

Effects of Forest Restoration on Mesocarnivores in the Northern Redwood Region of Northwestern California

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ABSTRACT

Restoration efforts are underway in the logged second growth forests in the Redwood National and State Parks complex to accelerate the return of old growth forest conditions that have been lost. Mesocarnivores are ideal focal suite of species to evaluate the effects of forest change because they include species such as the Humboldt marten, highly adapted to complex coastal forest conditions of hunting and opportunistic generalists such as the gray fox that typically respond positively to human-altered ecosystems. From 2009-2010 we studied how several species of mesocarnivores and key habitat components for the Humboldt marten have responded to old growth and second growth forest characteristics, forest roads, and restorative thinning. Stands restoratively thinned 15-30 years ago have regenerated moderately dense shrub layers composed of native, shade tolerate shrub species approaching the conditions in old growth redwood stands and stands used by the Humboldt marten. Suitable resting structures for martens, including large diameter trees, snags, and downed logs with cavities or platforms have been significantly reduced in second growth stands compared to old growth stands and stands used by martens. Regional occupancy modeling revealed that dense shrub cover, measured at a spatial scale close to each species' home range size, most significantly increased the probability of marten occurrence and decreased the probability of occurrence of the fisher and gray fox. Road density only affected martens, where it reduced the probability of occurrence. Camera survey results for carnivores on paired road and creek locations revealed that 80% of the detections of generalist carnivores occurred on roads while 80% of detections of habitat specialist carnivores occurred off-roads, along creeks. Restorative thinning and road removal will affect mesocarnivores over the short term (1-3 decades) by restoring dense shrub cover and reducing its fragmentation, factors that will likely benefit habitat specialists like the Humboldt marten by reducing the distribution and abundance of larger-bodied generalist mesocarnivores that can kill them. However, because mesocarnivores have large home ranges, restoration actions will have to be strategically located to have the greatest impact. Large-diameter standing and downed woody structures, critical for providing resting and denning locations for the Humboldt marten are depauperate in second growth landscapes. Because the restoration of the natural recruitment of these structures will likely take >200 years, alternatives for creating suitable structures will be necessary to improve habitat conditions in the interim.

BACKGROUND

The goals of forest restoration efforts in the redwood region are to return natural conditions to sites where they have been significantly altered. To date, forest restoration has focused on restorative thinning to accelerate the recruitment of late-seral forest conditions and the closure or removal of roads. It is unclear how wildlife species will respond to these changes. Intermediately sized mammalian carnivores (mesocarnivores) are important indicators of ecosystem integrity due to their wide-ranging habits, reliance on numerous prey populations, and often highly specialized habitat requirements. Understanding their ecology in relation to changes in the structure and function of the habitats they require will allow managers to predict their responses to restoration.

Redwood forests are more than big trees to terrestrial mesocarnivores, they are highly productive and structurally complex ecosystems. For terrestrial carnivores that chase down smaller-bodied prey, old growth redwood forests offer a challenging obstacle course of dense stems and foliage near the ground in which to capture a meal. The Humboldt marten (*Martes americana humboldtensis*), the smallest of all marten subspecies, appears to have adapted to this environment and its small size allows it to negotiate thick understory tangles (Hagmeier 1961). Unfortunately, few areas of sufficient size and suitability -- dense spatially extensive shrub cover underneath an old growth tree canopy -- remain in the redwood region to support marten populations (Thornburg et al. 2000).

The Humboldt marten is endemic to the redwood region (Grinnell and Dixon 1926) and was common in the early twentieth century (Grinnell et al. 1937) but was feared extinct towards the end of the century due to the absence of verifiable detections for over a 50 year period (Zielinski and Golightly 1996). Remarkably, in 1996, the first marten was detected from the only known population remaining, currently occupying an area <5% of the historical range of the Humboldt marten, adjacent to second growth forest in Redwood National and State Parks (RNSP; Slauson 2003). Surveys in 2002 found that martens still had not recolonized RNSP (including the Mill Creek addition), despite the presence of a nearby population located <2 kilometers to the west of the Rock Creek area and well within their dispersal range (Slauson and Zielinski 2003). The marten is one of the most highly specialized species in the redwood region. Martens appear to require numerous large and old woody structures (e.g., live trees snags with cavities, downed logs with cavities) for resting refugia and large patches of dense, spatially extensive shrub cover to exclude larger-bodied mesocarnivores (Slauson et al. 2007, Slauson and Zielinski 2009a). Restoration of marten populations to more of their former range represents one of the best indicators of ecosystem recovery in the redwood region and should be one of the long-term goals guiding restoration efforts.

The distribution of carnivores is largely determined by the interaction of a number of factors including habitat structure, prey availability, mesocarnivore community interactions, and physical factors. The marten is smaller than most mesocarnivores and thus is likely to be excluded by larger-bodied species through interference competition and direct killing. Martens in North America typically occupy forests in locations that receive frequent deep, soft snowfall during the winter (e.g., high elevations of the Sierra Nevada and Cascade mountains). Martens are well adapted to cope with deep, soft snow due to having one of the lowest foot loadings (low mass per unit foot surface area) of all mesocarnivores (Krohn et al 2004). Where snowfall is not so frequent or deep, dense fisher populations have been shown to limit the distribution of marten populations (Krohn et al. 2004). Deep, soft snow is a physical factor, that limits the ability of larger-bodied mesocarnivores (e.g., fisher and gray fox) with higher foot loading to occupy these regions. Snowfall is rare in the redwood region, but dense shrub cover is not, and shrubs likely represent another physical factor that discriminates against the larger-bodied mesocarnivores. In the last century this dense, spatially extensive shrub layer has been highly fragmented by road building and reduced by stand management methods developed to maximize wood production. Site preparation after logging typically reduces shrub cover. The high densities of replanted trees limit the amount of light reaching the ground and further reduce shrub cover. Species of mesocarnivores that were not historically common in the redwood region (i.e., fisher, gray fox)

have now become quite common in these second growth habitats with highly altered shrub structure (Grinnell et al. 1937, Klug 1996, Slauson and Zielinski 2004).

The fisher (*Martes pennanti*) was historically distributed throughout much of northwestern California, but it was less common in the coastal redwood forests than it was in the interior Douglas-fir forests (Grinnell et al. 1937). During the late nineteenth and early twentieth centuries nearly all records (95%) for fishers in Humboldt and Del Norte counties were >20 km from the coast. However, during the latter portion of the twentieth century the fisher has expanded its range in the redwood region and now occupies many areas of second growth forest in the northern redwood region (Slauson and Zielinski 2004). The gray fox has followed a similar pattern, although historical data is not as complete as for the fisher. Nevertheless, contemporary occurrence data suggest that fishers and gray foxes are either absent from, or extremely rare, in the largest remnant patches of fog-influenced old growth forests in the redwood region within Redwood National and State Parks (Slauson and Zielinski 2003), the Smith River National Recreation Area, and Six Rivers National Forest (Slauson and Zielinski 2004). While the fisher has received deserved conservation attention, due to its more severe decline throughout the Pacific states, its presence in most of the northern redwood region appears to be without precedent and appears to represent an expansion into areas formerly occupied by martens. If the goal of the restoration of second growth is to return old growth conditions (including dense shrub layers) where they have been lost, these efforts will have beneficial effects on marten and will probably discourage larger-bodied competitors like the fisher and gray fox.

Using mesocarnivores like the marten, fisher, and gray fox as focal species to help predict, design, and monitor restoration efforts will provide large-scale models of how wildlife responds to such efforts. We quantitatively assess the current suitability of second growth areas of Redwood National and State Parks for the Humboldt marten at three spatial scales: microhabitat, stand, and home range. Secondly, we will investigate the effect of road density on the occurrence of martens, fishers, and gray foxes in the redwood region. Finally, we will use the information gained from these new efforts to evaluate how future restoration efforts can best be planned to benefit restoration of the Humboldt marten to Redwood National and State Parks.

