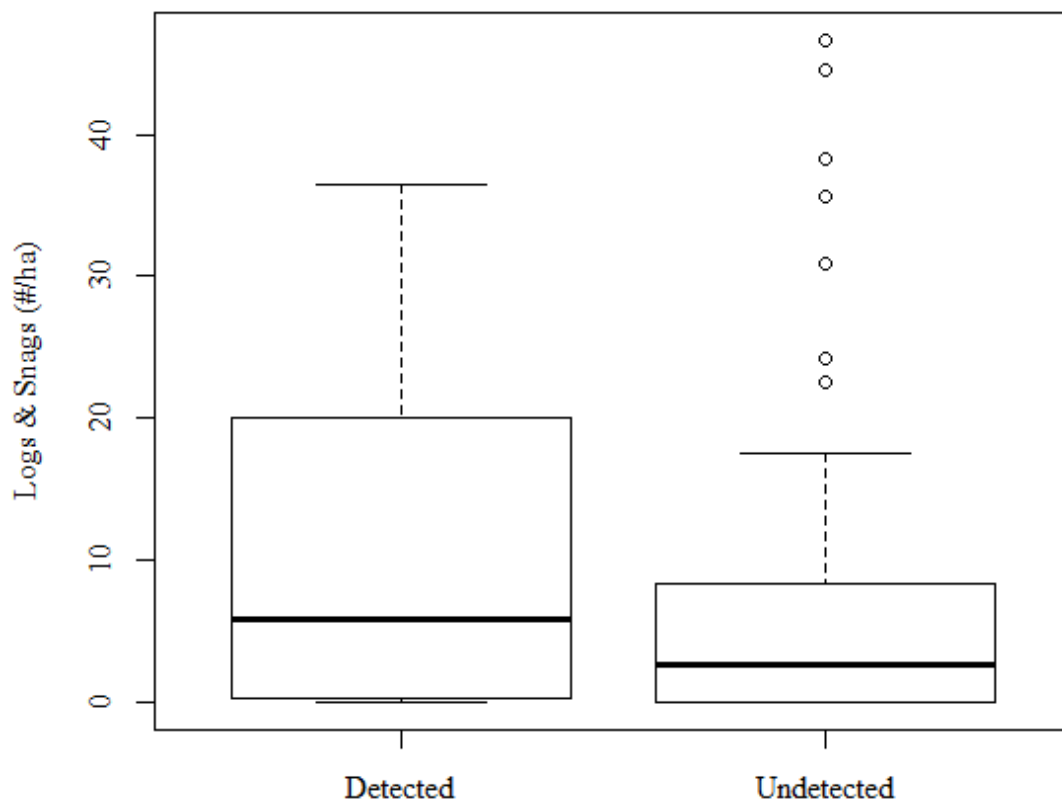


Figure 14. Box and whisker plot for mean density of logs and snags at stations where martens were detected ($n = 24$) and not detected ($n = 78$) in northern California, USA, 2017 – 2018. The box depicts the interquartile range (middle 50%), and the whiskers depict the minimum/maximum values of each field.

Within occupied sample units, stations with detections were significantly further from the nearest road, with detections occurring 108 m further away from the nearest road than non-detections (mean = 238 m, 95% CI = 133 – 343 m; Table 12). Regardless of sample unit level occupancy, all stations with detections compared to non-detections revealed that distance to the nearest stream significantly influenced stand level use, with detections occurring 111 m closer to the nearest stream (mean = 180 m, 95% CI = 125 – 236 m; Table 13). Shrub cover, logs, snags were not significantly different for detected

and non-detected sites in either of the univariate analyses, although shrub cover was marginally significant ($P = 0.086$) for paired stations within occupied sample units, with detections occurring in stands with 7% higher shrub cover (mean = 37%, 95% CI = 28 – 46%; Table 12). None of the covariates were significantly different between all serpentine and non-serpentine detections; however, shrub cover was marginally significantly different ($P = 0.054$), with detections occurring in serpentine stands with 17% higher shrub cover than in non-serpentine stands (mean = 47%, 95% CI = 32 – 63%; Table 13).

Table 12. Comparative average values for 5 stand-scale variables for sample units ($n = 16$) with a detection at one station and a non-detection at the other station surveyed in northern California, USA, 2017 – 2018. Standard error is in parentheses. Bold numbers represent P values < 0.05 for paired t-tests.

Variable	Detection ($n = 16$)	Non-detection ($n = 16$)	P
Distance to Stream (m)	152 (30)	231 (39)	0.133
Distance to Road (m)	238 (53)	136 (44)	0.049
Shrub Cover (%)	37 (5)	30 (4)	0.086
Logs (#/ha)	7.5 (1.9)	5.6 (1.7)	0.350
Snags (#/ha)	3.7 (1.6)	1.2 (0.5)	0.183

Table 13. Comparative average values for 5 stand-scale variables at stations where Humboldt martens were and were not detected in serpentine habitat ($n = 24$), non-serpentine habitat ($n = 78$), and all sample units combined ($n = 102$) surveyed in northern California, USA, 2017 – 2018. Stations were classified as occurring in serpentine habitat if the station grid point fell on serpentine soil, and in non-serpentine habitat if the station grid point fell on non-serpentine soil. Standard error is in parentheses. Bold numbers represent P values < 0.05 for two-sample t-tests for each habitat type.

Variable	Serpentine Detection ($n = 5$)	Serpentine Non-detection ($n = 19$)	Non-serpentine Detection ($n = 19$)	Non-serpentine Non-detection ($n = 59$)	All Detections ($n = 24$)	All Non-detections ($n = 78$)
Distance to Stream (m)	201 (63)	396 (79)	175 (33)	256 (26)	180 (28)	291 (28)
Distance to Road (m)	141 (57)	223 (51)	211 (47)	215 (36)	196 (39)	217 (30)
Shrub Cover (%)	47 (8)	40 (4)	30 (4)	26 (2)	33 (4)	29 (2)
Logs (#/ha)	3.5 (2.9)	0.6 (0.4)	9.0 (2.3)	7.0 (1.4)	7.9 (1.9)	5.4 (1.1)
Snags (#/ha)	1.3 (0.9)	0.9 (0.3)	3.3 (1.4)	1.7 (0.4)	2.9 (1.1)	1.5 (0.3)

Among the five covariates used to model habitat use at the home range level (Table 2), marten detections were higher at non-serpentine sample units with lower elevation ($P = 0.002$) and greater stream density ($P = 0.031$, Table 14), with mean detections for non-serpentine sample units occurring 314 m lower in elevation (mean = 615 m, 95% CI = 545 – 684 m) and with 0.37 km/km² higher stream density (mean = 1.52 km/km², 95% CI = 1.27 – 1.78 km/km²). For all sample units combined, marten detections were higher at lower elevations ($P = 0.008$, Table 14), with mean detections for all sample units occurring at 688 m (95% CI = 599 – 777 m). None of the covariates influenced use between detections and non-detections within serpentine sample units; however, elevation, slope, and percent size class 5 per sample unit were significantly different between sample units with detections in serpentine habitat compared to sample units with detections in non-serpentine habitat (Table 14). Detections in serpentine habitat occurred 368 m higher in elevation (mean = 983 m, 95% CI = 855 – 1110 m, $P = 0.00$), 13% lower slope (mean = 38%, 95% CI = 32 – 45%, $P = 0.00$), and in sample units with 18% less size class 5 trees (mean = 1.0%, 95% CI = 0.0 – 2.0%, $P = 0.04$) than detections in non-serpentine habitat (Table 14).

