Mitigation for energy development fails to mimic natural disturbance for birds and mammals

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A B S T R A C T

Using habitat mitigation to minimize or offset negative impacts of land use change on biodiversity is increasingly common and widespread. For example, where natural disturbance is undesirable (e.g., wildfire in oil and gas fields), mechanical approaches are frequently used to replace natural disturbance and improve habitat for particular species. However, the consequences of such actions for diverse animal assemblages have gone largely unexamined. To assess whether mitigation targeting single species can emulate natural processes and improve habitat for multiple species, we investigated the short-term response of birds and mammals to mechanical tree reduction and natural wildfire in a landscape altered by energy development. We found that no mammal species responded positively to mitigation for energy development in our study region. In contrast, four mammal species were positively associated with fire, and only a single species responded negatively. Similarly, only a single species of bird responded positively to mitigation. Fire had a positive effect on the density of three bird species and a negative effect on six bird species. We show that habitat mitigation intended to emulate natural disturbances and mitigate the negative effects of energy development has mixed but largely negative short-term consequences for birds and mammals. To sustain biodiversity in places undergoing rapid land use change, mitigation should explicitly measure both intended and unintended effects on diverse taxa.

1. Introduction

Manipulating ecosystems to improve habitat quality and mitigate for anthropogenic activities, such as energy development, is increasingly common. Global demand for energy production is predicted to increase by 40% in the next 20 years (International Energy Agency, 2009), and this trend is likely to have profound effects on biodiversity (Jones et al., 2015). Understanding if and under what circumstances mitigation is effective will be a major challenge for conservation scientists and practitioners in the coming decades (Northrup and Wittemyer, 2013).

Declining bird and mammal populations have led to numerous strategies to mitigate habitat loss from energy development. These include development by design (Kiesecker et al., 2010), biodiversity offsets (Tallis et al., 2015), habitat manipulation focused on single species (Bergman et al., 2015), and using mechanical methods to emulate natural processes where disturbance regimes have been fundamentally disrupted (Baruch-Mordo et al., 2013; Redmond et al., 2013). The latter two approaches are particularly prevalent in the western U.S.A, which has experienced unprecedented levels of natural gas development and also provides critical habitat for large migratory mule deer (*Odocoileus hemionus*) herds (Johnston, 2009).

Mature pinyon-juniper woodlands are considered poor foraging habitat for mule deer due to decreased biomass of forbs and shrubs important for sustaining deer populations during winter months (Bartmann, 1983). Although fire was historically the primary source of disturbance in this system – maintaining a mosaic of woodlands, shrublands and grasslands (Romme et al., 2009; Miller and Tausch, 2000) – wildfire is rarely compatible with energy development. This set of circumstances has led conservation practitioners to seek mechanical means of improving mule deer habitat in the midst of some of the U.S.A's largest oil and gas fields. This habitat mitigation strategy has provided measurable benefits to mule deer (Bergman et al., 2015), but the consequences of this and other single-species mitigation strategies on diverse animal assemblages have gone largely unexamined (Gallo and Pejchar, 2016).

Anthropogenic and natural disturbance could have similar or divergent effects on plant and animal communities during early successional stages (Hobson and Schieck, 1999; Andre, 1994; MacArthur and MacArthur, 1961). For example, mechanical tree removal and fire may differentially change the chemical composition of soils, which can influence plant recolonization and regeneration (Certini, 2005).

Furthermore, such interventions can disrupt population dynamics of birds and mammals, with cascading effects on community structure, composition, and species interactions (Gallo and Pejchar, 2016; Kalies et al., 2010). Therefore, mitigation designed for single species may have unintended consequences, such as changes in species co-occurrence (Miller et al., 2012), resulting in cumulative effects on natural communities (Brookshire et al., 2002).

This study examines how bird and mammal communities respond to anthropogenic attempts to mimic natural disturbance and mitigate the effects of energy development. In January 2013, 147 patches of woodland in northwestern Colorado, U.S.A, were mechanically removed (Fig. 1) to increase the productivity of mule deer forage in an oil and gas field. At the same time, wildfires burned approximately 3200 ha throughout the same area. These circumstances provided the unique opportunity to investigate whether birds and mammals respond differently to mechanical and natural disturbance, and to assess the outcome of single-species mitigation for energy development on diverse species assemblages. Specifically, we 1) compared the influence of mechanical disturbance and fire on bird densities and mammal habitat use, and 2) identified the environmental and anthropogenic characteristics associated with differences in bird densities and mammal habitat use among sites. Our findings provide insight into whether mitigation can emulate natural processes to improve habitat for multiple species in areas undergoing rapid land use change.

2. Materials and methods

2.1. Study area

This study was conducted from spring 2013 to fall 2014 in a pinyon-juniper ecosystem in northwestern Colorado, U.S.A (Fig. 2). Pinyon-juniper woodlands in this region consist of pinyon pine (*Pinus edulis*) and Utah juniper (*Juniperus osteosperma*), and dominant shrubs include antelope bitterbrush (*Purshia tridentata*), mountain mahogany (*Cercocarpus montanus*), big sagebrush (*Artemisia tridentata*), and rabbitbrush (*Chrysothamnus* spp.) (Sedgwick, 1987; O'Meara et al., 1981). The topography consists of high plateaus and deeply incised valleys, and elevation ranges from approximately 1800 to 2400 m. Dominant land use activities in the area include oil and gas extraction and domestic livestock grazing (Northrup et al., 2015). Between April and September 2012, 13 naturally-ignited wildfires burned approximately 3200 ha in the region before being suppressed by wildfire crews. In January 2013, approximately 444 ha of pinyon-juniper woodlands were mechanically removed within 147 treatments (Figs. 1c and 2b).