Project Objectives

1. Compare the availability of potential marten rest structures in stands occupied by martens to their availability in second growth stands.
2. Determine the current habitat suitability, using previously developed methods (Slauson et al. (2007), of all recently restoratively thinned stands.
3. Determine how road density affects the occurrence of martens, fishers, and gray foxes. Compare the use of roads versus the interior of stands with dense shrub layers for several species of mesocarnivores.

4. Use the information from this study to predict the future responses of fishers, martens, and gray foxes to the current plans for restoration in Redwood National and State Parks and to identify strategic areas for restoration to facilitate re-colonization for the Humboldt marten.

METHODS

We compared the habitat characteristics at areas currently occupied by martens to second growth areas in Redwood National and State Parks currently unoccupied by martens. We included a representative sample of restoratively thinned stands, including recent ($n = 21$) and 15-30 year old ($n = 6$; Veirs 1986, Keyes 2005) thinned stands, as well as a sample of adjacent unthinned stands ($n = 15$). In each stand we sampled the density of microhabitat elements (e.g., large downed logs) and stand characteristics (e.g., seral stage, shrub cover). At the microhabitat scale we compared the densities of potential rest structures in second growth stands and stands known to be occupied by martens. At the larger, stand and home range scales, we applied predictive habitat models, developed from the areas occupied by martens, to determine the change in habitat suitability following restoration. Finally, to assess the effects of road density, we measured mesocarnivore use of roads and also took a more regional approach, using our systematic survey database of mesocarnivore detections for the northern redwood region to evaluate the relative effects of road density and other key habitat characteristics on mesocarnivore distributions.

Habitat Assessments

Microhabitat: Rest and Den Site Availability

We established reference conditions for the availability of potential resting and denning structures by estimating their density in stands within known marten home ranges to the east of Redwood National and State Parks. Rest structures included large live trees with defects, snags, logs, and rock piles, the most common resting structures used by martens in the coastal population (Slauson and Zielinski 2009a). Each log, snag, and live tree structure must have been >60 cm in maximum diameter or diameter at breast height (DBH) and have a detectable feature (e.g., chamber, cavity, platform) which a marten could use for resting or denning. Each restoratively thinned and paired unthinned second growth stand was also sampled to compare potential resting and denning structure density. We recognized that it was necessary to reconcile the fact that places where martens occur may be different than the redwood second growth areas. To do so we referenced previously collected data from Slauson and Zielinski (2003) to provide additional reference conditions for the density of potential resting and denning structures in old growth stands throughout Redwood National and State Parks.

Density of potential resting structures was determined using multiple variable-length belt transects following the approach of Bate et al. (1999). Transect length was determined by the dimensions of each stand and contained enough total length to cover $>50\%$ of each stand. Transect width differed for trees and snags (wider) versus downed logs and rock piles (narrower) due to differences in detectability, each width was determined in each stand based on the distance the observer could reliably detect each structure type.

Shrub cover for each stand was measured along the same transects as potential resting structures were sampled. At each 10m interval along the transect, shrub cover and species dominance was visually estimated in a 1x1m quadrat. The quadrat was placed on alternating sides (right or left) of the transect at successive intervals. Mean shrub cover for each stand was estimated by taking the mean of all quadrat estimates. Shrub species rank dominance for each stand was calculated by summing all the ranks (1-3) from each quadrat.

Stand Scale Habitat Suitability

To determine the current habitat suitability of restoratively thinned and unthinned stands we applied a previously developed predictive model for the Humboldt marten (Slauson et al. 2007):

$$\text{Prob. of Occupancy} = 1 / (1 + \exp[-4.16 + (\text{Seral Stage}) + (0.036 * \% \text{ Shrub Cover}) + (2.41 * \% \text{ Conifer})])$$

This stand model combines information on the seral stage, density of the shrub layer, and conifer dominance of the overstory to produce a score, ranging from 0-1, representing the likelihood that a marten would occupy a stand. Stand scale habitat suitability was determined for all restoratively thinned stands and their adjacent unthinned stands. To provide a set of old growth redwood stands to evaluate habitat suitability, we included all the old growth stands (n = 69) throughout RNSP sampled by Slauson and Zielinski (2003), representing a random set of redwood reference stands. Finally, we included all 26 marten occupied and 133 unoccupied stands sampled earlier by Slauson et al. (2007).

Effect of Roads

Spatial Analysis

We used our existing survey database for the northern redwood region to investigate the relationships of mesocarnivore distribution to road density and other home range scale metrics of habitat structure and composition. The database used for this analysis contained 112 survey locations from 3 survey efforts. The first two survey efforts were the 1996-1997 “systematic surveys” (n = 78; Carroll et al. 1999) and 2002 Redwood National and State Park Surveys (n = 22; Slauson and Zielinski 2003) both which used the same survey protocol, a sample unit consisting of 6 track plate stations spaced ~500m apart in a pentagonal array. The third survey effort was the 2000-01 Humboldt marten population survey (n = 10; Slauson et al. 2007) which used 2 track plate stations per sample unit, spaced 250m apart. All three survey efforts used the same station-level protocol: once established each station was revisited every 2 days to remove tracks and replace bait. All stations were baited with single chicken drumsticks and had an olfactory lure (Gusto; Minnesota Trapline Products, Pennock, MN, USA).

Evaluation of the effect of road density on mesocarnivore distribution must include other habitat characteristics known or hypothesized to be important to each species in order to best understand the relative importance of roads. To create a suite of variables to model mesocarnivore distributions, we developed 7 habitat covariates (2 related to roads, 5 related to

habitat composition), representing home-range scale characteristics of the areas within a 1 and 2.5-km radius of each sample unit (Table 1). We used 2 GIS coverages to derive the habitat covariates. The first was a gradient nearest neighbor vegetation coverage (hereafter GNN layer), created by the Landscape Ecology, Modeling, Mapping, and Analysis program (<http://www.fsl.orst.edu/lemma/splash.php>) which uses a plot interpolation method to integrate field plot, remotely sensed, and mapped environmental data to map current vegetation. This vegetation layer is moderate to highly accurate ($r^2 = >0.60$) for predicted plot values of the coarse vegetation characteristics we selected. Three different structural habitat types were derived from the GNN layer: old forest (OG) defined by the combination of giant and large tree size classes, young forest (Y) defined by the combination of the shrub and pole developmental stages, and shrub cover (S) defined by the presence of shrub cover $>50\%$. The second coverage was a transportation layer, used to assess road density, that included all types of forest roads (e.g., paved, gravel, unimproved) created by the Six Rivers National Forest. The linear amount of road was converted to 30x30m pixel coverage, representing presence or absence of a road in each pixel.

Each sample unit was buffered with a 1 and 2.5 km radius circle, representing areas (1 km = 314 ha) equivalent for a typical male marten home range in coastal California (1-km radius; Slauson and Zielinski unpubl. data), equivalent to 2 home ranges for male gray foxes (1-km radius; Fryxell 1982), and equivalent to 50% and 100% of an average male and female fisher home range, respectively (2.5 km radius; Higley and Matthews 2009). Structured query language (SQL) was used to make selections from the vegetation and road coverages to develop predictors of mesocarnivore habitat. Selected habitat predictors were processed with a spatial analysis program (FRAGSTATS v 3.3, University of Massachusetts Landscape Ecology Program, <http://www.umass.edu/landeco/research/fragstats/fragstats.html>) to calculate landscape metrics associated with each sample unit. These metrics included the percent of the circle represented by roads (R) and each habitat type (e.g., OG, Y, S; Table 1) in the circle (PLAND), and for OG only, the number of habitat patches (NP) and number of distinct core areas (NDCA; Table 1).