Table 14. Comparative average values for habitat variables at sample units where Humboldt martens were and were not detected in serpentine habitat ($n = 9$), non-serpentine habitat ($n = 42$), and all sample units combined ($n = 51$) surveyed in northern California, USA, 2017 – 2018. Sample units were classified as occurring in serpentine habitat if $> 50\%$ of the habitat in the 1 km radius around each sample unit was serpentine, and in non-serpentine habitat if $< 50\%$ of the habitat in the 1 km radius around each sample unit was non-serpentine. Bold values indicate significant differences at $P < 0.05$ between detection and non-detection variables for the same habitat type. Asterisks (*) indicate significant differences at $P < 0.05$ between detection and non-detection variables for different habitat types (i.e., serpentine vs. non-serpentine detection).

Variable	Serpentine Detection ($n = 4$)	Serpentine Non- detection ($n = 5$)	Non-serpentine Detection ($n = 16$)	Non-serpentine Non-detection ($n = 26$)	All Detections ($n = 20$)	All Non-detections ($n = 31$)
Elevation (m)	983 (65)*	831 (74)	615 (36)*	929 (62)	688 (45)	913 (53)
Slope (%)	38 (3.2)*	43 (2.3)	51 (1.0)*	49 (1.3)	49 (1.5)	48 (1.2)
Stream Density (km/km ²)	1.12 (0.17)	1.39 (0.28)	1.52 (0.13)	1.15 (0.10)	1.44 (0.11)	1.19 (0.10)
Road Density (km/km ²)	1.04 (0.08)	1.10 (0.21)	1.76 (0.21)	1.43 (0.13)	1.62 (0.18)	1.38 (0.11)
Size Class 5 (%)	1.0 (0.0)*	3.0 (2.0)	19 (4.0)*	16 (2.0)	16 (4.0)	14 (2.0)

DISCUSSION

Marten Occupancy

Elevation and the amount of CWHR size class 5 forest habitat (hereafter ‘large trees’) present at the home range scale had the most influence on Humboldt marten occupancy in the study area. Elevation occurred in every top model from the 95% confidence set, indicating that elevation is a driving factor for marten habitat use in this population. Most marten detections occurred between 444 – 913 m elevation and martens disproportionately used sample units in the elevation range 400 – 699 m (Figure 8), suggesting that martens in this population use lower elevation habitat in comparison to what is available in the study area. Studies have shown that other populations of Humboldt martens along the coast of California and Oregon occur in low elevation areas with little to no snow fall (Slauson et al. 2009; Moriarty et al. 2016). Elevation is known to be important in other populations of martens (Kirk and Zielinski 2009; Slauson et al. 2009; Gompper et al. 2016; Zielinski et al. 2017), and in contrast to the coastal populations, martens in the Sierra Nevada and Cascade Range select for high elevation habitat between 1,350 – 3,200 m with high snowfall (Zielinski 2014). Data from my study suggest elevation is important for marten occurrence in the CA – OR EPA as well, although martens appear to be selecting lower elevation sample units in this region, contrary to my initial prediction.

The importance of elevation can be attributed to an array of biotic (i.e., changes in prey abundance, competition, predator avoidance) and abiotic (i.e., forest vegetation structure and composition, productivity of the soil types, available riparian habitat) factors (Stevens 1992; Wasserman et al. 2010; Eriksson et al. 2019). Elevation in this study area is likely associated with some of these factors, many of which I was unable to capture given the scope of the data. Application of occupancy models to sparse data can lead to poor estimations of occupancy (Nichols et al. 2008), and this is evident in my data by the large confidence intervals for estimating probability of occupancy at higher ranges of large trees (size class 5 > 20% [63 ha]). So few detections occurred in sample units with greater than 20% (63 ha) large trees available at the home range scale, and there were even fewer detections in sample units at both high elevation and with high amounts of large trees. It is evident from my best predictive model that the amount of large trees has some influence on probability of marten occupancy in this region, but I advise caution on the interpretation of these results given the sparseness of the data. Future survey efforts in this region should focus on sample units with greater amounts of large trees (i.e., size class 5 \geq 20%) to better draw conclusions on how large trees influence occupancy for this population.

Although the strength of the relationships reflected by my top model may depend on the small sample size, the top model in my study suggests that the importance of elevation on Humboldt marten occupancy reflects abiotic changes in forest structural composition at different levels of elevation. The amount of large trees at the home range scale was used to represent the importance of forest structural composition to marten

habitat use, as it is well known that martens prefer late-successional forests with large diameter trees for multiple life history requirements (Slauson et al. 2018). Large trees are typically associated with structural complexity of the forest, as they produce large snags and downed logs that provide cavities available for resting and denning (Kirk and Zielinski 2009; Moriarty et al. 2016; Delheimer et al. 2019). They also provide canopy cover for protection from aerial predators (Drew 1995), and many key prey species for martens reach their highest densities in these types of forest stands (Slauson et al. 2018). The importance of the amount of large trees on marten occupancy in this region was consistent with habitat selection in the larger California population of Humboldt martens (Slauson et al. 2007) and elsewhere for Pacific martens (Kirk and Zielinski 2009; Delheimer et al. 2019).

Within the last 150 years timber harvest has drastically decreased the number of large trees and snags in California, impacting species like the Humboldt marten. Along with this loss of large trees, marten populations in California have been declining over the past 30 years, with decreased detections coinciding with increased timber harvest (Delheimer et al. 2019). Growth and recruitment of these trees can take decades to centuries, with the loss of trees worldwide far outpacing the rate of recruitment. This pattern presents potentially dire consequences for cavity-dependent species such as the marten (Delheimer et al. 2019), highlighting the importance of preserving large trees in areas where they persist.

My study revealed that the influence of the amount of large trees on marten occupancy differed depending on the elevation. Overall, occupancy decreased

significantly with increasing elevation; however, when there were increased amounts of forest habitat with large trees present the decrease in probability of occupancy was not as dramatic. Similarly, at these higher elevation sample units, probability of occupancy increased as the amount of large trees increased in a sample unit. This suggests that higher elevation sample units provide harsher, less suitable conditions conducive to occupancy, but martens may be able to utilize areas of higher elevation as long as large trees are available.

At lower elevation sample units (< 800 m), the influence of amount of large trees on marten occupancy was contrary to what I expected: at lower elevation sites, martens occurred in areas with low amounts of large trees (Figure 7). This finding may be dependent on the small sample size and/or the inability to distinguish the sexes. The influence of home range habitat composition has been shown to be sex-specific in Pacific martens, influencing sex-specific densities and their spatial distributions. Slauson (2017) found that female Pacific martens are highly selective for habitat that is conducive to reproduction, selecting areas with increased amounts of older forest that contain suitable denning structures (i.e., large diameter live and dead trees) and abundant prey resources (Slauson 2017). Male Pacific martens exhibited equal selection for areas with greater amounts of older, large diameter trees (CWHR size class 5), but males also utilized areas with high amounts of mid-seral forest habitat (size class 4, 27.9 – 59.9 cm QMD) and consequently occupied many areas that females did not (Slauson 2017). This difference in habitat use can cause models that include males to be less accurate in identifying habitat features critical for supporting reproduction (Slauson 2017). Although the exact

number of reproducing females in my study area is unknown, females with kits were detected in two sample units containing high amounts of large trees (14% [44 ha] and 28% [88 ha] size class 5). These detections provide valuable insight on the prevalence of large diameter trees in known reproductive habitat and demonstrate their importance at the home range level for this population. Similar to the landscape composition in Slauson (2017), mid-seral forest habitat (CWHR size class 4) was far more prominent (48% of the study area) than larger size class 5 forest habitat in my study area (16% of the study area; Appendix E), with most sample units containing ~ 54% (170 ha) mid-seral forest habitat regardless of elevation. However, because I was unable to model for the effect of sex on habitat use, I was unable to determine if these low elevation sites with low amounts of large trees and high amounts of mid-seral forest habitat were predominantly occupied by males.