2.1.1. Treatment and reference sites

To compare bird densities and mammal habitat use between mechanical treatments ("mitigation sites") and wildfires ("fire sites"), we established 25 sampling sites within each site type (n = 50). Due to the dispersed geographic extent of the fires and the spatial clustering of the mitigation sites, we paired each treatment site with an undisturbed reference site (n = 50; Fig. 2). Reference sites were located in areas that had no detectable evidence of past mechanical disturbance or wildfire. We considered disturbance from livestock grazing to be constant across our study area.

2.1.2. Mitigation sites and paired reference sites

We randomly selected 25 of the 147 mitigation treatments (ranging in size from 0.8–4.5 ha, $\overline{x}$ = 2.70 ha ± 0.64 SE) and established one sampling point in the approximate center of each treatment (Fig. 2b). All selected mitigation sites were spaced at least 450 m apart ($\overline{d}$ = 4.2 km ± 1.3 SE). Using geographic information system (GIS), we randomly placed 25 reference sites in the vicinity of the mitigation sites (Fig. 2b). Reference sites were spatially buffered from all mitigation sites, including mitigation treatments that were not sampled, by at least 250 m (Fig. 2b). Each reference site was ground-truthed to verify

that it was within undisturbed pinyon-juniper woodlands.

2.1.3. Fire sites and paired reference sites

Using information obtained from the White River Bureau of Land Management office in Rio Blanco County, Colorado, we identified nine accessible wildfires that ranged from 3.2 to 2072 ha in size ($\overline{x}$ = 312 ha ± 224.86 SE). All fires burned at some point between July – September 2013, with the exception of one fire that burned during April 2013. We placed an initial sampling site within each fire area by choosing a random location in the approximate center of each area (Fig. 2c). We then placed additional sampling sites in each cardinal direction from the initially selected site, such that the sites were at least 250 m apart (Fig. 2c). Because we began allocating sites in the smallest fire first, our design allowed for one site in the smallest fire area and up to nine sites in the largest fire area for a total of 25 sites. Paired reference sites were established by walking from each fire-sampling site to a location > 250 m beyond the fire's nearest edge (Fig. 2c).

2.2. Bird surveys

We conducted 5-minute individual observer point counts at each of the 100 sampling sites (Dunn et al., 2006). Each site was surveyed 4 times/year between April and June by three to four trained observers. All birds detected visually or aurally were identified and their distance from the point count station was recorded. Surveys were conducted between 30 min after sunrise and on average no later than 1100 h. Surveys were not conducted during periods of fog, rain or high winds (> 3 on Beaufort scale). To account for observer and temporal bias, observers and starting times were rotated throughout the survey season. Due to the small size of some mitigation and fire areas, some sampling sites were located near undisturbed woodland; however, only birds detected within the treatment areas were recorded.

2.3. Mammals surveys

We randomly selected 22 of the 25 bird sampling sites within each of the four site types, and placed one unbaited remotely-triggered camera at each site (n = 88). To maximize detection probability, all cameras were located on wildlife trails, cattle trails, or unmaintained roads within 100 m of each sampling point. We used Reconyx P800 (n = 64; Reconyx, Holmen, WI, U.S.A), Cuddeback Attack (n = 13; Cuddeback Digital, De Pere, WI, U.S.A), and Cuddeback Capture (n = 11; Cuddeback Digital, De Pere, WI, U.S.A) cameras. Camera settings were the same for each camera of a particular model (see Appendix S1 in Supporting information). All cameras were deployed between April and June 2014, in a staggered entry design, and photo data were obtained for 149 days following each deployment. In order to ensure camera function, change batteries, and replace data cards, we checked each camera approximately every two weeks and downloaded photo data.

Volunteer observers were trained to identify species within each photo using the Colorado Parks and Wildlife Photo Warehouse (Ivan and Newkirk, 2016). Two observers viewed each photo and all animals were identified to species. To ensure consistency across species identifications, two authors (TG and LS) resolved all conflicting identifications between volunteers. Any animal that could not be identified to species was excluded from analyses, with the exception of two chipmunk species. Least chipmunk (*Tamius minimus*) and Uinta chipmunk (*Tamius umbrinus*) are difficult to differentiate in photographs and were collectively identified as Chipmunk. Camera data were standardized post hoc to include a 30-second quiet period between subsequent photos to ensure consistent trigger rate across camera types. Therefore, if multiple photographs were taken within a 30-second window, only one event was recorded for that 30-second time period.

Fig. 1. Mechanical disturbance in pinyon-juniper ecosystems across the western United States is often used to improve habitat for wildlife and mitigate for other drivers of habitat loss: (a) type of machinery used to reduce tree cover, (b) fine mulch layer left after disturbance, and (c) shrub and forb dominated habitat approximately six months after mechanical tree reduction. [Photo credits: Jason Tack: (a) & (b); Sara Bombaci: (c)].

