Pinyon-juniper removal has long-term effects on mammals

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ABSTRACT

Removing tree cover is a common forest management practice, and pinyon-juniper woodlands in the western United States have been the focus of tree reduction efforts for decades. The scale and intensity of tree removal practices are expected to increase as technology advances and as land managers are tasked with meeting multiple objectives, including fire prevention and habitat enhancement for livestock and wildlife of conservation concern. However, the long-term consequences of pinyon-juniper removal on animal communities are virtually unknown. The objectives of this study were to assess whether mammal habitat use differs between reference pinyon-juniper woodlands and stands that were mechanically disturbed by chaining more than 40 years ago, and to determine if these differences are associated with particular habitat characteristics. We used remotely triggered wildlife cameras to evaluate differences in mammal habitat use of historically chained sites ($n = 22$) and reference sites ($n = 22$) in northwestern Colorado. Our results demonstrate marked differences in habitat use between chained sites and reference woodlands for most detected mammal species. Bobcat, mountain lion, American black bear, golden-mantled ground squirrel, and rock squirrel all showed a negative response to historically chained sites, indicating long-term effects of tree removal on these species. In contrast, habitat use of chipmunk, mountain cottontail, and coyote did not differ between chained and reference sites. For most species, habitat use was influenced by specific vegetation characteristics, such as proportion of tree cover, which could be factored into management decisions. By understanding the long-term consequences of tree removal for diverse mammal species, we are better equipped to adapt forest management practices to benefit species of both economic and conservation concern.

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1. Introduction

Removing or reducing tree cover to benefit livestock or game species has been a common forest management practice for decades (Aro, 1971; Yahner, 1984; Redmond et al., 2013; Bergman et al., 2015). The scale and intensity of tree removal practices is expected to increase as technology advances and land managers are tasked with meeting multiple objectives, including fire prevention and enhancing forage and habitat for livestock and shrub-dependent wildlife in areas undergoing urbanization and energy development (Connelly et al., 2000; Redmond et al., 2013; Bergman et al., 2014). Although tree removal practices are widespread and pervasive in some forest ecosystems, little is known about the long-term effects of tree removal on wildlife communities (Bombaci and Pejchar, 2016).

During the last half-century, pinyon-juniper (P-J) woodlands have been a major focus of both forest conservation and tree

reduction efforts (Evans, 1988; Redmond et al., 2014). Collectively, P-J woodlands are the third largest vegetative community in the United States, covering over 40 million hectares (Romme et al., 2009). P-J woodlands are also an important source of food and cover for woodland-dependent wildlife species and forage for livestock (Schott and Pieper, 1987; Romme et al., 2009). However, both pinyon and juniper trees have been expanding into grasslands and shrublands for the past 150 years (Romme et al., 2009). Pinyon-juniper expansion into grasslands and shrublands reduces forage for livestock, increases fuel for wildfires and reduces habitat for economically important or rare species that depend on open habitats, such as mule deer (*Odocoileus hemionus*) and Greater Sage-grouse (*Centrocercus urophasianus*) (Terrel and Spillett, 1975; Evans, 1988). Tree removal and reduction has thus become a common tool for forest and wildlife management in P-J ecosystems (Aro, 1971; Bergman et al., 2014).

Historically, a mechanical technique known as chaining was the most common method for removing tree cover (Aro, 1971; Evans, 1988; Miller and Wigand, 1994; Redmond et al., 2014). Between 1950 and 1964, 1.2 million hectares of P-J were removed via chaining in the U.S. (Box et al., 1966). Chaining uproots trees and shrubs

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by dragging heavy anchor chains between two bulldozers across the forested landscape (Aro, 1971; Sedgwick and Ryder, 1986; Bureau of Land Management, 2008). Chaining is an efficient method for killing older, larger trees over a large area, and increasing herbaceous forage for livestock and economically important wildlife (Aro, 1971). Because chaining removes all or most trees, P-J woodlands are replaced with open grassland and shrubland habitats (Tausch and Tueller, 1977). Over time, the removal of P-J cover can shift the plant community from a woodland-dominated system to a shrub-dominated system (Redmond et al., 2013). Specifically, P-J removal can lead to reduced tree cover and increased cover of shrubs and perennial grasses (Evans, 1988; Yorks et al., 1994; Redmond et al., 2014). Although the use of chaining has tapered off since the 1970's (Redmond et al., 2013), it has been replaced with other tree removal methods that also reduce pinyon and juniper cover and increase herbaceous vegetation (Owen et al., 2009; Huffman et al., 2013; Redmond et al., 2014).

Regardless of the method employed, tree removal and subsequent changes to the plant community may fundamentally alter habitat use by mammals (Andren et al., 1994), particularly in slow-recovering systems, such as P-J woodlands (Schott and Pieper, 1987). Mammals contribute to important ecological processes, such as seed dispersal and nutrient cycling, and small and medium-sized mammals are prey sources for predatory birds and large carnivores (Holechek, 1981). Thus, understanding the long-term effects of the widespread practice of P-J removal on mammal species is both ecologically interesting and important for the conservation and management of ecosystems.