Model Development, Selection, and Evaluation

We hypothesized that both positive and negative relationships existed between road and habitat metrics and each species' distribution. We developed 8-12 *a priori* habitat models, based on existing information and our hypotheses, describing the relationships between species occupancy and home range scale metrics of habitat structure and composition (Burnham and Anderson 2002). We used resource selection functions (Manly et al 2002) to determine the habitat characteristics most important for species occupancy.

We independently ranked each species' set of models using Akaike's Information Criterion for small sample sizes AIC_c , (Burnham and Anderson 2002). We interpreted models by the comparison of ΔAIC_c values, which provides a measure of fit of data to the model (Anderson et al. 2000). To further interpret the relative importance of a model, given the *a priori* model set, we calculated Akaike weights (w_i) using ΔAIC_c values and created a 95% confidence set of models by considering all models whose cumulative weights equaled 0.95 (Burnham and Anderson 2002). To assess the relative importance of each variable in the selected models, we

assessed their frequency in the 95% confidence set of models and their effect sizes using odds ratios.

Road Surveys Using Cameras

To determine the species that use roads, we established paired remote camera sample units. One camera was located along a creek in the interior (>250 m from the edge/road) of a stand with dense (>70% cover), spatially extensive native shrub layers and the second was located on an adjacent, low human use, forest road. We selected creeks for comparison, because they represent a naturally occurring linear feature. Each camera was run for a total of 70 days, the first 28 days no olfactory lure was used, the second 28 days fisher, gray fox, and bobcat urine was sprayed 2-3 m in front of each camera, and during the final 14 days 3 chicken drumsticks and an commercial trapping lure (Gusto) was applied 2-3m in front of each camera. This sequence provided an initial period to collect unbiased information on the frequency of use of roads and creeks and then 2 levels of attractants to see if use patterns would change. Two types of remote camera units were used, Cuddyback Excite 2.0 and Scoutguard 5.0 megapixel cameras. Paired camera sample units were established in 3 different landscapes, defined by the 2.5 km radius surrounding the sample unit dominated by either old growth (>80%), old growth-second growth mix (>30%, <70% each), or second growth (>80%). In addition, each landscape surveyed had to have had a fisher or marten detected there within the last 10 years in order to be able to interpret the results relative to the two mesocarnivore species of highest conservation concern in the region.

An individual detection was recorded when a carnivore species was detected ≥ 1 time during each 24-hour period. This approach minimized the influence of short-term responses to olfactory lures. Detection rates were calculated by the following equation:

$$(\text{Total Detections}/\text{Survey Duration}) * 10$$

Detection rates were compared for roads versus creeks for each species and species guilds (habitat generalists versus specialists) using paired t-tests.

RESULTS

Habitat Assessments

Shrub Cover

We measured shrub cover along 1,060 m of transects in 6 stands occupied by martens, 900 m in 9 second growth stands thinned 15-30 years ago and 2,100 m in 21 second growth stands thinned in the last 2-7 years. Shrub cover was significantly greater in stands thinned recently ($t = 3.16$, $df = 18$, $P = 0.003$) and 15-30 years ago ($t = 3.88$, $df = 5$, $P = 0.003$) than in paired unthinned stands (Figure 1, Table 2). However, mean shrub cover was still significantly lower in stands thinned 15-30 years ago ($t = 2.26$, $df = 6$, $P = 0.03$) and recently thinned stands ($t = 5.97$, $df = 16$, $P < 0.001$) compared to stands occupied by martens (Figure 1). Mean shrub cover in stands

thinned 30 years ago did not differ statistically from stands occupied by martens ($t = -0.66$, $df = 3$, $P = 0.066$), but was still lower (Figure 1, Table 2) and overall more patchily distributed in thinned stands (K. Slauson pers. obs.).

The rank dominance of shrub species was similar between marten occupied, old growth redwood stands, and restoratively thinned stands (Table 3). Control stands reveal the severe decline and loss of the dominant shrub species found in marten occupied stands (e.g., salal [*Gaultheria shallon*], rhododendron [*Rhododendron macrophyllum*], evergreen huckleberry [*Vaccinium ovatum*]) and adjacent thinned stands (Table 3).

Fruiting and flowering by dominant shrub species (e.g., evergreen huckleberry, salal) was rarely observed in thinned stands, with only 38% (5/13) of stands supporting flowering and fruiting shrubs. Within these stands, flowering and fruiting was limited to individual shrubs with the most solar exposure (least overhead canopy cover). No flowering or fruiting was observed in any control stands, with many plants showing signs of moderate to severe decline in vigor and little new shoot growth. In contrast, fruiting and flowering was observed in 100% (6/6) of stands known to be occupied by martens.

Rest and Den Site Availability

Thinned stands contained significantly fewer potential resting and denning structures than stands known to be occupied by martens (Table 4). Only stands thinned 15-30 years ago had large logs at a similar densities to marten occupied stands, likely reflective of past practices of leaving cut trees if they had significant heart rot. In other cases several logs had been piled together, creating chambers potentially suitable for marten use.

Stand Scale Habitat Suitability

Application of the stand scale resource selection probability function revealed that the changes to date from restorative thinning have increased stand suitability values for martens beyond unthinned stands (Figure 2). However, structural conditions have not yet returned to those within the range of stands used by martens (Figure 2). The trajectory of restoratively thinned stands suggests that suitable shrub cover will establish within 10-20 years (Figure 1). Although restoration of shrub cover will result in increases in stand habitat suitability values, they will likely remain below the suitability range for martens until old growth tree characteristics return to the stands.

Effect of Roads

Mesocarnivore Occupancy Modeling Results

Marten--Five models were included in the 95% confidence set, 2 of which best fit the data (Models 1-2, Table 5). All models in the 95% confidence set contained the 3 variables with the highest importance weights (Table 5): shrub cover, road density, and old forest. All five models within the 95% confidence set included the shrub cover variable (Table 5).

In all top models, the odds of marten occurrence increased most significantly with dense shrub cover and decreased with road density. Using the estimates from Model 2, a 10% increase in the percent of dense shrub cover within a 1-km radius was associated with a 98% increase in marten occurrence (odds = 1.98, 95% CI = 1.12 to 3.50), after accounting for road density. For road density, a 0.5% increase in the amount of roads in a 1-km radius resulted in a 19% decrease in marten occurrence (odds = 0.81, 95% CI = 0.67 to 0.97), after accounting for dense shrub cover.

Fisher--The 95% confidence set contained only 3 models, 1 of which was well supported as the top model (Model 1, Table 5). In all the models in the 95% confidence set, the probability of fisher occurrence decreased with dense shrub cover, old forest, and young forest. Using the estimates from the top model (Model 1, Table 5), a 10% increase in the percent of dense shrub cover within a 2.5-km radius was associated with a 61% decrease in fisher occurrence (odds = 0.39, 95% CI = 0.20 to 0.77), after accounting for old and young forest. For old forest, a 10% increase in the amount of old forest in a 2.5-km radius resulted in a 50% decrease in fisher occurrence (odds = 0.50, 95% CI = 0.30 to 0.90), after accounting for dense shrub cover and young forest. For young forest, a 10% increase in the amount of young forest in a 2.5-km radius resulted in a 15% decrease in fisher occurrence (odds = 0.85, 95% CI = 0.49 to 1.46), after accounting for dense shrub cover and young forest.