2.4. Vegetation surveys

To assess the influence of habitat characteristics on bird density and mammal habitat use, we measured a variety of vegetative parameters. In 2013, we conducted surveys in a 10 × 10-m plot, offset from each point count site by approximately 5 m in a random direction (McElhinny et al., 2005). Species, tree height, crown area, diameter at breast height (DBH), and condition (i.e., live, dead, snag broken above 1 m) were recorded for each tree in the plot following Huffman et al. (2012). Trees (live and dead) were defined as stems > 1 m tall (Huffman et al., 2012). We estimated an index of forest stand age, modified from McElhinny et al. (2005), by dividing the total DBH of all trees within the plot by the plot size (DBH/100 m^2). We calculated percent tree cover by dividing the total area of overstory canopy within the plot by the plot area. In 2013 and 2014, we measured percent cover of shrub, grass and forb species using a 25-m line intercept beginning at each point count site and heading in a random compass direction (Canfield, 1941).

Differences between years for each vegetation characteristic were tested using ANOVA in R (R Core Team, 2015), and no significant differences were found. Therefore, the two years of vegetation data for each variable at each site were averaged and incorporated into the below analyses. We used a two-sample t-test to compare vegetation characteristics between reference types (mitigation and fire) and found no significant differences, so we combined the two sets of reference sites ($n = 50$) for subsequent statistical analyses.

2.5. Statistical analyses

2.5.1. Modeling the effects of mitigation and fire on bird density

We used Bayesian hierarchical open population binomial mixture models (Kéry and Schaub, 2012; Kéry and Royle, 2010) to quantify the effects of mitigation and fire on bird densities. Binomial mixture models estimate abundance using repeated count data while accounting for imperfect detection (Kéry and Schaub, 2012). To ensure consistent survey area across point count stations, we truncated the data to include only birds detected ≤ 52 m (area of the smallest disturbance) from the point count station, and infer our results as bird species density (individuals/ha).

To quantify the effects of mitigation and fire on the density of each bird species, we let y_{ijk} be the total number of individuals counted at site i ($i = 1,2,...I$), during survey j ($j = 1,2,...J$) in year k ($k = 1,2$). We assumed closure throughout each year; therefore, observed counts would arise as a binomial random variable,

$$y_{ijk} \sim \text{binomial}(N_{ik}, p_{ijk}), \tag{1}$$

where N_{ik} is the total number of individuals available to be counted in year k at site i, and p_{ijk} is the survey-specific detection probability. We modeled our latent variable N_{ik} as a Poisson random variable,

$$N_{ik} \sim \text{Poisson}(\lambda_{ik}), \tag{2}$$

where λ_{ik} is the expected number of individuals at site i for year k. To quantify the influence of disturbances on the density of bird species, we modeled λ_{ik} as a function of disturbance type at site i using a log link,

$$\log(\lambda_{ik}) = \omega_{g[i]} + X_i \boldsymbol{\beta}. \tag{3}$$
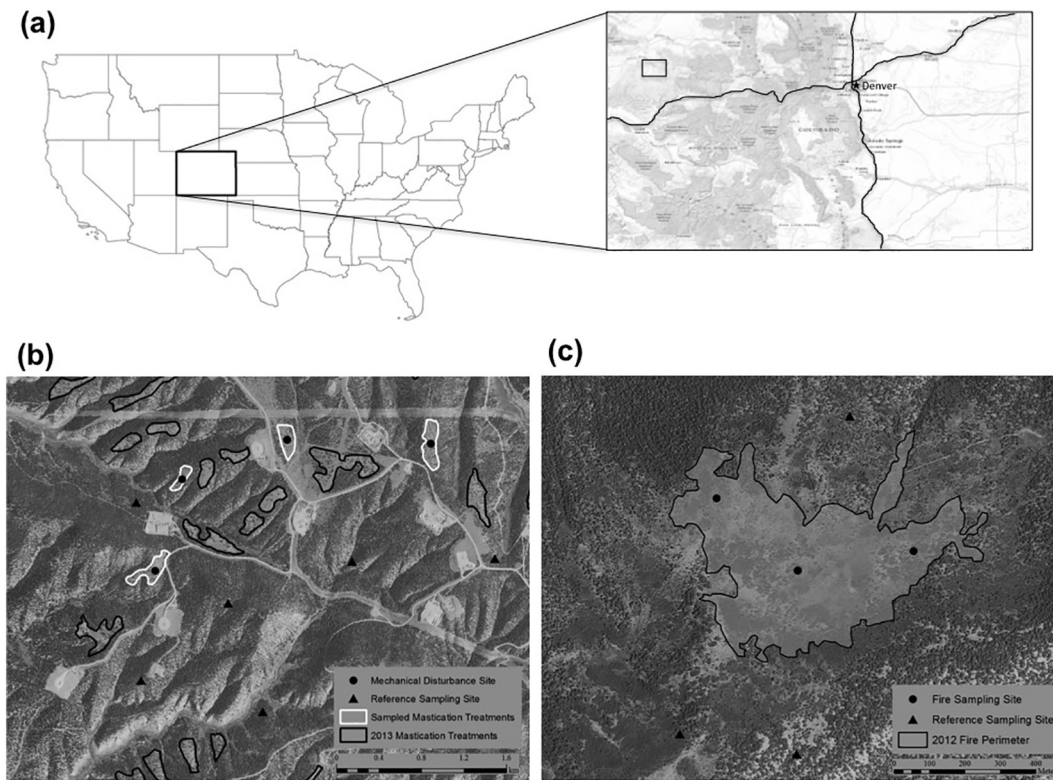
Fig. 2. (a) Location of study area in northwestern Colorado, U.S.A, (b) a portion of study area illustrating a subset of mitigation and paired reference sites, and (c) a portion of study area illustrating a subset of fire and paired reference sites.