The short and long-term effects of tree removal on medium and large-sized mammals in temperate and arid forest systems remain poorly understood (Crooks, 2002), and most studies of small mammals evaluated effects only shortly after tree removal. For example, habitat use of generalist rodent species (e.g., deer mouse, *Peromyscus maniculatus*) increased immediately following chaining (Baker and Frischknecht, 1973; O'Meara et al., 1981; Sedgwick and Ryder, 1986). Specifically, O'Meara et al. (1981) and Sedgwick and Ryder (1986) recorded greater numbers of least chipmunks (*Tamius minimus*) in chained sites than in undisturbed references sites, but found a decrease in the total abundance of pinyon mouse (*Peromyscus truei*) – a pinyon-juniper specialist. Sedgwick and Ryder (1986) also found that golden-mantled ground squirrels (*Callospermophilus lateralis*) were caught less often in chained sites than in reference sites. In New Mexico, lagomorphs preferred chained sites to reference sites immediately following disturbance (Kundaeli and Reynolds, 1972; Howard et al., 1987). With the exception of Howard et al. (1987), these aforementioned studies occurred in the few years following tree removal. Inference about changes in species composition immediately following habitat disturbance (e.g., 1–3 years) may or may not predict long-term effects on community dynamics (Stouffer et al., 2011). Although long-term effects on species can go undetected in short-term studies (Laurance et al., 2002; Laurance et al., 2011), these baseline studies provide the unique opportunity to revisit historic mechanically disturbed sites and compare short and long-term changes to mammal habitat use.

We investigated whether tree removal intended to increase forage for livestock and mule deer has long-term consequences for other mammal species. Using remotely-triggered wildlife cameras, we compared mammal habitat use within areas of P-J woodlands that were chained >40 years ago and reference woodlands in the Piceance Basin of Northwest Colorado, USA. Our research objectives were to (1) evaluate differences in habitat use between historically chained and reference sites, and (2) identify vegetation characteristics that influenced habitat use in our study area. Where mammal habitat use is associated with particular vegetation characteristics, we suggest incorporating these characteristics into future forest management practices, with the objective of minimizing impacts on species of conservation concern.

2. Methods

2.1. Study site

We examined mammal habitat use in historically chained and intact P-J woodlands on public land managed by the Bureau of Land Management in the Piceance Basin of northwestern Colorado, U.S.A. Dominant land uses in this P-J ecosystem include oil and gas extraction and domestic livestock grazing (Northrup et al., 2015). The area is topographically diverse and consists of high plateaus and deeply incised valleys. Our sampling sites ranged from approximately 1500–2400 m in elevation. Woodlands are dominated by pinyon pine (*Pinus edulis*) and Utah juniper (*Juniperus osteosperma*) (Sedgwick, 1987). The dominant shrubs are antelope bitterbrush (*Purshia tridentata*), mountain mahogany (*Cercocarpus montanus*), big sagebrush (*Artemisia tridentata*), rabbitbrush (*Chrysothamnus* spp.), common chokecherry (*Prunus virginiana*), and Saskatoon serviceberry (*Amelanchier alnifolia*) (O'Meara et al., 1981; Sedgwick, 1987).

2.2. Site selection

To assess habitat use of mammals in chained and reference woodlands, we established sampling sites in areas that historically underwent mechanical tree removal via chaining ("chained sites") and P-J woodlands that had not been mechanically disturbed or subject to any large-scale disturbance ("reference sites"). We identified areas that had been chained in the 1950's – 1970's using local knowledge from land managers and aerial imagery. We visited each historically chained location to confirm that no additional disturbance (i.e., prescribed fire, wildfire, or mechanical tree removal) had occurred since the initial disturbance. This was evidenced by the presence of many large, decaying, fallen trees and the absence of charred debris. Nine chained areas ranging in size from 3 to 1243 ha were identified. Using Geographic Information Systems (GIS), we established 22 sampling sites throughout these areas. We placed our first sampling site within each chained area by picking a random location in the approximate center of an accessible portion of the area. We then placed additional sampling sites in each cardinal direction, such that all sites were at least 250 m apart. Because we began allocating sites in the smallest chained areas first, our design allowed for one site in each of the smallest areas and up to 6 sampling sites in the largest areas (Fig. 1).