Although martens occur in areas with low amounts of large trees and high amounts of mid-seral forest habitat, there may be other elements associated with these lower elevation sites, such as higher stream density, that I was unable to capture due to the limitations of the data. I used stream density as an indicator of the amount of riparian habitat available at the home range scale, as riparian zones are known to be important foraging areas for martens (Zielinski 2014). Riparian habitat in montane areas provide superior habitat for many key prey species for martens, as they provide areas with ample water, increased vegetation productivity, and greater forage availability (Doyle 1990). The effect of riparian areas on productivity is even stronger at lower elevations as water moves from areas of high elevation to low elevation, beginning with small headwater

streams accumulating and sending water downstream to increasingly larger channels (NRC 2002). These large streams likely influence a wider band of adjacent vegetation than smaller, high elevation streams. In my study, stream density was found to be significantly higher at the univariate level for sample units with detections and was present within the 95% confidence set of the occupancy models. Stream density was also higher in low elevation sample units dominated by mid-seral forest habitat, suggesting that increased riparian habitat may contribute to martens' ability to occupy these areas with low amounts of large trees. Further research is necessary to better understand the factors driving the use of lower elevation sample units with high amounts of mid-seral habitat in this population, particularly in regard to the influence of riparian habitat available at the home range level.

Due to the limited number of sample units that fell on serpentine habitat, I was also unable to model the influence of forest structural and compositional characteristics in that habitat type. Nine sample units contained more than 50% serpentine soil, with martens detected at nearly half ($n = 4$) of these sample units. The differences in habitat use between serpentine and non-serpentine habitat have prompted researchers to assess habitat selection for these habitat types separately (Slauson et al. 2007). Because my sample size for detections on serpentine soil was low, I removed them from my analysis to ensure my assessment of occupancy on non-serpentine habitat was not confounded by soil type. I believe this was justified as managers recommend focusing survey efforts on non-serpentine habitat, as previous research has revealed that although martens are found in serpentine habitats, these regions support lower numbers of females and may provide

more unstable occupancy than areas on forest habitat in more productive soils (Slauson et al. 2019).

In addition to these abiotic factors, there may be other biotic factors that influence marten occupancy at lower elevations that I was unable to capture. For instance, species richness tends to decline as elevation increases due to changing climatic conditions along the gradient, with a general trend of plants and animal species richness being much lower on mountaintops than it is in lowland areas (Stevens 1992). This trend could be influencing habitat use in this population of martens if a greater species richness of prey is available at the sample units with more productive soil types at lower elevation. Habitat quality for martens is in part dictated by prey availability (Buskirk 1992). Martens have a high metabolism and limited fat reserves relative to other carnivores and must consume approximately 25% of their body weight daily to survive (Eriksson et al. 2019). I was unable to capture the influence of prey availability in this study, and further research is needed to determine if abundance of prey influenced habitat use of martens at lower elevation sample units.

Competitive interactions and potential predation may also influence marten habitat use along an elevation gradient. Fishers (*Pekania pennanti*) were detected at three sample units, two occurred at higher elevations and one co-occurred with a marten detection at a lower elevation sample unit (Appendix F). Martens and fishers are known to occur together in different parts of the state and exhibit similarities in diet and foraging strategies (Zielinski and Duncan 2004; Zielinski et al. 2010; Sweitzer and Furnas 2016; Croose et al. 2019). Previous literature has identified direct competition between fishers

and martens for food and space (Zielinski and Duncan 2004; Zielinski 2014; Zielinski et al. 2017; Green et al. 2018), influencing differences in habitat selection by the two species at the landscape scale and limiting the distribution of martens, the smaller competitor (Fisher et al. 2013; Suffice et al. 2017). Furthermore, fishers are known to directly influence marten populations through predation (Suffice et al. 2017; Wilk and Raphael 2018). Marten and fisher habitat is generally stratified by elevation, with martens utilizing higher elevation forests that receive considerable snowfall (Zielinski et al. 2017). Martens' high foot surface area to body mass ratio allows them to move more adeptly on deep, soft snow in these areas, providing martens with a competitive advantage over larger-bodied fishers whose distribution is limited by this type of snow (Zielinski 2014). However, when martens and fishers occur in sympatry, martens have been found to use lower elevation habitat with low snowpack and rely on spatial and temporal avoidance patterns to minimize risk associated with encounters with fisher (Zielinski et al. 2017). Since both species are present within the study area it is possible that fishers influence marten selection of lower elevation sample units. Although the exact relationship, if any, with fisher co-occurrence in this area is unclear, understanding their interactions across the study area will be critical for assessing how fishers influence martens in this region.

In the coastal Oregon population of Humboldt martens, prey availability and predator avoidance play a key role in martens being able to exploit an area of young, low-lying coastal forest not typically associated with marten occupancy (Eriksson et al. 2019). Although extensive older and mature forests occur inland along the central coast of

Oregon, they currently do not support populations of marten (Moriarty et al. 2016). Eriksson et al. (2019) aimed to address this puzzling trend and found that a higher abundance of prey along the dunes and a significantly lower presence of bobcats (*Lynx rufus*), a significant predator of martens (Slauson et al. 2018; Wilk and Raphael 2018), allowed martens to utilize the younger forests along the coast. This study showcases the importance of understanding how biotic factors influence habitat use and highlights the need to incorporate species interactions into inferences on species distributions rather than relying solely on variables, such as elevation, that are likely correlated with the biological factors influencing a species' distribution.

Detection Probability

The time of the year stations were placed (session: June or July/August) and the number of days the stations were operable (duration) had the most influence on detection probability in my study. Detection probability was higher for stations that were operating in July and August, and lower for stations that were operating in June. This activity pattern may be attributed to martens' reproductive strategy, as mating occurs from late June to early August with a peak in July (Slauson et al. 2018). It is possible that this higher detection rate occurred as martens were moving more extensively in search of mates during this time period. In contrast to the high detection rate in July and August, detection probability may have been lower in June as female movement is more restricted during this time period. Females give birth in March and April (Slauson et al. 2018), and their movement may be limited to areas near the denning location during June when they

are tending to young and may increase as young mature and require increasing nutritional support.

In addition to session, detection probability increased the longer the station was deployed. This is intuitive, as an increase in survey effort (i.e., the number of days a station was deployed) increases the number of opportunities to detect a marten if it is present in the area. Standard protocol suggests surveying sites for a minimum of 21 days to maximize detection probability (Slauson and Moriarty 2014), and this appears to be sufficient in July and August as overall detection probability in these later months was 0.98 after 5 survey checks (approximately 20 days). However, overall detection probability was lower in June (0.75) after 5 survey checks, suggesting that surveyors should aim to place stations during late June to early August for 21 days to increase likelihood of detecting resident martens, or plan to account for potential temporal variation when modeling the detection process.

During the 2017 summer surveys, track plates were established alongside camera stations, with one camera and one track plate station deployed in each sample unit using the same configuration described by Slauson and Moriarty (2014). Previous studies have indicated that there is no difference in detection probability for martens between remote cameras and track plates (Moriarty et al. 2011), but the first season of this study suggested a marked difference in detection between the two device types due to frequent destruction of track plates by bears. Due to differences in detection probability between cameras and track plates (Figure 5), I removed track plates from the second field season and used two cameras per sample unit in 2018. If using two cameras per sample unit is

not possible, I recommend checking track plate stations more frequently or keeping the station out longer if persistent bear damage to track plates is an issue.