Our data matrix (X_i) was set up as a design matrix so that effect size could be compared between disturbance types. To account for potential site dependency that is not accounted for by disturbance type, we used a multilevel model (Gelman and Hill, 2007) to include a random effect (ω_g) on geographical grouping ($g = 11$). Mitigation sites and associated reference sites were placed into a single group because they were spatially aggregated (Fig. 2b). Sampling sites within each fire area were grouped with the paired reference sites at that fire (Fig. 2c). We 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),

$$\omega_g \sim \text{normal}(\mu_\omega, \sigma_\omega^2). \tag{4}$$

Based on previous analyses (T. Gallo, unpublished data), we had reason to believe that for all species, detection probability was best explained by the individual survey observer. Therefore, we modeled detection probability as a function of the observer who conducted the survey at site i, survey j, and year k on the logit scale:

$$\text{logit}(p_{ijk}) = \alpha_o + \alpha_1 observer_{ijk}. \tag{5}$$

Conventional 'vague' priors were used for all parameters. Specifically, we assumed $\boldsymbol{\beta} \sim$ normal (0,100), $\boldsymbol{\alpha} \sim$ normal (0,100), $\mu \sim$ normal (0,100), and $\sigma \sim$ uniform (0,100). One fire area, containing three fire- and three reference-sampling sites, was removed from bird density analyses due to inaccessibility in 2013. We were able to fit this model to data from 12 bird species.

2.5.2. Modeling the effects of mitigation and fire on mammal habitat use

To quantify the effects of mitigation and fire on mammal habitat use, we used a similar binomial mixture model as described above. However, we exchanged the abundance parameter (N; Eqs. (1) and (2)) with an activity parameter (A) and used photos per day as our count data (Gallo et al., 2016). Specifically, we let y_{ij} be the total number of photos counted each day j, at site i,

$$y_{ij} \sim \text{binomial}(A_i, p_i), \tag{6}$$

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

$$A_i \sim \text{Poisson}(\lambda_i), \tag{7}$$

where λ_i is the expected habitat use at site i. To quantify the effects of mitigation and fire on mammal habitat use, we modeled λ_i as a function of disturbance type at each site using a log link,

$$\log(\lambda_i) = \omega_{g[i]} + X_i\boldsymbol{\beta}_i. \tag{8}$$

Again, our data matrix (X_i) was set up as a design matrix so that effect sizes could be compared among disturbance types. To account for potential site dependency, we used a multilevel model and included a random effect, ω_g, as described in Eq. (4). Detection radius varied by camera type, so we modeled the detection probability as a function of camera type (*camera*) at each site on the logit scale:

$$\text{logit}(p_i) = \alpha_o + \alpha_1 camera_i \tag{9}$$

Vague priors were used for all parameters. All sites were included in mammal analyses and we were able to fit this model to data from 9 mammal species.

2.5.3. Modeling the effects of environmental and anthropogenic parameters on bird density and mammal habitat use

To assess the effects of environmental and anthropogenic parameters on bird densities and mammal habitat use, we used similar hierarchical binomial mixture models as previously described for each taxon. However, in these models we replaced our predictor variables in Eqs. (3) and (8) with environmental and anthropogenic covariates that we hypothesized would best explain variation in bird density and mammal habitat use based on life history strategies and behaviors of each species (Rodewald, 2015; Degraaf and Wentworth, 1986; De Graaf et al., 1985).

For bird species showing evidence of a positive or negative response to mitigation and/or fire, we included in our models seven environmental covariates: proportion of tree cover, shrubs, grasses, and bare ground, forest age, number of snags (standing dead trees), and elevation calculated from a digital elevation model, and two anthropogenic covariates: size of disturbed area, and well pad density (number of natural gas well pads within 1 km of the point count station (Toms et al., 2005; see Northrup et al. (2015) for natural gas well pad digitization methods)). For all mammal species, we included in our models five environmental covariates: proportion of tree cover, shrubs, and grasses, forest age, and elevation, and three anthropogenic covariates: size of the disturbed area, distance to the nearest road, and well pad density. To calculate well pad density, we used species-specific scales based on body size, home range, and/or size of core habitat selection. Specifically, we used number of well pads within a 4 km radius buffer for coyote (Hinton et al., 2015; Fisher et al., 2011) and bobcat (Lovallo and Anderson, 1996), and number of well pads within a 500 m radius buffer for golden-mantled ground squirrel, chipmunk, rock squirrel (average home range of sciurid species; Harris and Leitner, 2004), mountain cottontail (Trent and Rongstat, 1974), American badger (Lindzey, 1978), and mountain lion (Fisher et al., 2011). Each environmental and anthropogenic covariate was calculated using ArcGIS 10.3 (Esri, Redland, CA, U.S.A). All covariates were scaled to have a mean of zero and standard deviation one. All covariates were tested for correlation and no covariates were highly correlated ($|r| > 0.7$). We were able to fit these models for all species previously analyzed with the exception of American black bear (*Ursus americanus*).

