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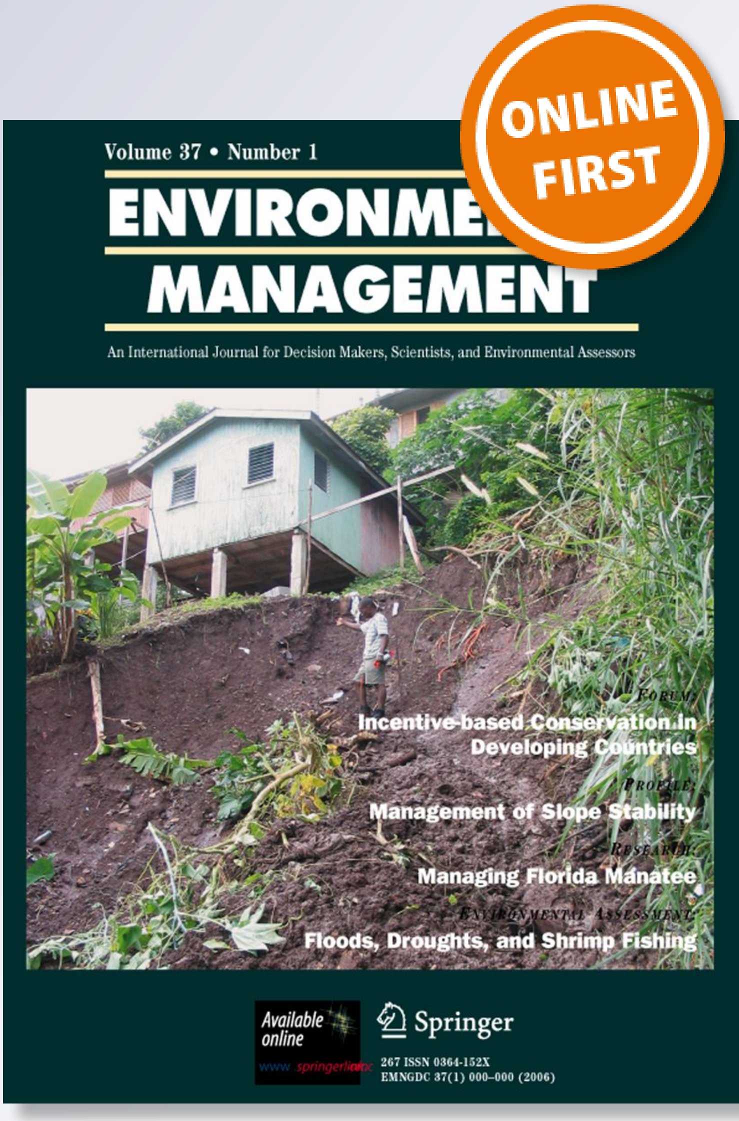

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Abstract Elk *(Cervus elaphus)* are known to shift habitat use in response to environmental modifications, including those associated with various forms of energy development. The specific behavioral responses underlying these trends, however, have not been effectively studied. To investigate such effects, we examined elk response to habitat alteration near natural gas wells in Las Animas County, Colorado, USA in 2008–2010. We created 10 1-ha openings in forests adjacent to 10 operating natural gas wells by removing standing timber in 2008, with concomitant establishment of 10 1-ha control sites adjacent to the same wells. On each site, we estimated elk use, indexed by pellet density, before and after timber removal. Concurrently, we measured plant production and cover, nutritional quality, species composition and biomass removed by elk and other large herbivores. Species richness and diversity, graminoid and forb cover, and graminoid and forb biomass increased on cut sites following tree removal. Differences were greater in 2010 than in 2009, and elk and deer removed more plant biomass in 2010 than 2009. Elk use of cut sites was 37 % lower than control sites in 2009, but 46 % higher in 2010. The initially lower use of cut sites may be attributable to lack of winter forage on these sites caused by timber removal and associated surface modification. The increased use of cut sites in 2010 suggested that elk possessed the behavioral capacity, over time, to exploit enhanced forage resources in the proximity of habitat modifications and human activity associated with maintenance of operating natural gas wells.