In addition to these survey-specific variables, I found that detection probability was not higher in stands with site-specific habitat variables used to represent more productive stands (i.e., increased shrub cover, higher density of logs, snags, size class 5 stands, etc.). This is contrary to what I expected, as I predicted martens would be more active and thus more likely to be detected in stands with more suitable features. Many species exhibit habitat preferences within their home range, with different space use and varying centers of activity present throughout the home range (Hemson et al. 2005). However, for martens, habitat selection is strongest among all spatial scales during the process of establishing home ranges, with individuals establishing home ranges in areas that will support year-round life history needs. Although martens typically select for more productive forest stands when establishing their home ranges, they will still make use of less productive stands if they provide different features necessary for varying life history needs, including prey abundance, predator avoidance, and structural complexity near the ground in different stands (Slauson et al. 2018). Consistent with previous literature, martens were not detected at a higher rate in my study area in more productive stands within their home range, suggesting that they are able to make use of the less productive stands within their home range.

Stand Scale Habitat Relationships

Due to the limited number of total detections, I was unable to assess stand scale habitat selection of Humboldt martens using multi-scale occupancy models. I found that when I tried to fit my data to the multi-scale occupancy model framework, extrinsic non-identifiability prohibited the estimation of parameters in the models, and researchers have been cautioned against using this modeling technique with sparse data sets as it can lead to poor estimates of occupancy (Nichols et al. 2008). Although I was unable to use this method to assess multi-scale habitat occupancy due to low sample size, this study showcases the survey design that is needed to implement this method on a larger scale. Standard Humboldt marten survey protocol is to place two stations within each sample unit (Slauson and Moriarty 2014); thus by ensuring the stations are placed within separate stands researchers can assess stand level habitat selection using non-invasive survey techniques. Following the framework of this study, researchers can assess fine-scale habitat use without the use of radio-collared animals. However, my study demonstrates that a sample size > 51 sample units and an unadjusted occupancy of 0.39 is likely necessary to support this level of model complexity.

Univariate comparisons of paired stands in sample units with and without detections in the same sample unit suggests that detections occurred more often in stands located further away from roads. Roads can negatively influence marten occupancy by the direct threat via roadkill, and the indirect threat of increasing the interactions between martens and their predators, particularly bobcats, and competitors that forage along roads

(Zielinski 2014). Furthermore, univariate comparison of all stands with and without detections suggests that detections were more frequent in stands located closer to streams. Streams are indicative of riparian habitat in or adjacent to a stand, and are important to martens for foraging, providing rest structures, and improving connectivity between habitats (Zielinski 2014). It is possible that proximity to road and stream habitats are important for martens at the stand level, but I was unable to capture this result in a multi-scale occupancy framework. Future research should aim to address the influence of roads and stream habitat at the stand level.

Sparse data also limited my ability to incorporate soil type into the occupancy modeling process. Instead, the comparisons of detections in serpentine and non-serpentine areas, as well as what is known from previous literature, help to better explain the trends on serpentine soil in this population. Martens use stands of all seral stages on serpentine soil, including young forests with canopy cover ranging from sparse to dense, so long as there is ample shrub cover available (Slauson et al. 2007). This is consistent with my finding of martens using sample units on serpentine soil with very little size class 5 trees (>2%) but with higher amounts of shrub cover (47%). They also make use of the interstitial spaces in boulder piles for resting sites, as structures generally used for resting (i.e., large trees, snags, and logs) are uncommon in this habitat type (Slauson et al. 2019). The amount of logs (3.5/ha) and snags (1.3/ha) were lower in serpentine stands compared to non-serpentine stands, suggesting that martens likely rely on other structures, such as boulder piles, for resting in these serpentine stands. It's likely that

martens in this population are able to occupy areas in serpentine habitat by making use of the different features in this habitat that support their life history needs.

MANAGEMENT IMPLICATIONS

In response to numerous efforts to list the Humboldt marten under federal and state protections, a conservation assessment and strategy was developed to address the most important conservation needs of the Humboldt marten (USFWS 2015; Slauson et al. 2018). Of these needs a comprehensive range-wide habitat suitability model was developed to identify areas where suitable habitat occurs and where new populations may occur (USFWS 2015; Slauson et al. 2019). This model identified the CA – OR EPA as suitable habitat and prompted my investigation to determine if a population existed in this area. This study provided the first systematic survey of the CA – OR EPA and addressed one of the key conservation objectives outlined by the conservation strategy: we now have a better understanding where martens occur in this area, and where to prioritize future survey efforts in this region. Furthermore, my findings of a breeding (and potentially viable) population in this area support the predictions of the habitat suitability model generated (Slauson et al. 2019), suggesting that it performs well when predicting where additional populations may occur and where researchers should prioritize future survey efforts. The model predicts that connectivity between this newly identified population of martens and surrounding populations becomes linear and narrow, suggesting that these areas should be prioritized for conservation to promote connectivity between populations. It is predicted that less than 20% suitable habitat exists throughout the current range of Humboldt martens in coastal California and coastal Oregon (Slauson

et al. 2019); thus understanding how martens are selecting habitat in this population is critical for developing strategies for connectivity and conservation.

Based on this study, I recommend that future studies address the factors driving habitat use along an elevation gradient. Prey availability, competition and predation by fishers, and forest structural composition are likely contributing to selection for low elevation sample units, but data were lacking to address these biotic factors, and sparse data limited my ability to assess fully the influence of forest composition, riparian habitat, and soil productivity in my study area. The habitat suitability model predicts suitable habitat exists beyond the CA – OR EPA (Appendix G) and martens were detected in sample units outside of the EPA, so it is likely that the population extends beyond the 2017 – 2018 survey area. It is clear from the interaction between elevation and large trees that forest composition is important to this population, but further research is needed to identify what extent forest composition plays in habitat use. The 2017 – 2018 survey area contained limited amounts of size class 5 trees, but areas beyond the survey area contain high amounts of size class 5 trees and should be investigated (Appendix E). Furthermore, martens were detected in serpentine habitat, but limited data made it difficult to understand why martens in this population were able to utilize this habitat type. Additional areas beyond the survey area occur in serpentine habitat and should be investigated to better explain these patterns (Appendix H). Future surveys should prioritize 1) areas identified by the habitat suitability model to contain highly suitable habitat, 2) areas with relatively high amounts of size class 5 trees, and 3) areas in serpentine soil to understand better the distribution and extent of this population.

The survey results reported here are important for managers, as the majority of the study area is managed by the U.S. Forest Service, and timber harvest (i.e., stand and patch clear-cuts, commercial thinning) and other forest management practices (i.e., retention of wildlife habitat, seed-tree/shelterwood cuts) do occur in this area. In the last 60 years, approximately 7.5% of the area has experienced clear-cutting (Appendix I). With new information on where martens occur in this area, we can better identify areas to conserve for this population of martens. Because retention for wildlife habitat management does occur in this area, I recommend prioritizing areas for retention with greater amounts of large trees (size class 5 \geq 60.0 cm QMD), especially in areas with and adjacent to areas with verified marten detections.

Few studies have clearly identified the factors that influence survival in populations of marten (Slauson et al. 2018). Previously, it was reported that martens exhibit higher survival and production rates in old growth forests as compared to post clear-cut forests (Thompson and Colgan 1994). This is likely due to greater rates of prey capture and reduced predation in old growth forests compared to the more open habitats in logged forests. Larger trees are known to be important to marten ecology (Payer and Harrison 2003) and should be preserved in this area, and management strategies aimed at preserving key features important for marten survival and reproduction can be implemented to maintain structural complexity in areas that will be harvested. A recent study examined the hypothesis that reduced forest structure limited Humboldt marten populations in northern California in areas that have been intensely managed for timber harvest (Delheimer et al. 2018). Artificial rest boxes were distributed in known marten

ranges to assess use and feasibility of using such boxes to improve lower quality marten habitat. The study revealed that martens used artificial rest boxes for resting and reproductive activities, indicating that they may be an option for future management aimed at improving lower quality habitat for dispersing and eventually breeding martens.