2.5.4. Estimations and inference

Posterior distributions of model coefficients were estimated using Markov chain Monte Carlo (MCMC) methods implemented in JAGS using the *rjags* package in R (Plummer et al., 2006). Model convergence was assessed by checking that the Gelman-Rubin diagnostic statistic for each parameter was < 1.1 and visually inspecting the trace plots of MCMC samples (Gelman et al., 2008). Model fit was assessed using post predictive checks (Kéry and Schaub, 2012). We compared the posterior distributions of model coefficients and examined overlap of posterior distributions with zero. Similar to Harris et al. (2017), we considered any covariates to have evidence of a significant effect if 95% Bayesian credible intervals (BCI) did not overlap zero, and discuss moderately significant effects if the 90% BCI did not overlap zero. Although mule deer and elk (*Cervus canadensis*) were detected at a majority of our sites, these species are migratory in our study region (Northrup et al., 2014). Sampling sites were located across both the winter and summer ranges of these species, which resulted in spatial correlation, hampering model convergence. Therefore, we chose to exclude deer and elk from our analyses.

3. Results

A total of 56 bird species were detected across all sites during 2013–2014 (see Table S1 in Supporting information). Thirty-five bird species were observed in mitigation sites, 41 species in fire sites, and 51 species in reference sites. Ten species were detected in fire sites but not detected in mitigation sites, whereas eight species were detected in mitigation sites but not in fire sites (Table S1).

Mountain bluebird (*Sialia currucoides*) was the only bird species that responded positively to mitigation treatments (Fig. 3b). All other species showed little to no response to mitigation (Fig. 3b). Blue-gray gnatcatcher (*Polioptila caerulea*), *Empidonax* flycatcher, green-tailed towhee (*Pipilo chlorurus*), and spotted towhee (*Pipilo maculatus*) showed a significant negative response to fire sites (Fig. 3b), and Brewer's sparrow (*Spizella breweri*) and white-breasted nuthatch (*Sitta carolinensis*) showed a moderately negative response. Mountain bluebird showed a significant positive response to fire sites, and hairy woodpecker (*Leuconotopicus villosus*) and lark sparrow (*Chondestes*

grammacus) showed a moderately positive response (Fig. 3b). Broad-tailed hummingbird (*Selasphorus platycercus*) and house wren (*Troglodytes aedon*) showed little to no response to either disturbance type (Fig. 3b).

Most measured habitat characteristics differed across mitigation, fire, and reference sites (Table 1). The magnitude and direction of the effects of environmental (i.e., proportion of tree cover, shrubs, grasses, and bare ground, forest age, number of snags, elevation) and anthropogenic (i.e., size of the disturbed area and well pad density) parameters on bird densities differed by species (Fig. 4). However, at least one environmental parameter had a significant effect on the density of each species, with the exception of *Empidonax* flycatcher (Fig. 4a–g). At least one anthropogenic parameter had a significant effect on each species, except mountain bluebird, spotted towhee, and white-breasted nuthatch (Fig. 4h–i).

From a total of 13,112 camera trap nights, twenty-six mammal species were detected across all sites. Eighteen mammal species were observed in mitigation sites, 17 species in fire sites, and 26 species in reference sites (see Table S2 in Supporting information). Two species were detected in fire sites, but not in mitigation sites, and three species were detected in mitigation sites, but not in fire sites (Table S2).

No mammal species showed a positive response to mitigation. Bobcat, golden-mantled ground squirrel, and chipmunk showed a significant negative response to mitigation, and American black bear and coyote showed a moderately negative response (Fig. 3a). Coyote (*Canis latrans*) and mountain cottontail (*Sylvilagus nuttallii*) showed a significant positive response to fire, and bobcat (*Lynx rufus*) and golden-mantled ground squirrel (*Callospermophilus lateralis*) demonstrated a moderately positive response, whereas American badger (*Taxidea taxus*) showed a moderately negative response to fire (Fig. 3a). Rock squirrel (*Otospermophilus variegatus*) showed no response to either disturbance type (Fig. 3a). Anthropogenic parameters had the greatest influence on habitat use for all mammal species except bobcat. However, the magnitude and direction of the effects of environmental and anthropogenic parameters on mammal habitat use differed by species (Fig. 5).

4. Discussion

Mitigation is often used to offset anthropogenic impacts and improve habitat quality, yet the consequences for diverse animal assemblages are poorly understood (Bombaci and Pejchar, 2016). We found that mitigation meant to emulate natural disturbance and wildfire had strong and divergent short-term effects on the density of birds and habitat use of mammals. Most strikingly, no mammal species responded positively to mitigation, yet several species did appear to benefit from fire. Landscape-level anthropogenic disturbances (e.g., well pad density and distance to road) also had a significant influence on most bird and mammal species. Finally, bird densities and mammal habitat use were correlated with specific vegetation characteristics (e.g., tree diameter and cover), which could be incorporated into future efforts to offset the negative effects of energy development on biodiversity.