Gray Fox--The 95% confidence set contained 8 models, 4 of which best fit the data (Table 5). All 4 models included shrub cover. The probability of gray fox occupancy decreased with increased shrub cover. Using the estimates in the top model (Model 1, Table 5), a 10% increase in the percent of dense shrub cover within a 1-km radius was associated with a 50% decrease in gray fox occurrence (odds = 0.50, 95% CI = 0.25 to 1.0), after accounting for the number of old forest patches. For old forest patches, an increase of 10 in the number of old forest patches in a 1-km radius resulted in a 20% increase in gray fox occurrence (odds = 1.20, 95% CI = 0.97 to 1.48), after accounting for dense shrub cover.

We evaluated the scale sensitivity of the strength of the effect of the shrub cover variable for each species by comparing the univariate p-values for each spatial scale (Figure 3). P-values were minimized when dense shrub cover was measured closest to the home range size of each species. This indicates how the amount of dense, spatially extensive shrub cover most directly influences the process of home range establishment by individuals of each species.

Camera Surveys

From 01 May to 16 December 2009, 20 remote camera sample units were surveyed in California State Parks (n = 8), Redwood National Park (n = 3), and Six Rivers National Forest (n = 9; Figure 4). Seven carnivore species were detected; 3 habitat generalists and 4 habitat specialists (Table 6). The survey protocol performed well for most species, with near perfect probability of detection for all but 2 species, mountain lion (*Felis concolor*) and mink (*Mustela vison*, Table 6).

Three species showed positive responses to both attractants: gray fox, fisher, and marten (Table 7). Detection rates for these species increased when either the 3 urines or Gusto+chicken

were added. Marten and fisher both had the strongest positive response to Gusto+chicken (Table 7). Addition of urine did have a positive response for bobcats, but the presence of Gusto+chicken did not alter their detection rate.

Habitat generalist carnivores were detected on roads significantly more than forest interiors, while habitat specialists used forest interiors significantly more than roads (Figure 5, Table 5). Although fishers and martens showed the strongest increase in detections when attractants were added, the presence of Gusto+chicken did not increase their detections on roads, with only 2 fisher and 0 marten detections occurring on roads when Gusto+chicken used.

During our camera surveys, we detected at least one marten in two locations in Prairie Creek Redwoods State Park (Figure 6). These detections are >9 km west of the nearest known marten detections and are the first in recent times to occur south of the Klamath River. Surveys in 2010 have confirmed the continued presence of a marten in the same area (K. Slauson unpubl. data). This appears to be a recent recolonization as surveys conducted in 2002, <200m from the detection locations, did not detect martens.

DISCUSSION

Potential Marten Rest and Den Site Availability

Potential rest and dens structures have been severely reduced in logged stands. These findings are consistent with the comparison of logged second growth and old growth stands in Redwood National and State Parks (Slauson and Zielinski 2003). However, logged stands in the Mill and Rock creek watersheds are more depauperate of potential rest structures than older second growth stands (Veirs, Whiskey 40) sampled in this study and by Slauson and Zielinski (2003) throughout Redwood National Park. This finding is undoubtedly linked to the reduction in the practice of leaving felled trees with extensive heart rot.

Resting structures are a critical component of habitat for martens and are used daily, to provide thermal benefits and security from predation while resting. Arboreal resting structures constituted 54% of those used by martens in coastal northwestern California in the summer and fall (Slauson and Zielinski 2009a). Elsewhere in their range, martens shift to using more ground-based resting structures covered by snow during the winter due to their increased thermal benefits (Schumacher 1999). However, this seasonal shift is not expected in the coastal forests martens inhabit, due to the lack of significant snow pack. The minimum ages of live and dead woody structures used by martens in coastal northwestern California was 176 and 254 years, respectively (Slauson and Zielinski 2009a). Given the time required to naturally regenerate suitable rest structures, alternative approaches will be necessary to provide the adequate types and number of resting structures during the next 1-2 centuries.

One alternative approach could involve developing artificial structures for resting. Slash piles, left after logging often have chambers, and have been shown to be used by martens. Use of slash piles is typical during the summer, likely due to their poor thermal benefits during winter (Raphael and Jones 1994). However, the creation of inner chambers to provide protection from

rain and increased thermal cover may increase their use in winter. British biologists have designed a ‘marten den box’ (Vincent Wildlife Trust 2010) used by pine martens (*Martes martes*) in young forests. These boxes could be used in slash piles as well as elevated on live trees. The interstitial spaces in large rock piles have also been used by martens (Slauson and Zielinski 2009a) and could be an additional longer-lived alternative to slash piles. Existing large logs and trees could be enhanced through cavity creation, which has been successful in the restoration of limited resources for an endangered forest bird, the red-cockaded woodpecker (*Picoides borealis*). Finally, large logs with natural or created cavities could also be moved into sites where they are especially depauperate.

Response of Shrub Cover to Thinning

Shrub cover positively responded to thinning of the overstory. Stands thinned 2-7 and 15-30 years ago had a 3 and 5-10 times increase in mean shrub cover compared to their respective unthinned control stands. If left unthinned, many control stands will lose most individual shrubs and head on a developmental trajectory very different from surrounding reference conditions. Only the oldest thinned stands (Veirs, Whiskey) showed regeneration of the shrub layer to the extent present in marten occupied stands, suggesting that 20-30 years may be required after thinning to regenerate suitably dense and spatially extensive shrub cover.

Dominant shrubs that produce flowers and fruits support additional foraging opportunities for martens. Martens frequently consume fruit, which appeared in >80% of 420 scat samples primarily from June until November (Slauson unpubl. data). Indirectly, flowering and fruiting shrubs support numerous prey populations (e.g., bald-faced hornets [*Dilovespula maculata*]) and attract migratory species (e.g., band-tailed pigeons [*Columbia fasciata*], varied thrushes [*Ixoreus naevius*]) that collectively increase the foraging value of stands where flowering and fruiting occurs.

Most shrubs showed responses to thinning with increased shoot growth, but the presence of flowering and fruiting was nearly absent from recently thinned and very sparse in old thinned stands. In comparison, shrub layers in all marten occupied stands showed fruiting and flowering. While recently thinned stands may simply require more time for shrubs to have the resources to support flowering and fruiting, the old thinned stands have had 1-3 decades. Fruit production is related directly to the availability of soil nutrients and the amount of photosynthate available, thus canopy closure directly affects this latter resource and can limit fruit production (Lee 1988). This suggests that stands thinned 20-30 years ago have either reduced soil nutrients or that overstory canopies have become/remained restrictive to flower and fruit production. Given that some shrubs in recently thinned stands had responded by fruiting, the reduction in soil nutrients does not appear to be the cause. We suspect that the single layer tree canopies in regenerating stands versus multi-layered of old growth, marten occupied stands may result in markedly different solar radiation exposure when overall canopy cover is similar. This has been shown to be the case for how other soft-masting species, which decrease fruit production in even-aged versus uneven-aged silvicultural systems as canopy cover increases (Perry et al. 1999). Restoration of fully productive shrub layers may require increased solar radiation to the shrub layer either through time as the canopy becomes multi-layered or through additional thinning.

Effects of Roads and Dense Shrub Cover on Mesocarnivore Distribution

The pattern of road use by habitat generalists versus specialists was striking in that habitat generalists dominated the use of roads and habitat specialists dominated the riparian areas in the forest interior. This supports the hypothesis that roads benefit species least adapted for capturing prey in the dense shrub understory of coastal forests. We cannot determine whether species are simply adjusting their movements to use roads or whether roads are facilitating species use of coastal forest landscapes. However, roads favor the generalists (i.e., bobcats, gray foxes) which also prey on martens and fishers (the forest specialists). Habitat specialists that must cross roads to move between habitat patches are more likely to encounter predators there, farther away from escape cover.