Reference sampling sites ($n = 50$) had been previously established across similar elevations and soil types (i.e., loam) within the study area for an ongoing wildlife-monitoring program. All reference sites were randomly placed on the landscape using GIS and were buffered from disturbed areas (e.g., other areas of tree removal or fire) by at least 250 m. Each reference site was ground-truthed to verify that it was within P-J woodlands. We randomly selected 22 reference sites for this study from the larger pre-existing set of reference sites using GIS to maintain a consistent sampling effort between the chained and reference sites (Magurran, 2004). Because five of the nine historically chained areas were spatially aggregated on the landscape, we stratified reference sites such that 16 sites were randomly selected from locations near the large cluster of chained areas (Fig. 1B). The remaining 6 sites were geographically dispersed across the study area (Fig. 1A). This design ensured that all reference sites were within 15 km of the historically chained areas (Fig. 1).
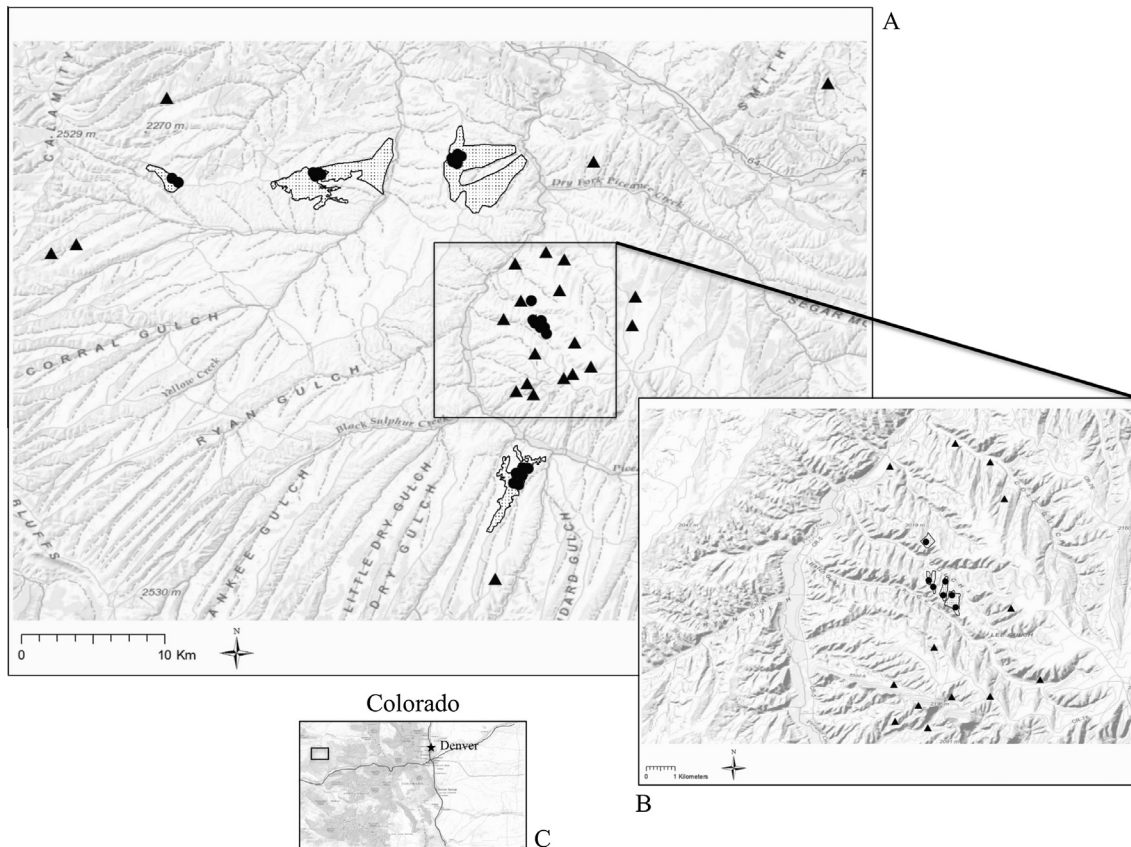
Fig. 1. Location of historic treatment and reference study sites in the Piceance Basin in northwestern Colorado, U.S. Stippled polygons represent historically chained areas. Black circles mark chained sites and black triangles mark reference sites. Map (A) shows the full extent of study area, inset (B) illustrates the distribution of chained and reference sites in and around the cluster of small chained areas, and inset (C) shows the location of the study site within the state of Colorado, USA (Basemap Source: ESRI, Redlands, CA, USA).

2.3. Wildlife camera trapping

To quantify mammal habitat use, we placed one unbaited remotely-triggered camera at each sampling site. To maximize detection probability, we preferentially established all cameras on wildlife trails, livestock trails, or unmaintained roads (e.g., two-tracks) situated within a 100 m radius of each sampling point. We used three models of cameras: Reconyx PC800 ($n = 30$; Reconyx, Holmen, WI, USA), Cuddeback Attack ($n = 10$; Cuddeback Digital, De Pere, WI, USA), and Cuddeback Capture ($n = 4$; Cuddeback Digital, De Pere, WI, USA). We allocated sampling effort evenly within each site type (chained or reference) among the three camera models. We deployed cameras during April – June 2014, and each camera collected relative activity data (photos per day) for each species for 149 days following deployment. We checked each camera approximately every two weeks to change batteries, replace data cards, and download photographs.

Volunteer observers were trained to identify species within each photo. Two observers viewed each photo, and all animals captured were identified to species. To ensure consistency across species identifications, two of the authors (TG and LS) resolved all conflicting identifications between volunteers. Any animal that could not be identified to species was excluded from the analysis, with the exception of two chipmunk species. Least chipmunk and Uinta chipmunk (*Tamius umbrinus*) are difficult to consistently and accurately differentiate from wildlife camera photographs; therefore, they were collectively recorded as "chipmunk." The Colorado Parks and Wildlife Photo Warehouse was used to store and manage data and to generate species occurrence results

(Ivan and Newkirk, 2016). Camera trap data were standardized to include a 30-s quiet period between subsequent photos to ensure a similar trigger rate among camera types.

2.4. Vegetation surveys

To assess the relationship between habitat use and vegetation characteristics, we measured a variety of vegetative parameters (Table 1). We sampled vegetation parameters in a 10 × 10-m plot offset by ∼5 m from each sampling point in a random compass direction (McElhinny et al., 2005). We recorded crown area and diameter at breast height (DBH) for each tree following the methods used in Huffman et al. (2012). Trees (live and dead) were defined as >1 m in height (Huffman et al., 2012). We calculated percent tree cover by dividing total crown area by plot size (100 m^2), and estimated an index of forest stand age by dividing

Table 1
Summary statistics of vegetative parameters (means and 95% confidence intervals) in historically chained sites and reference sites in northwestern Colorado.