Habitat mitigation in the form of mechanical tree removal was intended to benefit mammals by altering vegetation structure and composition. However, mammal habitat use did not increase in mitigation sites during our study (Fig. 3a). In fact, most species responded negatively to mitigation, even when some demonstrated a positive response to natural wildfire during the same time period (Fig. 3a). These results could have cascading effects on animal and plant communities. The loss or decline of predator species alters species interactions and co-occurrences, modifying species assemblages (Estes et al., 2011). Mammals also play an important role in structuring plant communities via seed dispersal (Hämäläinen et al., 2017; Wall, 1997; Wunderle, 1997), herbivory (Maron and Crone, 2006), and nutrient cycling (Holechek, 1981). Therefore, declines in mammal habitat use may affect plant community composition and recolonization (Brookshire et al., 2002),
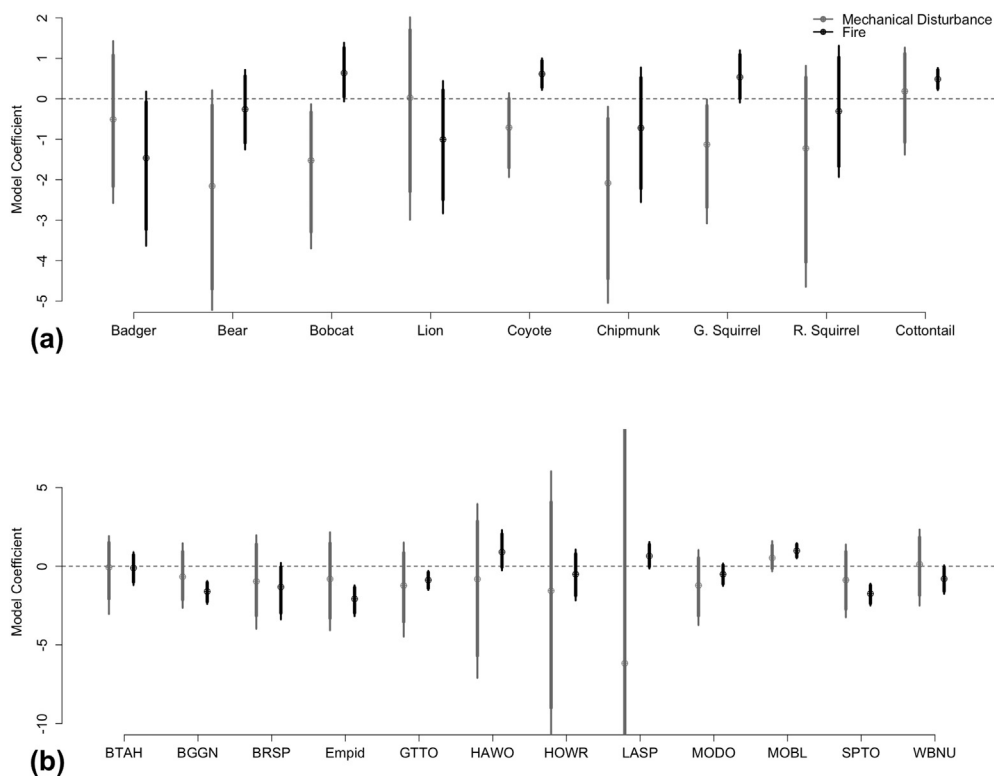
Fig. 3. Median model coefficient values and 95% (thin vertical line) and 90% (thick vertical line) Bayesian credible intervals for the effect of mitigation and fire on (a) mammal habitat use and (b) bird density in northwestern Colorado, U.S.A. Bird species are abbreviated with four-letter codes; see Table S1 for common and Latin names of bird species.

Table 1

Vegetation parameters (means and 95% confidence intervals) in mitigation, fire and undisturbed reference sites in northwestern Colorado, U.S.A.

Parameter	Mechanical	95% confidence intervals		Fire	95% confidence intervals		Reference	95% confidence intervals	
		Lower	Upper		Lower	Upper		Lower	Upper
Mean shrub cover	0.30	0.22	0.39	0.11	0.06	0.16	0.36	0.27	0.46
Mean grass cover	0.08	0.06	0.10	0.09	0.06	0.13	0.10	0.07	0.12
Mean proportion of bare ground	0.23	0.17	0.29	0.54	0.47	0.61	0.35	0.30	0.40
Mean forest cover	0.07	0.04	0.09	0.05	0.02	0.09	0.26	0.20	0.33
Mean DBH/plot (cm)	0.06	0.01	0.12	0.24	0.11	0.37	0.72	0.52	0.92
Mean number snags	0.84	0.00	1.78	3.18	0.84	5.53	0.45	0.22	0.67

ultimately influencing successional trajectories.

Habitat structure and heterogeneity play important roles in shaping bird abundance (MacArthur and MacArthur, 1961), and mitigation and fire sites differed in their vegetative structure and cover. These parameters were important predictors of bird densities. For example, lark sparrow and hairy woodpecker responded positively to fire sites (Fig. 3b). Fire sites had a significantly lower shrub cover compared to reference sites, and had four and six times the density of snags compared to mitigation and reference sites, respectively (Table 1). Lark sparrows prefer open grassland habitats and woodland edges (Lusk et al., 2003; Martin and Parrish, 2000), and hairy woodpeckers prefer nesting in snag cavities (Raphael and White, 1984). Thus, vegetation structure left by fire may retain important habitat for these species. Further, tree diameter was positively associated with cavity nesting birds and mammal species (Figs. 4e and 5d). Therefore, preserving large stands of mature trees near or within treated areas might maintain habitat for these species. Accounting for vegetation characteristics associated with diverse species should be an explicit component of future habitat mitigation efforts.

Some measure of anthropogenic disturbance influenced the habitat use of all but two mammal species (Fig. 5f–h) and the density of all but two bird species (Fig. 4h–i). These results demonstrate that managing small-scale vegetation characteristics alone will not fully account for factors influencing animals in areas with high anthropogenic

disturbance. To be cautious of model overparameterization and ensure model fit, we chose to use relatively simple models to examine main effects alone, without considering additive effects or interactions between habitat characteristics. Future research should test for these potential interactions, and subsequent plans for habitat mitigation via mechanical disturbance should explicitly account for them.