The most important factor determining the distribution of all 3 mesocarnivores was the presence of dense shrub cover. This provides strong support for the importance of the maintenance and restoration of this structural layer for marten conservation and restoration. Furthermore, it highlights the importance of a physical factor structuring the mesocarnivore community and mediating carnivore interactions.

At the home range scale, road density was an important factor contributing to limiting marten distribution. Although road density is correlated with other factors known to negatively affect martens (e.g., percent of the landscape logged, Slauson et al. 2007), our findings for high road use by potential marten predators suggests that the potentially negative effects of roads should be further investigated.

Responses of Mesocarnivores to Current and Future Restoration

Overall our findings illustrate the multiscale responses of mesocarnivores to changes in forest structure and composition from logging in the northern redwood region. Second growth landscapes are used by larger-bodied mesocarnivores that are not typically detected in contiguous patches of old growth coastal forest and show a negative association with one of the main structural components of these forests, dense shrub cover. Furthermore, forest roads are frequently used by generalist mesocarnivores and may be facilitating their increased distribution in coastal forests. Both the loss of old growth forest habitat, old forest elements (large live and dead trees), and the increased abundance of larger-bodied mesocarnivores have likely contributed to the decline and lack of recovery of the Humboldt marten. However, restoration actions, road removal and thinning, are likely to benefit martens by returning larger portions of the landscape to conditions favoring their size and foraging adaptations and reducing larger-bodied generalists (e.g., gray foxes, bobcats) that can kill them.

The challenges for restoration are great in the Redwood National and State Park complex. Collectively, the complex includes >24,000 hectares of logged second growth forest and includes >500 km of logging roads. To date, road removal has dominated most of the restoration

actions, with >300 and >50 km of roads removed by the national and state parks, respectively. Thinning has just begun on a large scale, with ~4% and ~6% of second growth stands treated by 2010 in the National and State Parks, respectively.

To be of the greatest benefit, restoration actions should select combinations of roads for removal and stands for restorative thinning that will: (1) buffer existing old growth patches and (2) connect adjacent areas of old growth. For example, Redwood National Park's restoration plan for the second growth and road removal in the Lost Man Creek watershed achieves the first of these criteria by explicitly targeting restoration of stands and removal of roads in proximity to the remaining old growth there. Although we recognize there are multiple objectives for road removal and restorative thinning, we have yet to see the considerations of large-scale connectivity guide the selection of restoration areas in any redwood national or state park units (RNP 2008, CSP 2010).

How roads are removed will likely have alternative effects on mesocarnivores. Roads that are completely removed using landform restoration will reduce access by generalist mesocarnivores but road decommissioning (blocking vehicle passage but leaving the road) will offer no change in access for use by mesocarnivores until the road bed is revegetated. The cost of landform restoration will likely limit the annual amount of road removal using this technique, which emphasizes the need to strategically select sections of roads that can buffer existing old growth patches and help restore connectivity between old growth patches.

One of the most critical elements lacking in the second growth landscapes are large woody structures with suitable resting and denning locations for martens and other wildlife. Because natural regeneration of these structures may take >200 years, alternatives will be required to provide adequate numbers of suitable structures until natural processes of recruitment are restored. Much like the need to return large wood to creeks to restore critical habitat for salmonids, large woody structures or surrogate structures (e.g., marten den boxes) need to be strategically returned to the landscape to accelerate the restoration of one of the most threatened mammals in the redwood region. Given that the only remnant Humboldt marten population is estimated to number <100 individuals (Slauson et al. 2009b) and individuals have been detected <1 km from the Mill Creek acquisition, short term measures that can increase habitat suitability may be critical to ensuring persistence and recovery of this population.

The scale at which restoration is needed and is being undertaken in the northern redwood region is both daunting and globally unprecedented. While the research we have described herein contributes to the beginning of our understanding of mesocarnivore response to restoration, we will need to continue to add to this knowledge base to refine management and restoration actions.

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Table 1. Definitions and abbreviations for variables measured at 1-km and 2.5-km radius circles around each sample unit used to model mesocarnivore distributions from surveys conducted from 1996-2002 in coastal northwestern California, USA.

Variable	Abbreviation
%Landscape Old Forest ^a	OG_Pland
Number of Habitat Patches of Old Forest ^a	OG_NP
Number of Distinct Core Areas of Old Forest ^a	OG_NDCA
% Landscape with Dense Shrub Cover ^a	S_Pland
% Landscape of Young Forest Habitat ^a	Y_Pland
% Landscape with Roads ^b	R_Pland
% Landscape Young Forest and Roads ^a	YR_Pland

^a Measured from the gradient nearest neighbor (GNN) vegetation coverage produced by the Landscape Ecology, Modeling, Mapping, and Analysis program (<http://www.fsl.orst.edu/lemma/splash.php>).

^b Measured from the transportation layer provided by the Six Rivers National Forest.

Table 2. Mean shrub cover measured in forest stands from 2002-2010 in coastal northwestern California, USA. Stands were sampled in 3 groups, Reference stands that included old growth redwood stands and old growth stands occupied by martens, and stands restoratively thinned either 15-30 years ago (Old Thin) or 207 years ago (New Thin). The 2 thinned stand groups also included measurements of paired control stands, where thinning was not conducted.

Group	Treatment (n)	Mean Shrub Cover (SD)	95% Confidence Interval
Reference			
	Marten Occupied (6)	71.7% (10)	63 – 80%
	Marten Occupied (26)*	74.0% (20)	66 -- 82%
	Old Growth Rwd (69)**	86.3% (15)	83 -- 90%
Old Thin			
	Total (6)	46.8% (25)	22 – 72%
	Veirs (3)	66.5% (12)	
	Whiskey 40 (3)	33.0% (19)	
	Control (3)	6.2% (4)	2 – 10%
New Thin			
	Total (13)	31.9% (19)	20 – 44%
	Control (8)	11.8% (10)	4 – 44%

*From Slauson et al. (2007).

** From Slauson and Zielinski (2003).

Table 3. Rank-order shrub species dominance for 6 most dominant shrub, shrub form tree, and fern species determined from transect sampling from 2002-2010 in coastal northwestern California, USA. For each species the sum of the ranks and the number of stands it was present, in parenthesis, are presented. The 3 most dominant shrub species in each stand type are highlighted.

Plant Species	Thinned 15-30		Thinned 2-7		Marten Occupied		Old Growth Rwd (n=90)*
	Thin (n=5)	Control (n=3)	Thin (n=13)	Control (n=7)	Stands (n=6)	Slauson 2003 (n =26)**	
Evergreen huckleberry	82 (4)	21 (3)	86 (9)	53 (4)	0 (0)	35 (14)	143 (NA)
Salal	47 (5)	6 (2)	55 (6)	3 (1)	97 (2)	27 (10)	69 (NA)
Rhododendron	21 (4)	0 (0)	22 (5)	10 (2)	76 (2)	19 (9)	85 (NA)
Tanoak	6 (1)	0 (0)	19 (3)	2 (1)	55 (4)	14 (6)	NA
Huckleberry oak	0 (0)	0 (0)	0 (0)	0 (0)	61 (2)	17 (6)	NA
Sword Fern	17 (2)	3 (1)	51 (7)	24 (4)	5 (1)	NA	189 (NA)

* Results from Slauson and Zielinski (2003).

**Results from (Slauson 2003) are for rank-order estimates from single plots in each stand.

Table 4. Mean densities (#/ha) of potential resting and denning structures in recently thinned, not recently thinned, and old growth stands in coastal northwestern California. Each structure must have been >60cm in maximum diameter and have a detectable feature (e.g., chamber, cavity, platform) that a marten could use for resting or denning.