Keywords *Cervus elaphus* · Colorado · Elk · Habitat modification · Natural gas · Ponderosa pine

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Introduction

Elk (*Cervus elaphus*) are a ubiquitous megafauna of the US and Canadian Rocky Mountains, where they are esteemed for sport hunting and conservation value. Elk are exposed to human presence and activity in various forms, including human residence, road networks and vehicular traffic, recreational activities, agriculture, logging, mining and energy development. Among these and other forms of habitat modification, development associated with resource extraction or energy production changes landscapes by altering composition of vegetation communities, creating noise and requiring infrastructure in the form of roads and pipelines (Nellemann and Cameron 1998). Habitat loss can occur through construction of well pads and associated service roads, with additional indirect loss through avoidance or altered habitat selection by elk. Oil and gas wells and their associated service infrastructure of roads, pipelines and maintenance workers are common in the conterminous United States, particularly in the Intermountain West, and increasing in the face of rising demands for energy and desire to reduce dependence on energy from foreign sources. In Colorado, for example, applications for permits to drill for oil and gas increased by 750 % from

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1996 to 2008 (Colorado Oil and Gas Conservation Commission 2008). Responses of wildlife to human-caused stimuli, such as those generated from energy development activities, can be categorized as avoidance, tolerance, or attraction (Whittaker and Knight 1998). Such responses are mediated by scale-, time- and place- dependent variables, resulting in diverse physiological, behavioral, and population-level consequences. Elk have been shown to retain a high level of home-range fidelity in the face of various and sometimes extensive environmental changes including logging (Edge and others 1985; Vore and others 2007), exploratory oil development (Van Dyke and Klein 1996) and wind power development (Walter and others 2006), which suggests a capacity to tolerate such changes under certain conditions. However, elk may avoid, flee or hide from some kinds of disturbances, such as use of all terrain vehicles and other related recreational activities, at distances of up to 3 km (Preisler and others 2006; Naylor and others 2009). Elk also generally avoid roads (Czech 1991; Rowland and others 2000), including roads constructed in association with energy development (Sawyer and others 2007; Harju and others 2011; Webb and others 2011a), and avoidance is greater when forest cover is absent (Lyon 1979) or predation risk is high (Rumble and others 2005).

Elk may mitigate the effects of human disturbance behaviorally by shifting habitat selection within their home range on a temporal scale, such as increasing use of dense cover habitat during peak periods of human activity (Van Dyke and Klein 1996). Similarly, avoidance of roads lessens during periods when human traffic and related activity decline (Edge and Marcum 1985; Edge and others 1985). Such behavior is consistent with risk aversive behavior in elk, which, under some conditions, can lead them to increase use of affected areas. For example, elk increase use of areas associated with human activity or human-caused habitat modification when such areas can provide protection from wolf predation (Hebblewhite and Merrill 2009), increase proximity to human residences and agriculture in areas experiencing development for oil and natural gas (Dzialak and others 2011a) and increase use of explicitly protected refuge areas when exposed to hunting pressure (Proffitt and others 2010).

Although aversion to predation risk is an important driver of habitat selection in elk, forage acquisition also affects habitat selection, and may lead elk to tolerate some kinds of habitat change in order to meet their demands for sufficient quantity and quality of forage. An elk's choice of diet is a complex product of maximizing nutritional quality and digestibility while minimizing predation risk and foraging effort, and elk must accomplish such optimization within a complex integrative context of place-specific spatial, vegetative and climatic variables (Morgantini and Hudson 1985; Fortin and others 2005; Christianson and Creel 2007; Proffitt and others 2010). Thus, elk are highly opportunistic in their response to forage availability, quality and quantity, and such opportunism also can lead to rapid response to some kinds of habitat modification. For example, elk are more likely to forage in areas of high herbaceous biomass (Frair and others 2005), to increase foraging effort on burned sites following prescribed fire (Rowland and others 1983; Van Dyke and others 1991; Van Dyke and Darragh 2006a, b, 2007), to increase use of open canopy areas in predominately forested environments (Licoppe and de Crombrugghe 2003) and to select open grassland areas during winter (Proffitt and others 2010), even though such habitats are in some cases created by or associated with various kinds of disturbance.