Some limitations should be considered in interpreting our findings. First, we measured only the short-term effects of mitigation and fire on birds and mammals. Yet, these effects may either remain consistent or change over time if trajectories of ecological succession differ between treatment types. For example, possible differences in post-disturbance soil chemistry and soil structure (Certini, 2005) can have long-term consequences for plant structure and community composition (Keller et al., 2003; Fisher and Wilkinson, 2005). Pinyon-juniper woodlands are slow-recovering systems (Schott and Pieper, 1987; Redmond et al., 2013) and studies have shown that disturbance events can have long-term effects on birds and mammals (e.g., Gallo et al., 2016; Gallo and Pejchar, 2017). Thus, decadal-scale monitoring will be essential for measuring mitigation outcomes for biodiversity in some systems (Laurance et al., 2011).

Furthermore, the spatial scale at which mitigation treatments occurred within the landscape was smaller than the scale of the wildfires, and the distribution and landscape configuration of the two disturbance types also varied. Species perceive the environment at different scales
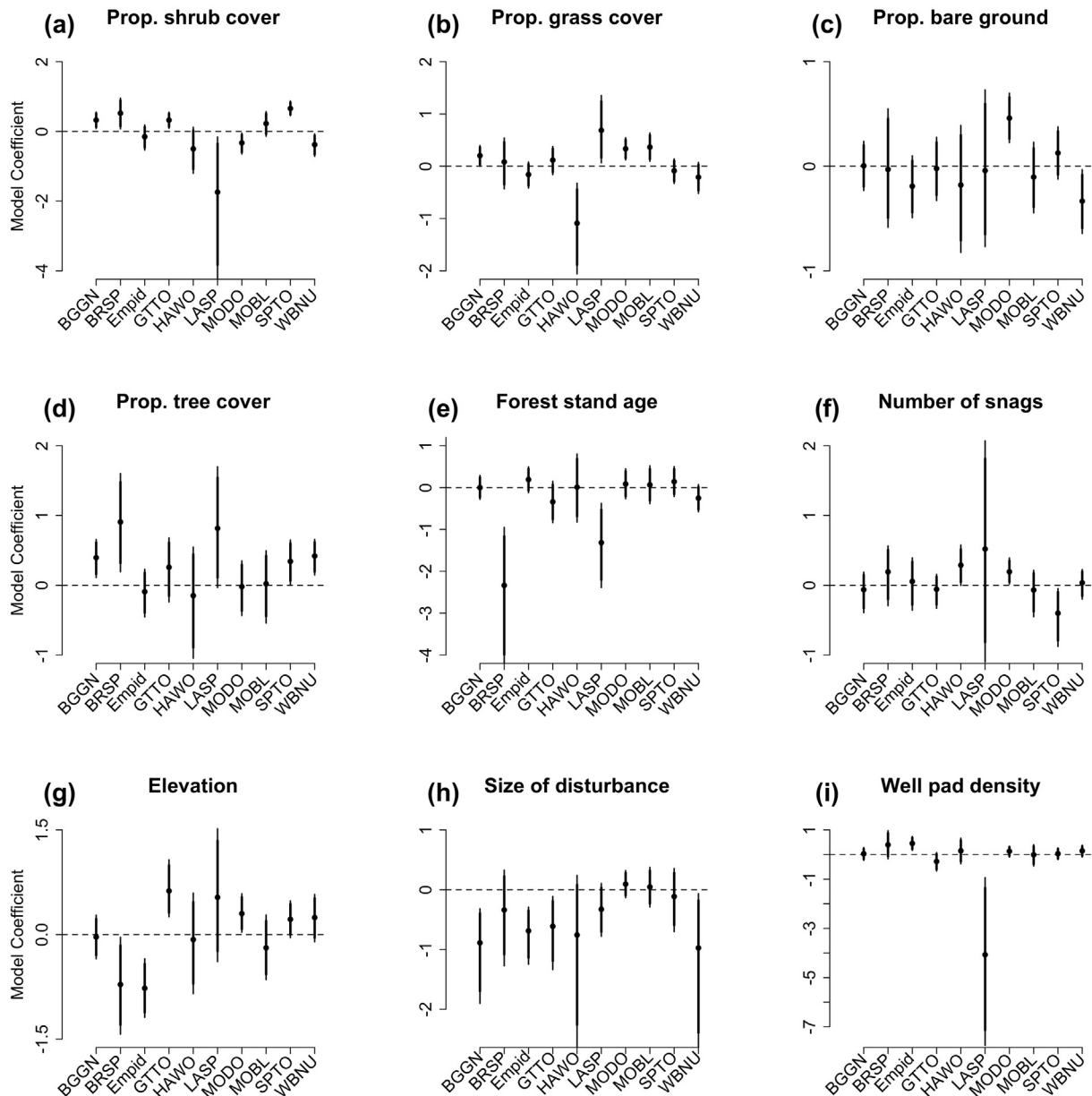
Fig. 4. Median model coefficient values and 95% (thin vertical line) and 90% (thick vertical line) Bayesian credible intervals from the models used to quantify the effects of environmental (a–g) and anthropogenic (h–i) covariates on bird densities in northwestern Colorado, U.S.A. Bird species are abbreviated with four-letter codes; see Table S1 for common and Latin names of bird species.

(Levin, 1992), and patterns measured at one scale may be driven by habitat use at another scale (Turner and Gardner, 2015). We accounted for the size of disturbance at each site in our modeling approach, but we did not have control over the spatial distribution, size, or extent of the habitat mitigation efforts. We recommend that future habitat mitigation efforts be explicitly designed to experimentally compare the effects of different mitigation efforts on mammals and birds, including controlling for size, extent, and spatial distribution.