Parameter	Chained	95% confidence intervals Lower	Upper	Reference	95% confidence intervals Lower	Upper
Mean shrub cover	0.27	0.21	0.33	0.15	0.09	0.21
Mean grass cover	0.11	0.09	0.13	0.09	0.05	0.13
Mean tree cover	0.03	0.01	0.05	0.28	0.16	0.4
Mean DBH/plot (cm)	0.07	0.03	0.11	0.79	0.48	1.1

the total DBH of all trees within each plot by plot size (DBH/plot; modified from McElhinny et al. (2005)). Percent cover of shrubs was measured using a 25-m line intercept beginning at each sampling point and heading in a random compass direction (Canfield 1941). At each site a 1-m^2 quadrat was placed at a random location on each side of the 25-m line. Percent cover of grass was calculated by averaging the proportion of grass cover between the two 1-m^2 quadrats for each site (Elzinga et al., 1998).

2.5. Statistical analysis

We used the following Bayesian hierarchical binomial mixture models, parameterized by Royle and Dorazio (2008) and Gelman and Hill (2007), to address our two specific research objectives: (1) compare mammal habitat use between historically chained sites and references sites, and (2) determine the importance of grass, shrub, and tree cover, and forest age (DHB/plot) for explaining potential differences in mammal habitat use among chained and reference sites. Binomial mixture models are traditionally used to estimate the number of individuals in a population using repeated count data and taking into account imperfect detection (Kéry and Schaub, 2012). We exchanged the number of individuals of a given species with the relative daily activity (detections per day) of that species and used the binomial mixture model to account for imperfect detection. This provides a more information rich estimate of habitat use than estimating an occurrence/non-occurrence response similar to the widely used occupancy modeling framework used for camera trap data of unmarked individuals (MacKenzie et al., 2006; O'Connell and Bailey, 2011; Kéry and Schaub, 2012).

2.5.1. Treatment model formulation

To quantify the long-term effects of chaining on mammal habitat use, we let y_{ij} be the total number of photos counted each day j, at each site i. These observed counts arise as a binomial random variable,

$$y_{ij} \sim \text{binomial}(\theta_i, p_i),$$

where θ_i is daily activity or "habitat use" at site i, and p_i is the site-specific detection probability. We then modeled the latent variable θ_i as a Poisson random variable,

$$\theta_i \sim \text{Poisson}(\lambda_i),$$

where λ_i is the expected habitat use at site i (Table S1). To quantify the effect of historical disturbance on mammal habitat use, we modeled λ_i as a function of disturbance or non-disturbance at each site using a log link,

$$\log(\lambda_i) = \omega_{g[i]} + \beta_1 chain_i.$$

Our data vector was set up so that β_1 was the model coefficient for the chained sites. Multiple disturbed patches contained multiple sampling sites (Fig. 1). Therefore, to account for potential site dependency within each disturbed patch, we used a multilevel model parameterized by Gelman and Hill (2007) to include a random effect ω_g on disturbance patch for the chaining sites and geographical grouping for the reference sites. Each chained area (Fig. 1) was given its own group, with the exception of the spatially aggregated chainings (Fig. 1B), which were placed together in a single group. There were a total of five chaining groups. Reference sites were divided into two groups – the clustering of reference sites (Fig. 1B) was placed in one group and the geographically dispersed reference sites (Fig. 1A) were placed in a second group. We then modeled the group level parameters using a normal distribution and allowed each group to have a common mean (μ_ω) and standard deviation (σ_ω),

$$\omega_g \sim \text{normal}(\mu_\omega, \sigma_\omega^2).$$

This distribution allows the estimates of ω_g to draw toward the mean (μ_ω), but not completely, creating a partial-pooling compromise among the estimates (Gelman and Hill, 2007). Because detection radius varied by camera type, we modeled the detection probability (p) as a function of camera type (camera) at each site on the logit scale:

$$\text{logit}(p_i) = \alpha_o + \alpha_1 camera_i$$

Vague priors were used for all parameters. Specifically, we assumed $\boldsymbol{\beta} \sim \text{normal}(0, 100)$, $\boldsymbol{\alpha} \sim \text{normal}(0, 100)$, $\mu \sim \text{normal}(0, 100)$, and $\sigma \sim \text{uniform}(0, 100)$.

2.5.2. Vegetation covariate model formulation

To address our second objective of evaluating the effect of percent cover of grass, shrub, and tree and forest age on habitat use for each species, we used a similar Bayesian hierarchical binomial mixture model as previously described. However, in this model our independent variables of percent cover of grass (grass), shrubs (shrub), and trees (tree) and forest age (dbh) are continuous variables scaled to have mean 0 and standard deviation 1 (Gelman et al., 2008):

$$\log(\lambda_i) = \omega_{g[i]} + \beta_1 grass_i + \beta_2 shrub_i + \beta_3 tree_i + \beta_4 dbh_i$$

We tested for correlations among covariates to ensure that no covariates were highly correlated ($|r| > 0.7$). Again, we assumed $\boldsymbol{\beta} \sim \text{normal}(0, 100)$, $\boldsymbol{\alpha} \sim \text{normal}(0, 100)$, $\mu \sim \text{normal}(0, 100)$, and $\sigma \sim \text{uniform}(0, 100)$.