Logging of marten habitat can negatively impact reproduction, foraging, and predator avoidance abilities, but managers can mitigate these effects by maintaining forest stand complexity, cover, and physical structures near the ground (Wilk and Raphael 2018). For instance, slash piles have been shown to be important in logged areas to retain ground level structure for resting and denning and to boost prey availability (Wilk and Raphael 2018). We can use data from this study to better inform a minimum amount of structures to preserve in areas with known martens, as well as surrounding areas where martens may occur. Consistent with results from the larger California population (Slauson et al. 2018), managers interested in promoting marten conservation in the CA – OR EPA should maintain and increase large patches of low-elevation forest habitat with large-diameter trees. Since timber production and forest management does occur in this area, managers should prioritize areas between 400 – 900 m elevation and maintain a minimum of 49.7 ha (15.8% per 1-km buffer) of continuous patches of large trees in areas with known marten home ranges. Managers should also aim to preserve a minimum shrub cover of 33%, 7.9 downed logs \geq 60.0 cm DBH per hectare, and 2.9 snags \geq 2 m in height and 60.0 cm DBH per hectare. Sparse data limited my ability to determine the optimal range of each structure to preserve, so it is important to acknowledge that these values represent the minimum value managers should aim to

preserve, rather than the optimal target. Furthermore, areas with ≥ 157 ha (50%) serpentine forest habitat, as well as areas with increased stream habitat (≥ 1.44 km/km²) should be prioritized. Preserving large trees and snags, implementing rest boxes, and retaining key ground level structures, such as logs and slash piles, may improve habitat in areas that will be logged, as well as along the perimeters of the current study population where martens were not detected in order to promote dispersal to areas that contain suitable habitat.

This research can be applied in a broader sense by understanding how management for the Humboldt marten can be viewed under the “umbrella species” concept and how conservation under this framework can be applied to similar species. The “umbrella species” concept is the idea that conserving habitat for one species with large spatial and broad habitat needs will in turn provide habitat for an array of species with more narrow needs (Moriarty et al. 2019). Oftentimes it is more efficient and cost effective to manage at the habitat level rather than the individual species level (Lindenmayer et al. 2014), but over simplistic goals for the umbrella species can lead to poor management of habitat characteristics necessary for the lesser known species (Moriarty et al. 2019). Marten species have a home range size around 50 times greater than what would be predicted of their body size and the range of habitat loss that they can tolerate is limited, leading martens to serve as an excellent umbrella species (Buskirk 1992). They are considered one of the most forest-sensitive carnivores in North America and are often used as a surrogate species for forest conservation initiatives (Sirén et al. 2015). This study revealed that elevation was the driving factor for habitat use in this

population of Humboldt martens, and the effects of habitat use changing along an elevation gradient have been well documented for a wide variety of species (Rahbek 1997; McLellan and Hovey 2001; Stewart et al. 2002; Buckley and Roughgarden 2005; Halsey et al. 2015; Zielinski et al. 2017). However, when applying the umbrella species concept to this population of martens, elevation alone may prove too broad for capturing habitat characteristics for other species. This study demonstrates the importance of considering additional habitat characteristics that may be important for capturing the needs of other wildlife populations when managing habitat under the umbrella species concept.

Northern spotted owls (*Strix occidentalis caurina*) are another prime umbrella species, and it is speculated that conserving spotted owl habitat can aid in the conservation of martens, as they both select for late-successional forests with high canopy and large trees with complex vegetation features (Moriarty et al. 2019). However, populations of Humboldt marten in Oregon can occur in stands with a much broader range of tree sizes than spotted owls if other important vegetation features such as high shrub cover are available (Moriarty et al. 2019). This showcases the need for managers to consider diversifying vegetation management to maintain habitat conditions at multiple spatial scales to capture the needs of different species.

Maintaining healthy populations of forest carnivores is necessary for the health of the ecosystem. In 2009, it was estimated that fewer than 100 individuals remained in the only remaining population of Humboldt martens in California at the time (Slauson et al. 2009). Because martens have been successfully reintroduced into their former range

through translocation efforts (Davis 1983), assessing the extent of area in which martens occur may influence future translocation efforts by determining suitable habitat available in this region. With the new knowledge that a breeding population of Humboldt martens exists north of the remnant population, determining the extent of available habitat for this additional population is critical to the survival of this subspecies.

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APPENDIX A

Appendix A: Comprehensive list of variables considered for inclusion in modeling detection probability (p), occupancy at the stand level (θ), and occupancy at the home range level (Ψ) during the exploratory analysis for predicting single and multi-scale occupancy for Humboldt martens in northern California, USA, 2017 – 2018.

Scale	Variable	Description	Source of data layer: ATTRIBUTE CODE (Shapefile name; Data source)
p	Year	Survey year (2017 or 2018)	<i>Raw data</i>
	Session_A	Survey Session (Jun/July/Aug)	<i>Raw data</i>
	Session_B	Survey Session (Jun/July+Aug)	<i>Raw data</i>
	Duration	Number of days station was out	<i>Raw data</i>
	OG	Old growth habitat at each stand point	SERIAL (SRF_rawvegwild; Six Rivers National Forest GIS Database)
	LS	Late seral habitat (old growth, late harvest, late mature, and late seral)	SERIAL (SRF_rawvegwild; Six Rivers National Forest GIS Database); POSTHAB_OG, POSTHAB_LS, POSTHAB (PostHab; Pacific Southwest Research Station)
	sc_eveg_4/5	Stand classified as size class 4 or 5	CWHR_SIZE (EVMid_R05_NorCoastEast; USDA Forest Service)
	sc_eveg_5	Stand classified as size class 5	CWHR_SIZE (EVMid_R05_NorCoastEast; USDA Forest Service)
	stream	Distance to nearest stream (m)	LENGTH (tl_2018_06015_linearwater; U.S. Census Bureau MAF/TIGER hydrography database)
	cc_eveg_s	% canopy cover	TOTAL_TREE_CC (EVMid_R05_NorCoastEast; USDA Forest Service)
	shrub	Average % shrub cover	<i>Raw data</i>
	TR	Trap response	<i>Raw data</i>
	DT	Device type (track plate or remote camera)	<i>Raw data</i>
	θ	stream_s	Distance to nearest stream (m)
road_s		Distance to nearest road (m)	LENGTH (tl_2017_06015_roads; U.S. Census Bureau MAF/TIGER roads database)
serp_s		Stand classified as serpentine	PARENT2 (SRF_SOILS; Six Rivers National Forest GIS Database)