Finally, although beyond the scope of our study, future research should examine the effects of mitigation on other important variables, such as fitness metrics (e.g., survival and fecundity), and the density and abundance of mammals. We also encourage future studies to evaluate the effects of single-species habitat mitigation on other taxa of conservation concern (e.g., reptiles and amphibians), including species that play important roles in food webs and ecological processes (e.g., arthropods; Debinski and Holt, 2000).

5. Conclusions

Habitat mitigation to offset the negative effects of energy development had profound short-term consequences for mammal habitat use and bird density in our study. Although meant to emulate natural disturbance and benefit wildlife through mechanical tree reduction, mitigation treatments showed no positive effects on mammal habitat use. In contrast, habitat use of coyote, bobcat and golden-mantled ground squirrel was positively associated with natural wildfires that occurred during the same time period. Mitigation also had little effect on most bird species, in contrast with fire, which influenced habitat use of most species. Thus, mechanical disturbance does not appear to emulate fire in providing suitable habitat for bird and mammal communities, at least in the short-term. Given the current scale and magnitude of anthropogenic land use change and its well-documented impacts on ecosystems (Foley et al., 2005), it is critical that we understand how our attempts at mitigation affect diverse natural communities.
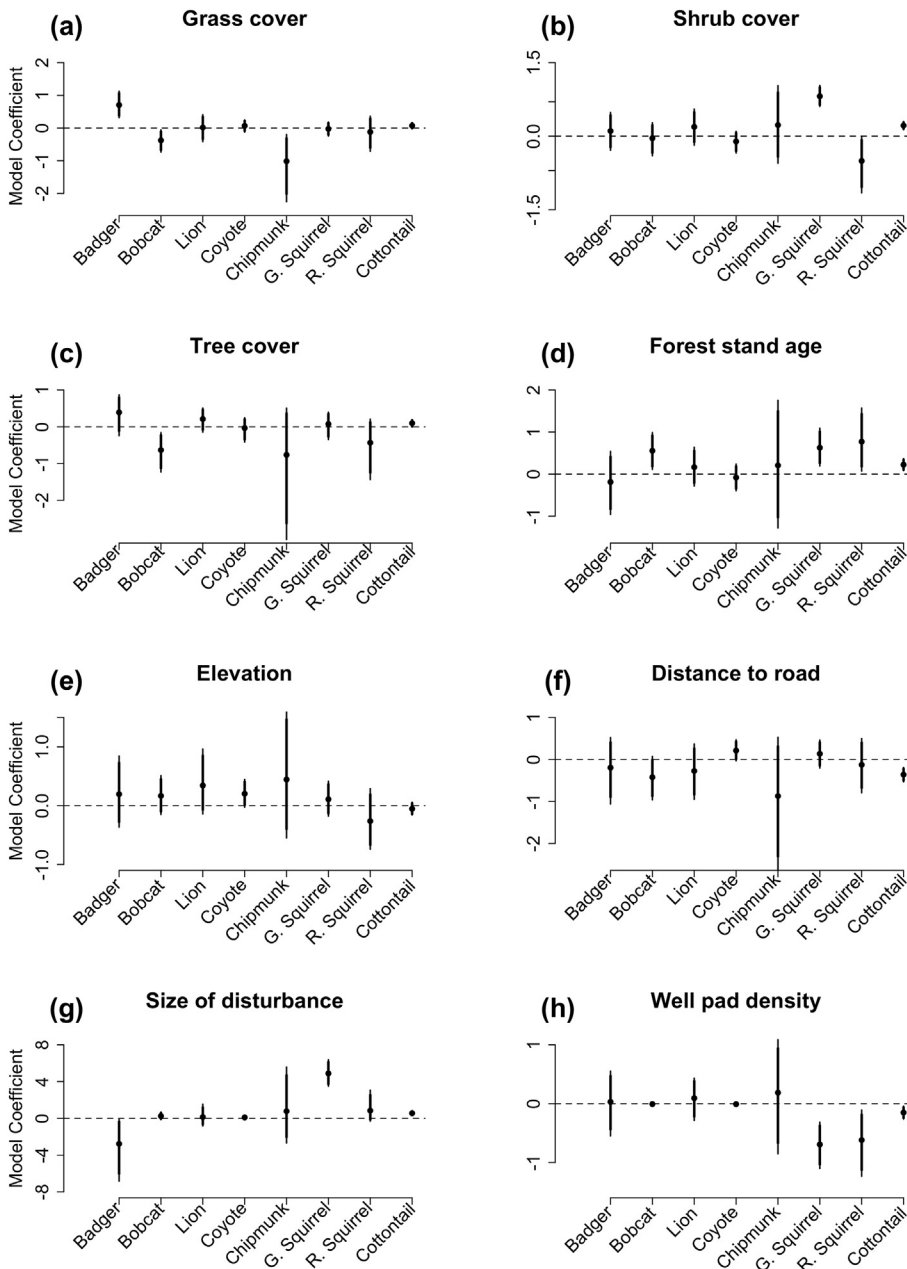
Fig. 5. Median model coefficient values and 95% (thin vertical line) and 90% (thick vertical line) Bayesian credible intervals for the effects of environmental (a–e) and anthropogenic (f–h) covariates on mammal habitat use in northwestern Colorado, U.S.A.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2017.05.023.

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