2.5.3. Model fitting and estimations

Posterior distributions of model coefficients were estimated using a Markov chain Monte Carlo (MCMC) algorithm implemented in JAGS using the rjags package in R (Plummer et al., 2006; R Core Team, 2015). JAGS models were run with 3 parallel chains for each model with the number of iterations ranging from 100,000 to 300,000, depending on species. Depending on the number of iterations, the first 50,000–100,000 iterations were discarded as burn-in. Model convergence was assessed by checking that the Gelman-Rubin diagnostic statistic for each parameter was <1.1 (Gelman and Rubin, 1992) and by visually inspecting the trace plots of MCMC samples. Due to both a small sample size and desire to suggest reasonable management recommendations, we chose to use relatively simple models to examine the main effect of each vegetation characteristic, without considering additive or interactive effects. To assess the relative influence of covariates on habitat use, we compared the posterior distributions of model coefficients and examined overlap of posterior distributions with 0. We considered any covariate to have evidence of an effect on mammal habitat use if the 90% credible intervals did not overlap 0. Although mule deer and elk (Cervus canadensis) were detected at a majority of our sites, these species are migratory in our region (Lendrum et al., 2013; Northrup et al., 2014); we expect that most individuals in these populations moved in or out of our system during the timeframe of our study, creating difficulties in model convergence. Therefore, we chose to exclude them from our analyses.

3. Results

A total of 21 mammal species were photographed across both site types. Eighteen species were photographed at chained sites and 19 species were photographed at references sites (Table 2). American black bear (Ursus americanus) and red fox (Vulpes vulpes) were never detected at historical chaining sites (Table 2). We were able to appropriately fit the treatment model to eight species –

Table 2
Mammal species and the number and proportion of sites (n = 22) that each species was detected on remotely-triggered wildlife cameras at historically chained and reference sites in pinyon-juniper woodlands in the Piceance Basin of Northwest Colorado.

| Species	Latin name	Chaining	Prop. sites	Reference	Prop. sites
American badger	*Taxidea taxus*	4	0.18	9	0.41
American black bear	*Ursus americanus*	0	0	4	0.18
Black-tailed jackrabbit	*Lepus californicus*	1	0.05	1	0.05
Bobcat	*Lynx rufus*	6	0.27	9	0.41
Bushy-tailed woodrat	*Neotoma cinerea*	1	0.05	1	0.05
Chipmunk	*Tamias sp.*	7	0.32	5	0.23
Cow	*Bos taurus*	2	0.09	9	0.41
Coyote	*Canis latrans*	15	0.68	14	0.64
Domestic dog	*Canis lupus familiaris*	3	0.14	4	0.18
Elk	*Cervus canadensis*	17	0.77	16	0.73
Golden-mantled ground squirrel	*Callospermophilus lateralis*	13	0.59	13	0.59
Human (non-researcher)	*Homo sapiens*	5	0.23	4	0.18
Long-tailed weasel	*Mustela frenata*	1	0.05	1	0.05
Mountain cottontail	*Sylvilagus nuttallii*	19	0.86	21	0.95
Mountain lion	*Puma concolor*	1	0.05	7	0.32
Mule deer	*Odocoileus hemionus*	20	0.91	19	0.86
Red fox	*Vulpes vulpes*	0	0	1	0.05
Rock squirrel	*Otospermophilus variegatus*	2	0.09	4	0.18
Striped skunk	*Mephitis mephitis*	1	0.05	2	0.09
Western spotted skunk	*Spilogale gracilis*	1	0.05	3	0.14
Feral horse	*Equus caballus*	6	0.27	4	0.18
Wyoming ground squirrel	*Urocitellus elegans*	0	0	1	0.05
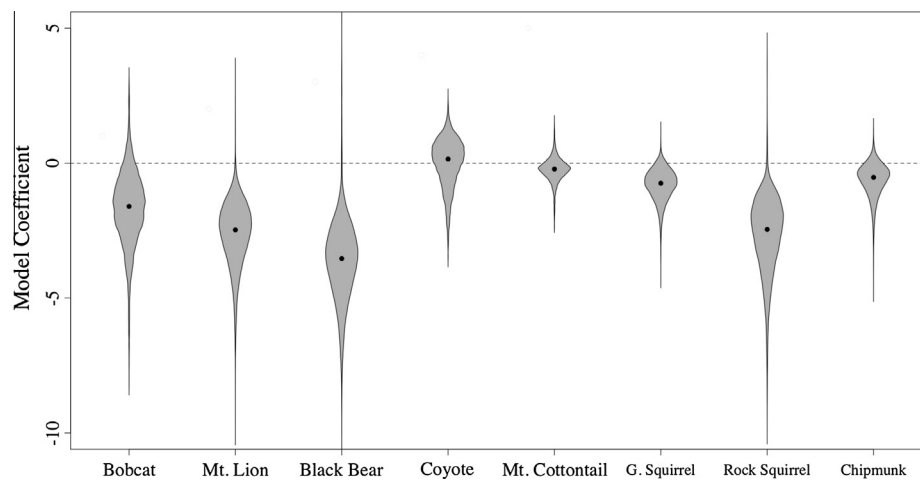
Fig. 2. Posterior distributions of model coefficient values for the effect of chaining on mammal habitat use in the Piceance Basin in northwestern CO, USA. Dashed line indicates coefficient value of 0. Black dots represent median posterior coefficient values. Posterior distribution with a large proportion above or below zero indicate strong evidence that chaining had an effect on habitat use.