Stand Type (n)	Structure Type #/ha (SE)		
	Logs	Snags	Live Trees
Thinned <9 Years Ago (17)	0.98 (0.48)*	0.07 (0.07)*	0.00*
Thinned 15-30 Years Ago (9)	6.02 (1.82)	0.18 (0.19)*	0.00*
Marten Occupied (7)	5.14 (1.72)	2.10 (0.54)	0.74 (1.13)

*Significantly lower t-test results for comparisons of means to marten occupied stands at $P < 0.05$.

Table 5. 95% confidence set of models predicting the probability of each species occurrence using regional survey data from coastal northwestern California and southwestern Oregon, USA. Each model is ranked according to ΔAIC_c value. OG = old growth, S = Shrub cover >50%, R = roads, Y = young forest, Pland= percent of the landscape, LPI = large patch index, NP = number of patches, Fisher = presence of fisher at the sample unit.

Species	Model #	Model Parameters		Model Ranking			
		Variables		ΔAIC_c	w_i^a	K^b	
Marten	1	OG_Pland*S_Pland	R_Pland	0.00	0.33	5	
	2	S_Pland	R_Pland	0.59	0.32	3	
	3	OG_Pland*S_Pland		1.95	0.13	4	
	4	OG_LPI*S_Pland		2.86	0.08	4	
	5	S_Pland		3.27	0.07	2	
Fisher	1	S_Pland	OG_Pland	Y_Pland	0.00	0.80	4
	2	S_Pland	OG_Pland		3.85	0.11	3
	3	S_Pland	*OG_Pland		5.46	0.05	5
Gray Fox	1	S_Pland	OG_NP		0.00	0.26	5
	2	S_Pland			0.92	0.16	4
	3	S_Pland	Y_Pland		1.32	0.13	5
	4	S_Pland	Fisher		1.52	0.12	8
	5	S_Pland	Y_Pland	R_Pland	2.23	0.09	4
	6	S_Pland	OG_Pland		2.92	0.06	5
	7	S_Pland	R_Pland		3.32	0.05	8
	8	S_Pland	*OG_Pland		4.32	0.03	8

^a w_i = Akaike weight, corrected for small sample sizes.

^b K = number of parameters in each model.

Table 6. Carnivore species detected at remote camera sample units surveyed from May-December 2009 in coastal northwestern California. Detection probability represents the probability that a species would be detected using the survey protocol, if in fact it was present.

Species	Detection Probability	Number of Observed Detections	
		Road (% total det.)	Forest Interior (% of total det.)
Habitat Generalists			
Gray Fox	100%	11 (69%)	5 (31%)
Bobcat	95%	5 (100%)	0 (0%)
Mountain lion	37%	7 (88%)	1 (12%)
Totals: Habitat Generalists		23 (79%)	6 (21%)
Habitat Specialists			
American marten	99%	2 (25%)	6 (75%)
Fisher	85%	3 (30%)	7 (70%)
Raccoon	94%	1 (14%)	6 (86%)
Mink	54%	0 (0%)	3 (100%)
Totals: Habitat Specialists		6 (21%)	22 (79%)

Table 7. Detection rates, calculated as # detections/10 survey days, for carnivore species at remote camera sample units from May-December 2009 in coastal northwestern California. Bolded detection rates are significantly different paired t-test results for roads versus forest interior (Interior) for each species at $P \leq 0.05$.

Species	N	Survey Treatment			
		No Attractants	Urine	Gusto+Chicken	
Gray Fox	10	Roads	0.88 (0.91)	0.45 (0.55)	1.36 (1.26)
		Interior	0.12 (0.29)	0.84 (0.18)	0.14 (0.45)
Bobcat	5	Roads	0.23 (0.15)	0.77 (0.89)	0.29 (0.64)
		Interior	0.0 (0.0)	0.05 (0.11)	0.0 (0.0)
Mountain lion	6	Roads	0.21 (0.15)	0.11 (0.20)	0.08 (0.22)
		Interior	0.0 (0.0)	0.0 (0.0)	0.08 (0.22)
<i>Habitat Generalists</i>	21	Roads	0.46 (0.66)	0.39 (0.59)	0.65 (1.00)
		Interior	0.04 (0.19)	0.09 (0.20)	0.08(0.01)
American marten	7	Roads	0.05 (0.12)	0.0 (0.0)	0.0 (0.0)
		Interior	0.05 (0.13)	0.73 (0.62)	0.86 (0.65)
Fisher	9	Roads	0.0 (0.0)	0.0 (0.0)	0.23 (0.36)
		Interior	0.11 (0.16)	0.0 (0.0)	1.29 (1.94)
Raccoon	7	Roads	0.04 (0.11)	0.0 (0.0)	0.0 (0.0)
		Interior	0.33 (0.5)	0.33 (0.28)	0.75 (0.19)
<i>Habitat Specialists</i>	23	Roads	0.03 (0.09)	0.0 (0.0)	0.09 (0.25)
		Interior	0.16 (0.31)	0.33 (0.47)	0.79 (1.33)

Figure 1. Box and whisker plots of percent mean shrub cover in forest stands in coastal northwestern California. Heavy black lines indicates the median values, boxes indicates upper and lower quartiles, lines represent maximum and minimum values, and open circles outlier values.