Scale	Variable	Description	Source of data layer: ATTRIBUTE CODE (Shapefile name; Data source)
	seral_jim	Seral stage of stand	SERAL (SRF_rawvegwild; Six Rivers National Forest GIS Database); POSTHAB_OG, POSTHAB_LS, POSTHAB (PostHab; Pacific Southwest Research Station)
	sc_jim_s	Size class	SIZECLASS (SRF_rawvegwild; Six Rivers National Forest GIS Database)
	sc_eveg_s	Size class	CWHR_SIZE (EVMid_R05_NorCoastEast; USDA Forest Service)
	cc_jim_s	% canopy cover	TOTAL_CC (SRF_rawvegwild; Six Rivers National Forest GIS Database)
	cc_eveg_s	% canopy cover	TOTAL_TREE_CC (EVMid_R05_NorCoastEast; USDA Forest Service)
	shrub	Average % shrub cover	<i>Raw data</i>
	cwd	Density of course woody debris (logs) \geq 60 cm diameter/unit area	<i>Raw data</i>
	snag	Density of snags \geq 60 cm diameter and 2 m height/unit area	<i>Raw data</i>
	log_snag	Density of snags & course woody debris (logs) \geq 60 cm diameter and 2 m height/unit area	<i>Raw data</i>
Ψ	elev_ave	Average elevation (m) across 1 km buffer	VALUE (srf_elev; Six Rivers National Forest GIS Database)
	slope	Average % slope across 1 km buffer	VALUE (srf_slope_pct; Six Rivers National Forest GIS Database)
	STREAM_hr	Stream density (km/km ²)	LENGTH (tl_2018_06015_linearwater; U.S. Census Bureau MAF/TIGER hydrography database)
	ROAD_hr	Road density (km/km ²)	LENGTH (tl_2017_06015_roads; U.S. Census Bureau MAF/TIGER roads database)
	SERP_hr	Proportion of serpentine habitat per 1 km buffer	PARENT2 (SRF_SOILS; Six Rivers National Forest GIS Database)
	CC_jim_hr	Area weighted mean canopy cover	TOTAL_CC (SRF_rawvegwild; Six Rivers National Forest GIS Database)
	CC_eveg_hr	Area weighted mean canopy cover	TOTAL_TREE_CC (EVMid_R05_NorCoastEast; USDA Forest Service)
	FIRE	Proportion of area burned after 1960	AREA (FirePerimeter; Six Rivers National Forest GIS Database)
	SC_eveg_4	Proportion of area size class 4 per 1 km buffer	CWHR_SIZE (EVMid_R05_NorCoastEast; USDA Forest Service)
	SC_eveg_45	Proportion of area size class 4 & 5 per 1 km buffer	CWHR_SIZE (EVMid_R05_NorCoastEast; USDA Forest Service)
	SC_eveg_5	Proportion of area size class 5 per 1 km buffer	CWHR_SIZE (EVMid_R05_NorCoastEast; USDA Forest Service)
	SC_jim_4	Proportion of area size class 4 per 1 km buffer	SIZECLASS (SRF_rawvegwild; Six Rivers National Forest GIS Database)
	SC_jim_45	Proportion of area size class 4 & 5 per 1 km buffer	SIZECLASS (SRF_rawvegwild; Six Rivers National Forest GIS Database)

Scale	Variable	Description	Source of data layer: ATTRIBUTE CODE (Shapefile name; Data source)
	SC_jim_5	Proportion of area size class 5 per 1 km buffer	SIZECLASS (SRF_rawvegwild; Six Rivers National Forest GIS Database)
	OG_jim	Proportion of old growth habitat per 1 km buffer	SERAL (SRF_rawvegwild; Six Rivers National Forest GIS Database); POSTHAB_OG, POSTHAB_LS, POSTHAB (PostHab; Pacific Southwest Research Station)
	LS_jim	Proportion of late seral (late harvest, late mature, and old growth) habitat per 1 km buffer	SERAL (SRF_rawvegwild; Six Rivers National Forest GIS Database); POSTHAB_OG, POSTHAB_LS, POSTHAB (PostHab; Pacific Southwest Research Station)
	PS_serp	Largest patch size (ha) serpentine	PARENT2 (SRF_SOILS; Six Rivers National Forest GIS Database)
	PS_veg_123	Largest patch size (ha) of class 1, 2, & 3	CWHR_SIZE (EVMid_R05_NorCoastEast; USDA Forest Service)
	PS_veg_4	Largest patch size (ha) of class 4	CWHR_SIZE (EVMid_R05_NorCoastEast; USDA Forest Service)
	PS_veg_5	Largest patch size (ha) of class 5	CWHR_SIZE (EVMid_R05_NorCoastEast; USDA Forest Service)
	PS_veg_45	Largest patch size (ha) of class 4 & 5	CWHR_SIZE (EVMid_R05_NorCoastEast; USDA Forest Service)
	PSnum_veg_123	# patch sizes of class 1, 2, & 3	CWHR_SIZE (EVMid_R05_NorCoastEast; USDA Forest Service)
	PSnum_veg_4	# patch sizes of class 4	CWHR_SIZE (EVMid_R05_NorCoastEast; USDA Forest Service)
	PSnum_veg_5	# patch sizes of class 5	CWHR_SIZE (EVMid_R05_NorCoastEast; USDA Forest Service)
	PSnum_veg_45	# patch sizes of class 4 and 5	CWHR_SIZE (EVMid_R05_NorCoastEast; USDA Forest Service)
	PS_jim_OG	Largest patch size (ha) of old growth	SERAL (SRF_rawvegwild; Six Rivers National Forest GIS Database); POSTHAB_OG, POSTHAB_LS, POSTHAB (PostHab; Pacific Southwest Research Station)
	PS_jim_LS	Largest patch size (ha) of late seral (late harvest, late mature, and old growth)	SERAL (SRF_rawvegwild; Six Rivers National Forest GIS Database); POSTHAB_OG, POSTHAB_LS, POSTHAB (PostHab; Pacific Southwest Research Station)

APPENDIX B

Appendix B: Marten detection photos taken from four different camera stations deployed in northern California, USA, 2017 – 2018. The top two photos depict multiple martens detected at one station.



APPENDIX C

Appendix C: Summary model output for modeling detection probability (p) for Humboldt martens studied in northern California, USA, 2017 – 2018.

Model	K	AICc	Δ AICc	Weights
{Psi(.) p(sess + dur)}	4	163.38	0.00	0.475
{Psi(.) p(sess)}	3	166.05	2.67	0.125
{Psi(.) p(dur)}	3	166.09	2.70	0.123
{Psi(.) p(road + stream)}	4	167.75	4.37	0.054
{Psi(.) p(logsnag)}	3	168.51	5.12	0.037
{Psi(.) p(logsnag + stream)}	4	168.65	5.27	0.034
{Psi(.) p(logsnag + road)}	4	168.93	5.54	0.030
{Psi(.) p(stream)}	3	169.17	5.79	0.026
{Psi(.) p(road)}	3	169.50	6.12	0.022
{Psi(.) p(.)}	2	170.37	6.99	0.014
{Psi(.) p(logsnag + sc5)}	4	170.86	7.48	0.011
{Psi(.) p(logsnag + shrub)}	4	170.96	7.57	0.011
{Psi(.) p(shrub + stream)}	4	171.12	7.73	0.010
{Psi(.) p(sc5 + stream)}	4	171.59	8.21	0.008
{Psi(.) p(shrub + road)}	4	171.86	8.48	0.007
{Psi(.) p(sc5 + road)}	4	171.95	8.57	0.007
{Psi(.) p(sc5)}	3	172.69	9.31	0.005
{Psi(.) p(shrub + sc5)}	4	175.09	11.71	0.001

K = number of parameters in the model

Δ AICc = difference in the Akaike's Information Criterion score (adjusted for small sample size) relative to the top model

Weights = Akaike weight (adjusted for small sample size)

APPENDIX D

Appendix D: Summary model output for modeling occupancy (Ψ) at the home range level for Humboldt martens studied in northern California, USA, 2017 – 2018.