bobcat (*Lynx rufus*), mountain lion (*Puma concolor*), coyote (*Canis latrans*), American black bear, mountain cottontail (*Sylvilagus nuttallii*), golden-mantled ground squirrel, rock squirrel (*Otospermophilus variegatus*), and chipmunk (*Tamius* sp.). We found that bobcat ($\beta = -1.6$, 90% CI [−3.37, −0.1]), mountain lion ($\beta = -2.47$, 90% CI [−4.18, −1.25]), American black bear ($\beta = -0.35$, 90% CI [−5.5, −1.96]), golden-mantled ground squirrel ($\beta = -0.75$, 90% CI [−1.59, −0.11]), and rock squirrel ($\beta = -2.46$, 90% CI [−4.54, −1.1]) had a negative response to chaining more than 40 years after tree removal (Fig. 2). Chipmunk ($\beta = -0.53$, 90% CI [−1.45, 0.06]), mountain cottontail ($\beta = -0.22$, 90% CI [−0.75, 0.24]), and coyote ($\beta = 0.15$, 90% CI [−1.25, 1.01]) showed little to no response to chaining, and we found no evidence of a positive response for any species (Fig. 2).

Most vegetation characteristics differed between chained and reference sites. For example, mean shrub cover was 12% higher at chained sites, and reference sites were characterized by 25% higher mean tree cover and older forest age compared to the chained sites (Table 1). The influence of these vegetation characteristics on mammal habitat use differed in both direction and

strength, and varied by species (Fig. 3 and Table A1). Although grass cover did not differ significantly between chained and reference sites, as a continuous variable grass cover had a positive effect on mountain cottontail and golden-mantled ground squirrel habitat use, but had a negative effect on bobcat and mountain lion habitat use. Increased shrub cover had a positive effect on bobcat habitat use, but a negative effect on rock squirrel habitat use. Mountain cottontail and chipmunk had a positive response to greater tree cover, whereas coyote had a negative response to greater tree cover. Older forest age had a positive effect on mountain lion habitat use, but a negative effect on bobcat and golden-mantled ground squirrel habitat use. We were unable to fit our vegetation covariate model to American back bear due to a lack of model convergence.

4. Discussion

Removing or reducing tree cover to benefit livestock or game species is widespread throughout the western U.S. (Aro, 1971; Redmond et al., 2013; Bergman et al., 2015), yet little is known
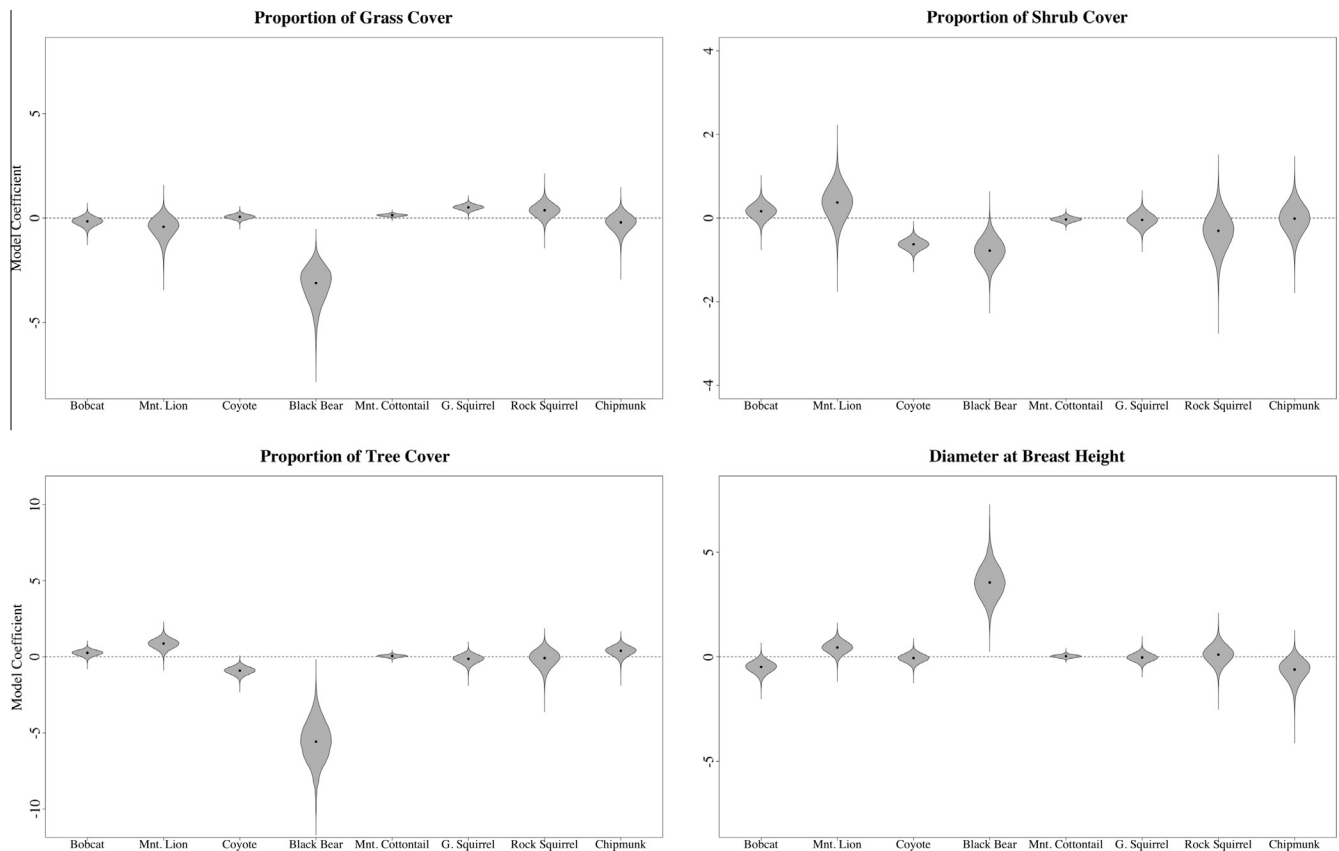
Fig. 3. Posterior distributions of model coefficient values for vegetation covariates fit to mammal habitat use models in the Piceance Basin, Northwest CO, USA. Dashed line indicates coefficient value of 0. Black dots represent median posterior coefficient values. Posterior distributions with a large proportion above or below zero indicate strong evidence that chaining had an effect on habitat use.