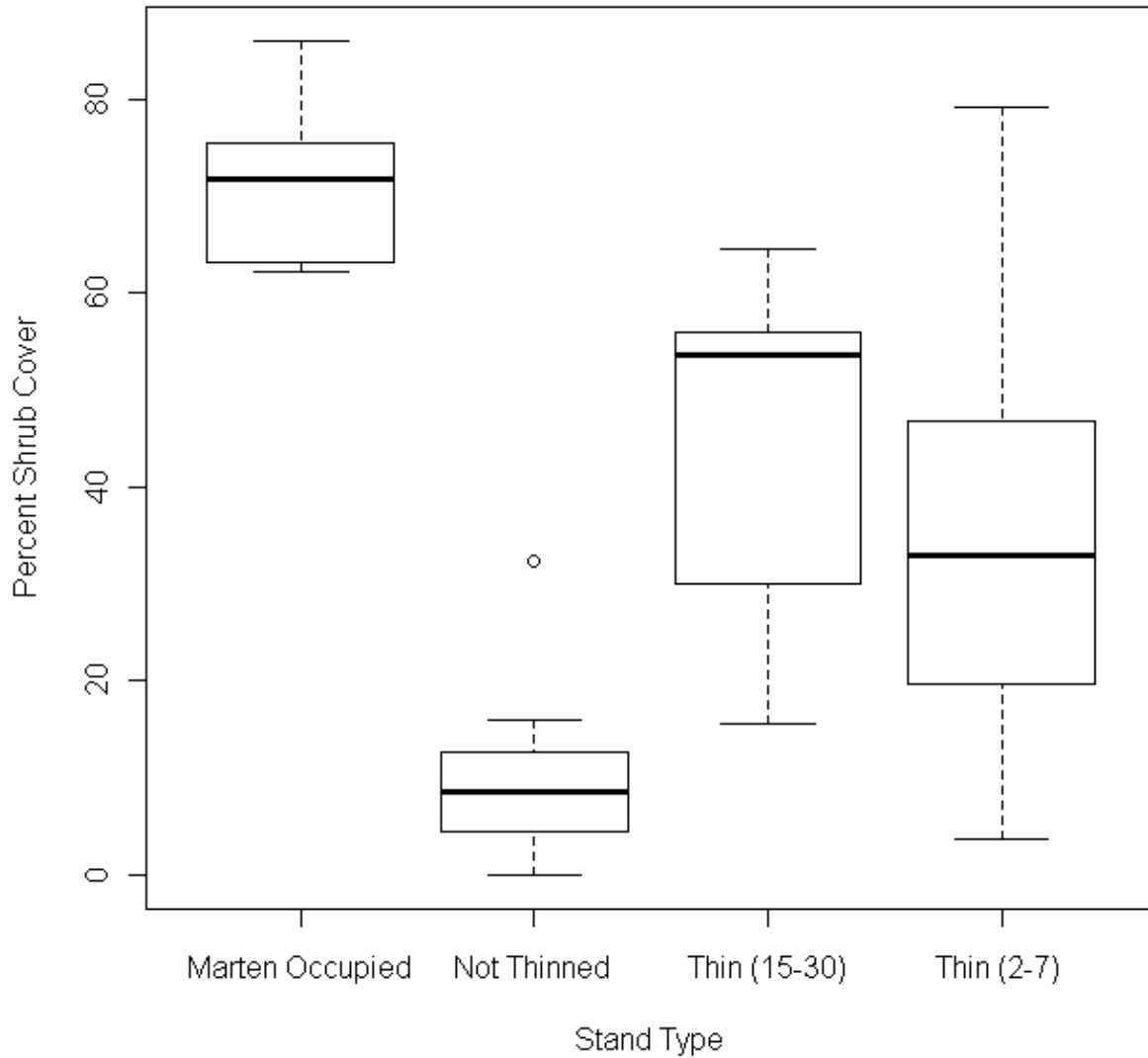


Figure 2. Box and whisker plots for the probability of stand scale occupancy for American martens in coastal northwestern California. Heavy black lines indicates the median values, boxes indicates upper and lower quartiles, lines represent maximum and minimum values, and open circles outlier values.

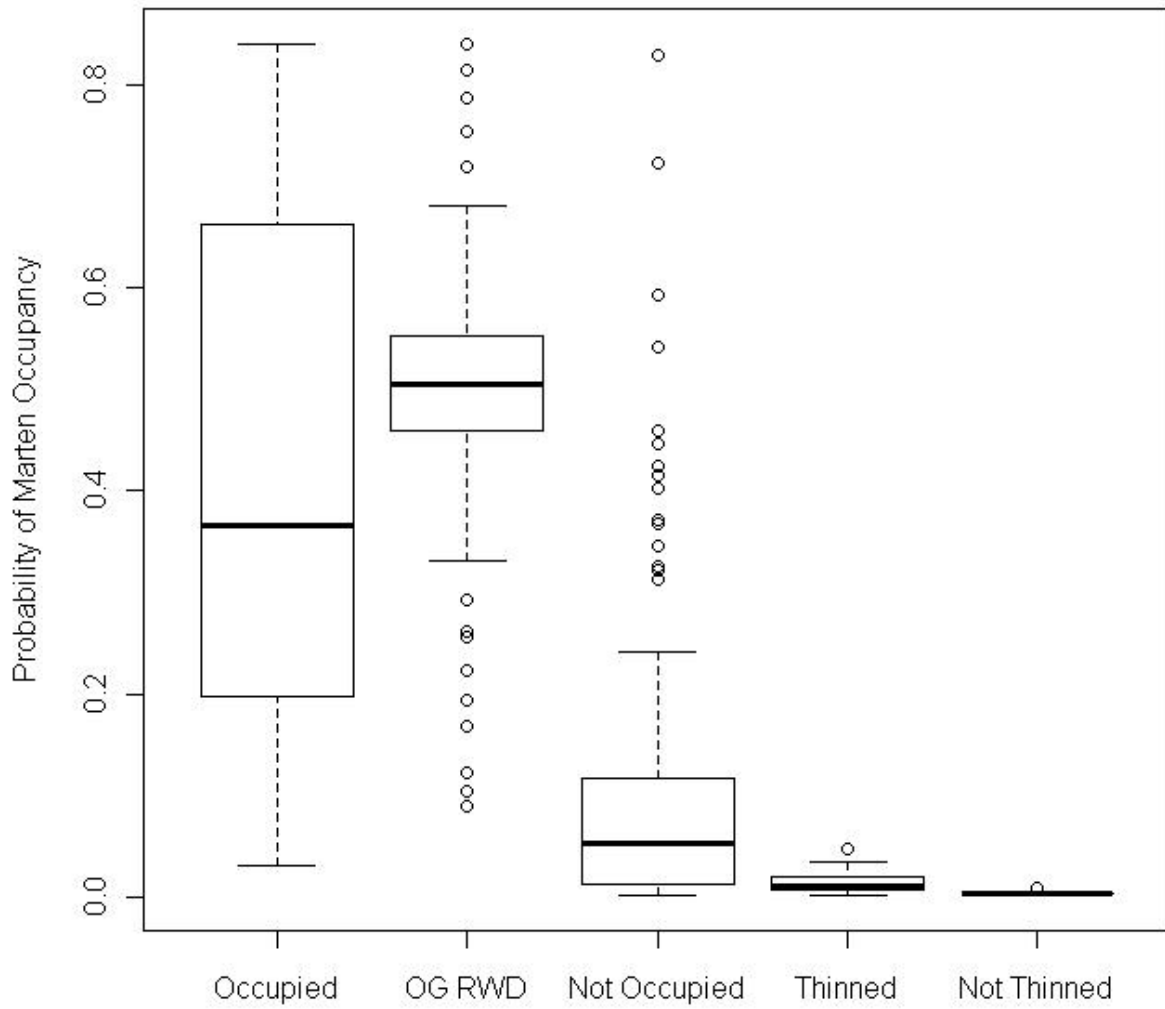


Figure 3. Scale-sensitivity for key habitat metrics, demonstrating the higher significance of the occupancy effect (positive for marten, negative to fisher and gray fox) when shrub cover is measured at spatial scales closer to each species' average home range size than at scales larger (marten and gray fox) or smaller (fisher). Y-axis equals the p-value for logistic regression models using the shrub cover variable measured at 1-km and 2.5 km radii around sample units.

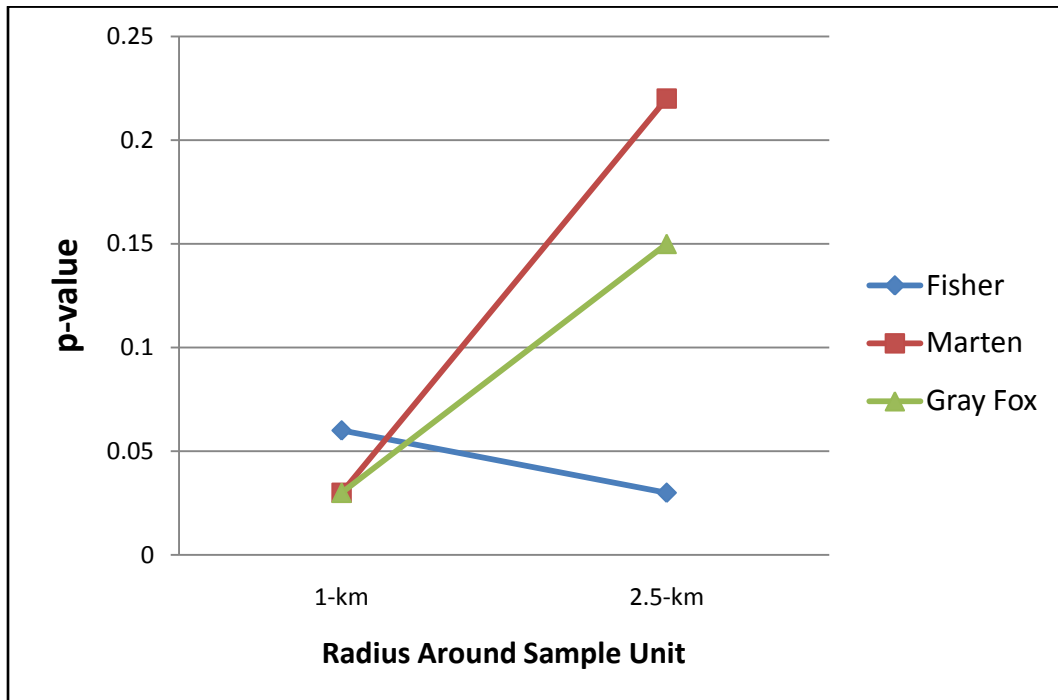


Figure 4. Distribution of remote camera sample units surveyed in coastal northwestern California in 2009.