Model	K	AICc	Δ AICc	Weights
{Psi(elev + SC5 + elev*SC5) p(sess + dur)}	7	148.99	0.00	0.671
{Psi(elev) p(sess + dur)}	5	151.79	2.80	0.165
{Psi(elev + stream) p(sess + dur)}	6	153.88	4.89	0.058
{Psi(elev + SC5) p(sess + dur)}	6	154.38	5.39	0.045
{Psi(elev + slope + SC5) p(sess + dur)}	7	155.55	6.56	0.025
{Psi(elev + stream + SC5) p(sess + dur)}	7	156.63	7.64	0.015
{Psi(elev + road + SC5) p(sess + dur)}	7	157.27	8.28	0.011
{Psi(stream) p(sess + dur)}	5	160.90	11.91	0.002
{Psi(elev + SC5 + slope + stream + road) p(sess + dur)}	9	161.34	12.35	0.001
{Psi(stream + slope) p(sess + dur)}	6	161.98	12.99	0.001
{Psi(stream + road) p(sess + dur)}	6	162.10	13.11	0.001
{Psi(stream + slope + road) p(sess + dur)}	7	162.42	13.43	0.001
{Psi(stream + SC5) p(sess + dur)}	6	162.98	13.99	0.001
{Psi(slope) p(sess + dur)}	5	163.24	14.25	0.001
{Psi(slope + road) p(sess + dur)}	6	163.34	14.35	0.001
{Psi(.) p(sess + dur)}	4	163.38	14.39	0.001
{Psi(stream + road + SC5) p(sess + dur)}	7	164.05	15.06	0.000
{Psi(stream + slope + SC5) p(sess + dur)}	7	164.25	15.26	0.000
{Psi(road) p(sess + dur)}	5	164.42	15.43	0.000
{Psi(slope + road + SC5) p(sess + dur)}	7	165.05	16.06	0.000
{Psi(SC5) p(sess + dur)}	5	165.08	16.09	0.000
{Psi(slope + SC5) p(sess + dur)}	6	165.13	16.14	0.000
{Psi(road + SC5) p(sess + dur)}	6	165.99	17.00	0.000
{Psi(.) p(.)}	2	170.37	21.38	0.000

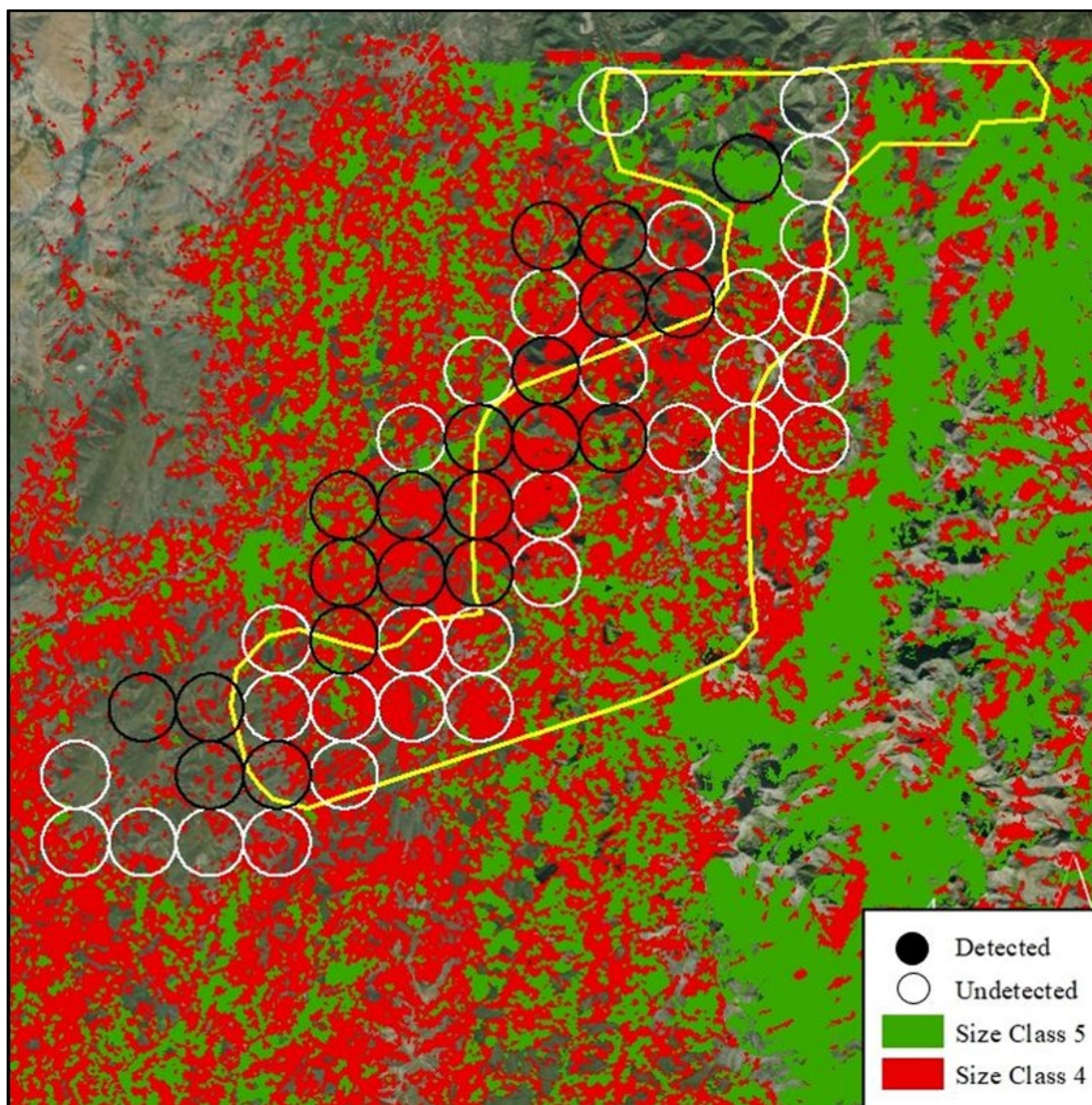
K = number of parameters in the model

Δ AICc = difference in the Akaike's Information Criterion score (adjusted for small sample size) relative to the top model

Weights = Akaike weight (adjusted for small sample size)

APPENDIX E

Appendix E: Amount of size class 4 (27.9 – 59.9 cm QMD) and size class 5 (≥ 60.0 cm QMD) habitat in and around the CA – OR EPA study area in the Six Rivers National Forest, northern California, USA. Circles depict the location of the 51 sample units placed in 2017 – 2018 where Humboldt martens were (black) and were not (white) detected.