about the long-term effects of tree removal on wildlife communities (Bombaci and Pejchar, 2016). We examined the long-term effects of pinyon-juniper removal on mammal habitat use in the Piceance Basin in northwestern Colorado. We found marked differences in habitat use between historically chained sites and reference woodlands for 5 out of the 8 species for which there was sufficient relative activity data. More than 40 years after chaining, bobcat, mountain lion, American black bear, golden-mantled ground squirrel, and rock squirrel all showed a negative response to historic chaining. These findings suggest that tree removal intended to benefit livestock and economically important wildlife species has long-term effects on a variety of non-target mammal species.

In many cases, vegetation characteristics helped explain variation in habitat use between chained sites and reference sites. Increased tree cover had a negative influence on coyote habitat use (Fig. 3), which is unsurprising because coyotes prefer open habitats (Gese et al., 1988; Kamler and Gipson, 2000). Bobcats preferred areas with high shrub cover, but were less likely to use areas with mature P-J trees, whereas mountain lions were more likely to use areas with mature P-J trees (Fig. 3). In previous studies, mountain lions and bobcats preferred a wide variety of habitat characteristics, but mountain lions have been shown to avoid large open areas in summer months (Koehler and Hornocker, 1991; Dickson and Beier, 2002). Further, mountain lions utilized mature woodlands during summer months, perhaps for enhanced protective cover and ability to stalk prey (Koehler and Hornocker, 1991). Mean DBH/plot, our index of forest age, was smaller in chained sites, and chained sites were dominated by big sagebrush and other low-statured vegetation (3% mean tree cover; Table 1). Therefore, mountain lions may utilize historically chained sites less

than intact woodlands because of their spatial extent and lack of protective cover. In Arizona, bobcats often used shrubland habitats but avoided large contiguous grasslands, and they showed no strong preference for any single habitat type (Lawhead, 1984). Bobcats and mountain lions have large home ranges that can encompass a wide assortment of habitat types (Lawhead, 1984; Koehler and Hornocker, 1991; Schonewald-Cox et al., 1991). Thus, it is possible that habitat characteristics at multiple scales influenced habitat use of mountain lions and bobcats in our region.

With respect to small mammals, we were only able to detect a small subset of the small mammal community using wildlife cameras, but the responses differed among those species we did observe. Chipmunk and mountain cottontail showed no long-term response to tree removal. However, rock squirrel and golden-mantled ground squirrel showed a negative response to P-J removal (Fig. 2). These results, >40 years after the initial chaining, are similar to those from studies conducted in the first few years after chaining occurred (Sedgwick and Ryder, 1986). Rock squirrel showed a negative response to increased shrub cover and golden-mantled ground squirrel showed a negative response to mature P-J trees. Both species showed a negative response to chaining, yet they both favored vegetation characteristics associated with chained sites (high shrub cover and low DBH/plot, Fig. 3). These conflicting findings make it difficult to explain why golden-mantled ground squirrel and rock squirrel showed a negative response to P-J removal in our study area. Both species are known to utilize forested and open-brushy habitats if there are rock outcroppings for shelter (Oaks et al., 1987; Bartels and Thompson, 1993). Both species also place the entrances of their burrows at the base of rock outcroppings (Oaks et al., 1987; Bihr and Smith, 1998). Rugged terrain and large rocky outcroppings

create a difficult work space for large machinery (i.e., bulldozers) to operate, and managers applying chaining treatments to an area often avoided rugged and rocky areas (McKenzie et al., 1984). Therefore, golden-mantled ground squirrel and rock squirrel may have avoided areas where P-J was historically removed not because of the vegetation characteristics of these sites, but instead because suitable habitat structures (e.g., rock outcroppings) are absent from sites selected for chaining.