The responses of elk and other large herbivores to habitat change and associated disturbance is scale-, time-, place- and change-specific in both type and magnitude of response, but remains an important question, not only because of its complexity, but because avoidance of altered habitats and human activities can lead to loss or reduced use of large proportions of otherwise available habitat (Dyer and others 2001). In caribou (*Rangifer tarandus*), for example, some investigations have documented avoidance of wells, seismic lines and well pads (Dyer and others 2001), while others have shown that caribou approach and use well pads and other elements of oil field infrastructure preferentially, particularly in summer months, to avoid parasitic insects more abundant on undisturbed tundra (Walsh and others 1992; Pollard and others 1996; Cronin and others 1998). When effective mitigation measures are employed, moose (*Alces alces*) have shown the capacity to habituate to the presence of above ground pipelines (Dunn and Quinn 2009) and elk to active oil drilling operations (Van Dyke and Klein 1996). In this study area, elk are more likely to be encountered close to gas well pads (Webb and others 2011b), but avoid associated service roads during daylight hours (Dzialak and others 2011b; Webb and others 2011a, b). The disparity and complexity of responses of large herbivores to disturbances associated with energy development is, in some cases, exacerbated because many past investigations of such responses employed observational data and correlational analyses of fine-scale behavior. A systematic understanding of such responses to habitat modifications and associated disturbances, however, would be better served by more extensive use of adaptive and experimental methods in which variables affecting such responses are intentionally manipulated by the investigator (Hebblewhite and others 2008) or explicitly modeled over time (Visscher and Merrill 2009). Responses of elk and other large herbivores have proven highly variable with respect to species, disturbance type, and landscape context. Responses of elk to environmental changes associated with energy development provide both a valuable opportunity and a specific case study in which to use such approaches to understand the capacities and thresholds of elk response to human-induced modifications at landscape levels, and their ability to exploit changes in resource availability, such as forage, when it occurs in proximity to environmental disturbance. Given the accelerating rate of energy development in the western United States, where the majority of US elk populations reside, there also is increasing need for a more definitive understanding of elk responses to different facets of such changes. Although response to factors such as human presence, vehicular traffic and predation risk have been studied in some detail, behavioral responses of elk to wells and well-pads, particularly during sustained long-term production rather than initial exploration, are not well understood.

To better understand patterns of elk behavior in response to the sustained habitat alterations associated with operating natural gas wells, we examined the response of elk to the intentional and managed creation of small forest openings and their associated increase in forage biomass production adjacent to operating natural gas wells in southern Colorado. Specifically, we compared such openings to undisturbed sites similarly adjacent to wells using measurements of vegetation composition, biomass and nutritional quality, elk pellet groups and amount of forage biomass removal as index variables of changes in plant communities and elk use associated with gas well development. The specific questions we sought to answer were: 1) How does tree removal affect plant community composition and nutritional quality in small forest openings? and 2) If production or nutritional quality of herbaceous vegetation increases following tree removal, will elk tolerate the presence of a natural gas well and demonstrate the behavioral plasticity to increase their use of sites with enhanced forage opportunities adjacent to the well? Answers to these questions could provide insight about the response by elk to gas wells and the potential abilities of elk to tolerate these and other kinds of habitat alterations. Such knowledge could enable more effective habitat management in human-altered landscapes as well as better prediction of the effects of future development in previously unaltered environments.

Study Area

Sarcillo Canyon, the locus of our study area, is a large, dry canyon in the eastern foothills of the Sangre de Cristo Mountains in southern Colorado, USA (37°12′ N, 104°49′ W). Topography is characterized by subdivision into smaller canyons and ravines separated by predominantly north–south ridges. Ridges and slopes were covered by extensive and relatively uniform stands of Ponderosa pine (*Pinus ponderosa*) forests, while canyon bottoms were often treeless and characterized by plant communities dominated by grass and forb species.

Sarcillo Canyon was located within a larger Colorado Division of Wildlife (CDOW) management unit, the Trinchera Data Analysis Unit (Trinchera DAU, Data Analysis Unit E-33, 8151 km^2), that was used by elk. The elk population in the Trinchera DAU was managed for size and sex ratio objectives determined by CDOW. Most hunting was conducted from late August through the end of November each year, although some, limited hunting opportunities extended through February. The adult elk population was limited mainly by hunting, although black bears (*Ursus americanus*), mountain lions (*Puma concolor*) and coyotes (*Canis latrans*) in the area were believed to affect calf survival. In 2006, the post-hunt population was estimated at 18,100 elk, with a current objective of 14,000–16,000 elk (Colorado Division of Wildlife 2007). In 2009, the post-hunt population was estimated at 19,280 individuals (A. Vitt, CDOW, pers. commun.).