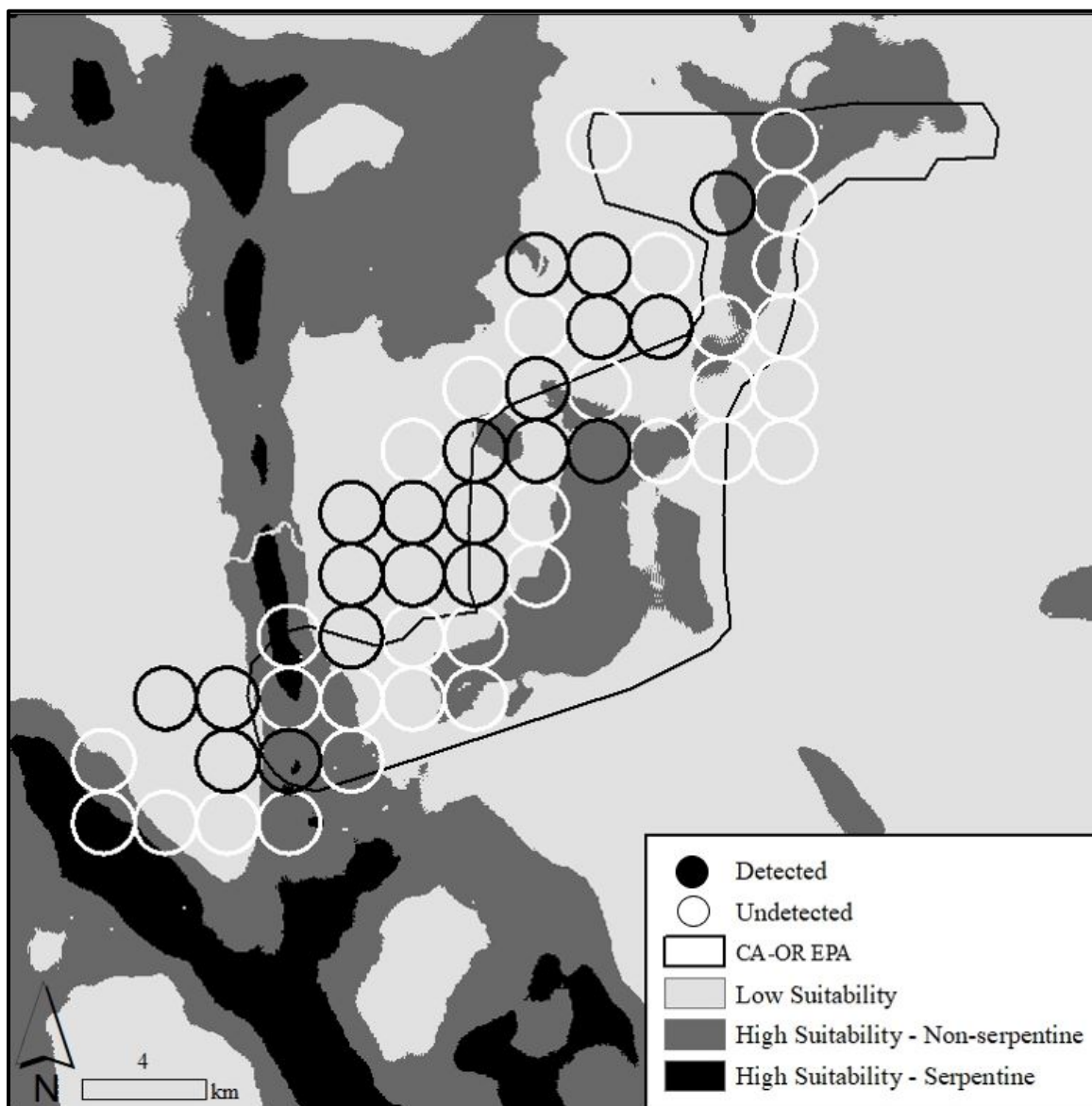
APPENDIX F

Appendix F: Sample units where fishers were detected and whether or not a marten was detected as well in areas surveyed in northern California, USA, 2017 – 2018, with detections indicated by an X.

Sample Unit	Elevation (m)	Fisher Detection	Marten Detection
14881	665	X	X
14925	1,272	X	
14926	1,135	X	

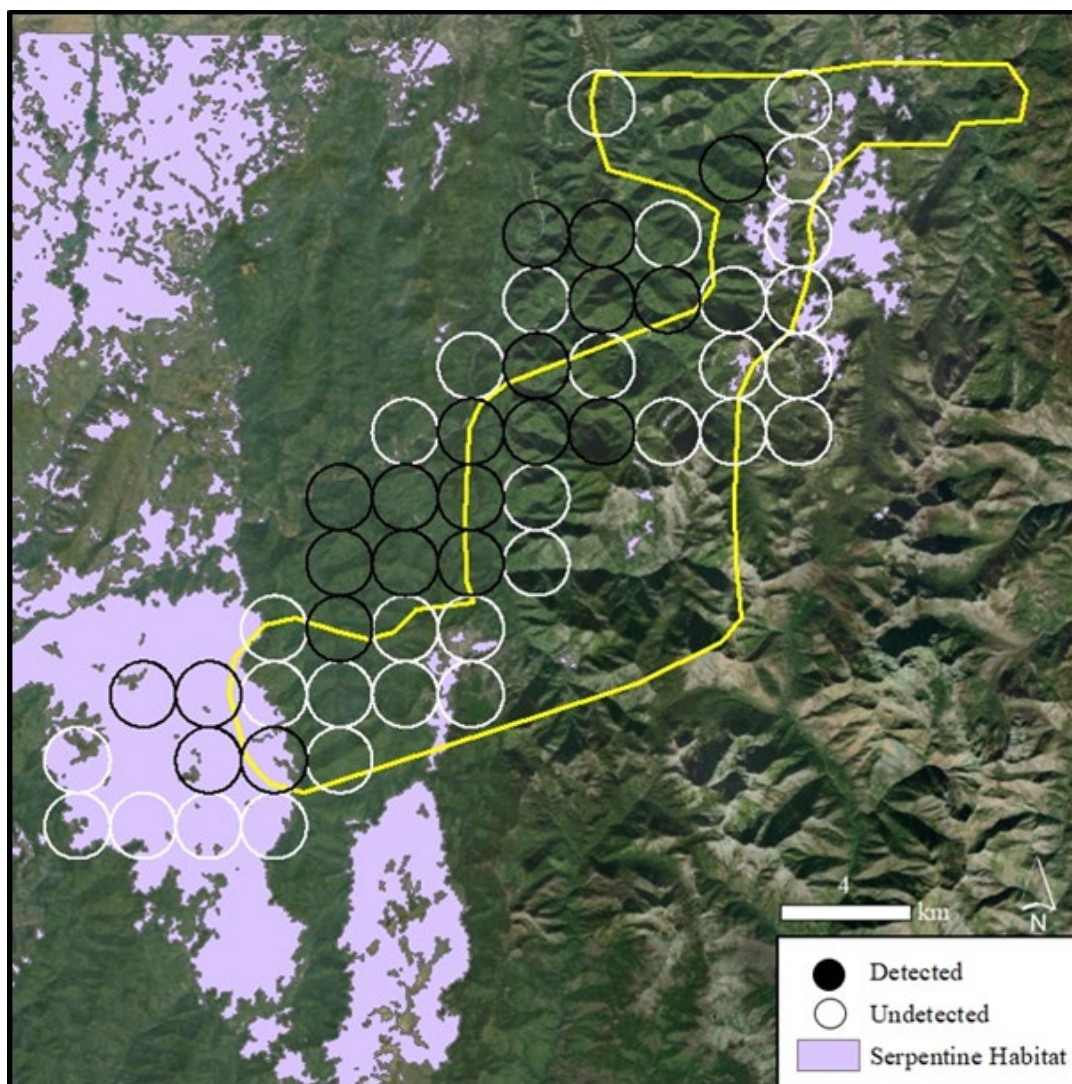
APPENDIX G

Appendix G. Amount of suitable habitat in and around the CA – OR EPA study area in the Six Rivers National Forest, northern California, USA. Areas of low and high suitability were generated with permission from models by Slauson et al. (2019). Circles depict the location of the 51 sample units placed in 2017 – 2018 where Humboldt martens were (black) and were not (white) detected.



APPENDIX H

Appendix H. Amount of serpentine habitat in and around the CA – OR EPA study area in the Six Rivers National Forest, northern California, USA. Circles depict the location of the 51 sample units placed in 2017 – 2018 where Humboldt martens were and were not detected.



APPENDIX I

Appendix I. Amount of habitat that has experienced timber production (i.e., stand and patch clear-cuts, commercial thinning, etc.) and forest management (i.e., retention of wildlife habitat, seed-tree/shelterwood cuts, etc.) in the CA – OR EPA study area in the Six Rivers National Forest, northern California, USA post 1950. Circles depict the location of the 51 Humboldt marten sample units placed in 2017 – 2018.