The strong relationships between habitat use and specific vegetation characteristics for some species could be factored into management decisions to account for the long-term effects of P-J removal on mammal communities. For example, modern tree removal techniques (e.g., hydrox; Wästerlund and Hassan, 1995) can be highly selective, such that some trees and other vegetation can be retained on the landscape (Wästerlund and Hassan, 1995; Crow and van Riper, 2010). We found that older forest age (DBH/plot) was positively associated with mountain lion habitat use (Fig. 3). Medium and large-bodied carnivores prefer a mosaic of habitats (Koehler and Hornocker, 1991; Dickson and Beier, 2002), and have large home ranges that encompass a wide variety of habitat characteristics (Schonewald-Cox et al., 1991). Selectively leaving patches of older trees within the treated areas might maintain habitat diversity for medium and large-bodied carnivores. However, these actions would have to be implemented across a large area, and may not be feasible with all tree reduction efforts. It is important to note that tree reduction projects have diverse goals and intended outcomes. Some objectives, such as creating habitat for Greater Sage-grouse, which cannot tolerate standing trees (Baruch-Mordo et al., 2013), may not be compatible with the above recommendations for enhancing habitat quality for mammal species.

An important shortcoming of our analysis is that our metric of habitat use only accounts for detections of individual species in a single season and does not address patterns in mammal abundance or density. Assessing the long-term effects of P-J removal on the density of various animal populations should be a future priority to better understand the effects of mechanical tree removal on mammals in a slow-recovering system. Further, landscape-level characteristics may have a greater influence on mammal habitat use than fine-scale vegetation parameters (Schonewald-Cox et al., 1991). Therefore, it may be important to incorporate landscape-scale attributes hypothesized to influence mammal habitat use, such as landscape connectivity metrics (see Kindlmann and Burel, 2008).

We chose to use relatively simple habitat use models to examine main effects alone, without considering additive effects or interactions between vegetation characteristics, environmental conditions, and anthropogenic factors. It is possible that anthropogenic factors, such as intensity of energy development or size of mechanical disturbances, may interact with vegetation characteristics to influence mammal habitat use. Future research should test for these potential interactions, and tree removal efforts in human-dominated landscapes should explicitly account for these interactions in future management plans.

Finally, the use of chaining tapered off significantly after the 1970's (Romme et al., 2009; Redmond et al., 2013), making it difficult to measure changes in mammal communities over a chronological time scale for this particular tree removal method. The broad geographical distribution of P-J ecosystems encompasses a wide variety of soil types, and gradients in precipitation and elevation, which could additionally affect rates and patterns of forest regeneration after disturbance (Tausch and Tueller, 1977; Schott and Pieper, 1987; Romme et al., 2009). Thus, we urge caution in generalizing our results to other regions.

In our study, tree reduction to increase forage for livestock and enhance habitat for game species had long-term consequences for mammal species, particularly mid-sized and large-sized carnivores. To maintain viable populations of diverse native species, future management actions that include tree removal should explicitly measure effects on both target and non-target mammal species. The hierarchical binomial mixture model that we used can be applied more broadly to camera trap data to predict mammal habitat use based on individual habitat characteristics. This information could be used to adaptively guide forest management decisions, while accounting for the costs and benefits of tree removal for different animal species. Given the magnitude of current anthropogenic pressure on ecosystems, it is critical that we understand the long-term effects of deliberate woodland reduction on native biodiversity.

Acknowledgments

Appendix A

See Table A1.

Table A1
Median coefficient values (Med.) and 90% lower (LCI) and upper (UCI) credible intervals for posterior distributions of vegetation covariates fit to mammal habitat use models in the Piceance Basin, Northwest CO, USA. Covariates with 90% credible intervals not overlapping zero (values in bold font) have a high probability of having an effect on mammal habitat use.

Species	Grass cover Med.	LCI	UCI	Shrub cover Med.	LCI	UCI	Tree cover Med.	LCI	UCI	Forest age Med.	LCI	UCI
Bobcat	**−0.33**	**−0.60**	**−0.09**	**0.26**	**0.04**	**0.47**	0.07	−0.17	0.31	**−0.72**	**−1.10**	**−0.38**
Mountain lion	**−0.78**	**−1.71**	**−0.16**	0.34	−0.10	0.74	0.39	−0.04	0.86	**0.50**	**0.17**	**0.83**
Coyote	0.05	−0.09	0.18	−0.01	−0.20	0.17	**−0.67**	**−1.05**	**−0.33**	−0.17	−0.49	0.14
Mountain cottontail	**0.17**	**0.10**	**0.24**	0.01	−0.07	0.09	**0.13**	**0.02**	**0.23**	−0.02	−0.11	0.07
Golden-mantled ground squirrel	**0.53**	**0.39**	**0.67**	0.03	−0.17	0.23	0.11	−0.21	0.39	**−0.26**	**−0.51**	**−0.01**
Rock squirrel	0.12	−0.45	0.65	**−0.67**	**−1.40**	**−0.03**	−0.19	−1.17	0.71	0.45	−0.15	1.12
Chipmunk sp.	−0.36	−1.10	0.19	−0.39	−1.22	0.19	**0.73**	**0.18**	**1.36**	−0.52	−1.19	0.03

Appendix B. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2016.06.029.

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