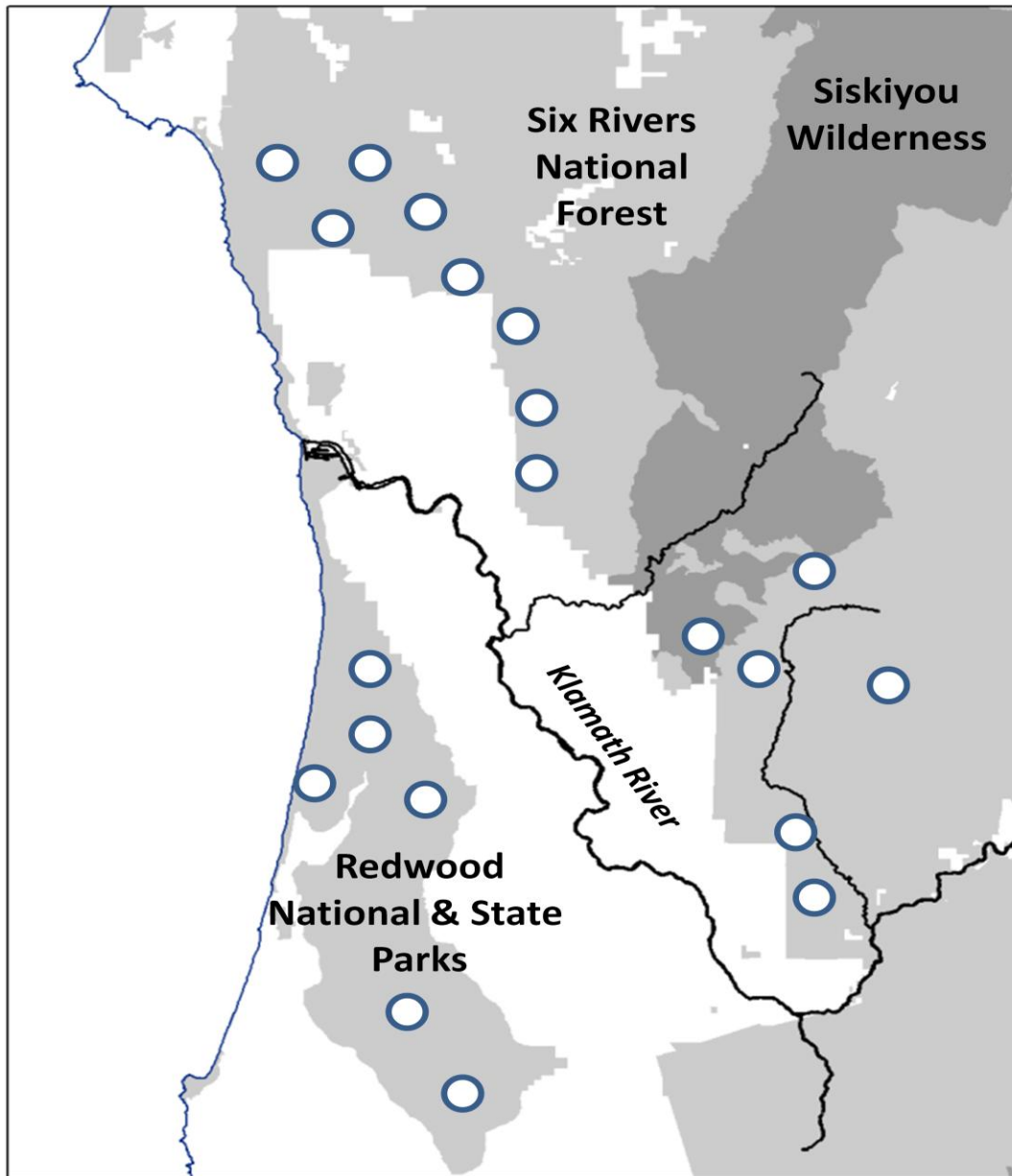


Figure 5. Percent of mesocarnivore station detections on paired road versus forest interior locations from May-December 2009 in coastal northwestern California.

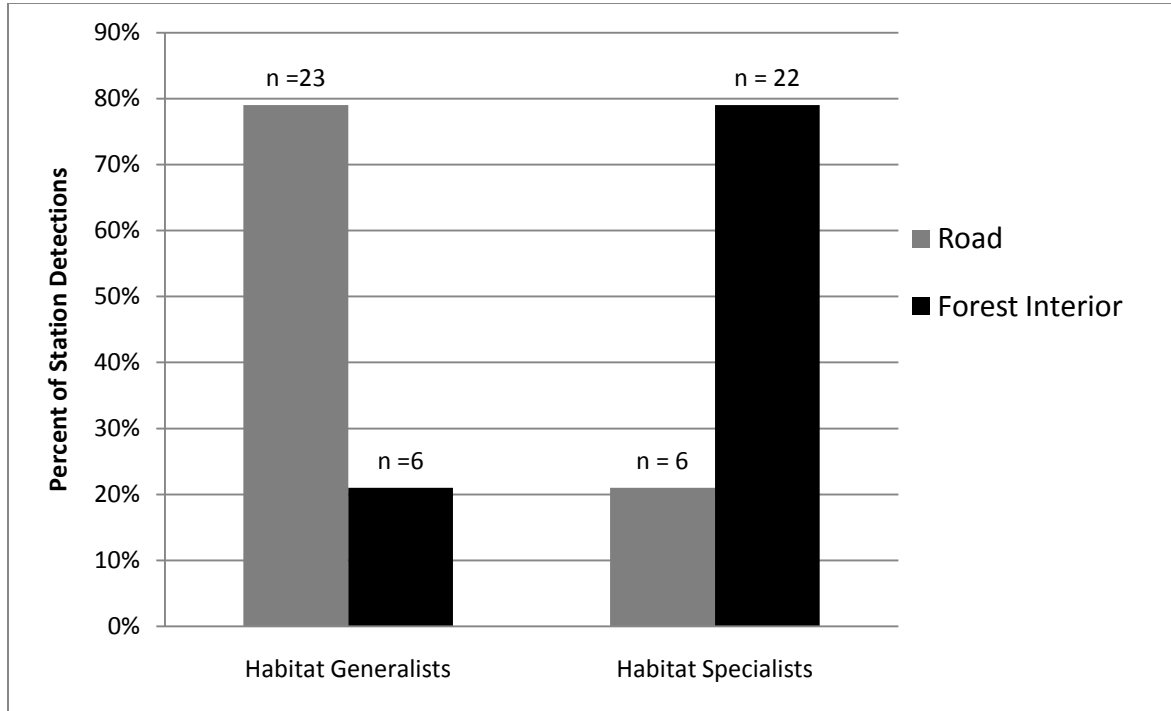


Figure 6. American marten detected by a remote camera in Prarie Creek Redwoods State Park, July 2009.