Development for the extraction of natural gas began in this region in the 1980s, and became more extensive during the 1990s when drilling efforts and associated supporting infrastructure of road and pipeline building increased as a result of improved efficiency of drilling techniques (Colorado Division of Wildlife 2007). In this area we selected 10 pairs of sites covered by Ponderosa pine forests and adjacent to active natural gas wells. We placed all sites on a single private property (the McDonald Ranch; 2892 ha; 2,220–2,360 m in elevation) to minimize habitat differences, ensure that land management practices were similar across study sites and reduce problems associated with obtaining landowner permission to access individual wells.

On the McDonald Ranch, exploration for extraction of coal bed natural gas began in 1995, and the density of wells on the ranch at the time of this study was 3 wells/km^2. Wells used in the study were $\geq$3 years old when the study began in 2008. Wells were visited daily by maintenance personnel, usually consisting of one visit by one or two employees in one vehicle. Roads to individual well pads had metal gates installed at the point they left a public road. Gates were secured by key or combination lock, with keys or combinations provided to well pad workers, the ranch owner and his employees, or other individuals specifically designated and authorized to visit or conduct work at the pad. Roads to gas wells terminated at the pad.

In addition to development for extraction of natural gas, the McDonald Ranch was used for free-range cattle ranching and fee-based sport hunting. Factors affecting landscapes around well pads included vehicular traffic, roads, pipelines, human residences and ranching operations.

Ponderosa pine dominated forested stands, with Douglas fir (*Pseudotsuga menziesii*), juniper (*Juniperus* spp.) and pinyon pine (*Pinus edulis*) present at low frequencies on some sites. Shrubs, primarily Gambel oak (*Quercus* *gambelii*) and mountain mahogany (*Cercocarpus montanus*), formed a sparse and intermittent shrub understory. Rock, soil and pine needles composed the majority of ground cover. Live groundcover of graminoids and forbs was of low frequency. Common graminoid species included blue gramma (*Bouteloua gracilis*), various sedges (*Carex* spp.), mountain muhly (*Muhlenbergia montana*) and little bluestem (*Schizachyrium scoparium*). White sagebrush (*Artemisia ludoviciana*), prairie sage (*A. frigida*), pussytoes (*Antennaria* spp.), nodding onion (*Allium cernuum*), Fendler's sandwort (*Arenaria fendleri*), fleabanes (*Erigeron* spp.) and groundsels (*Packera* spp. and *Senecio* spp.) were the most common forbs.

Local climate was characterized by hot, dry summers and short, mild winters. Average annual precipitation at Trinidad Lake (elevation 1868 m), the nearest permanent weather data collection site, was 44.5 cm. Winter temperature (December through February) averaged >0°C in all months (Western Regional Climate Center 2010). Winter and spring rainfall (1 December to 30 June) was 18.2 cm in 2008, 20.0 cm in 2009 and 20.0 cm in 2010 (Western Regional Climate Center 2010). In summer, extended periods without rain were common until late July or early August. At a weather station in Sarcillo Canyon installed near the center of the study area (elevation 2360 m), average summer temperature (June through August) in 2008 was 18.7 °C, in 2009 18.1 °C and in 2010 19.1 °C (Hayden-Wing Associates, pers. commun.).

Methods

Sampling of Elk Population and Plant Communities

We selected paired treated and control sites adjacent to 10 active wells in June 2008 after extensive review of a large pool of potential sites surrounding actively operating natural gas wells on the McDonald Ranch. Selected sites met all of the following criteria: (1) Sites were located in areas used currently by elk, as determined by the presence of recent elk pellet piles and by telemetry locations of ≥1 individuals of a group of 80 radio-collared elk that had been tracked by satellite in this area since 2006 (Hayden-Wing Associates, pers. commun.). Based on previously collected radio location data, elk used all areas where well pads were present (Dzialak and others 2011a, b; Webb et al. 2011a, b). Although such ubiquitous distribution made it impossible to choose pads whose surrounding area had never been used by elk, we considered the presence of elk on and around selected sites prior to treatment essential to effective study design in order that elk would directly observe and experience changes on every site during and following our experimental manipulation of vegetation in proximity to the well. As a result, any subsequent changes in elk use of sites would logically reflect responses of elk to such manipulation in the presence of an operating well, clearly establishing an obvious and direct link between vegetative manipulation, elk use, and tolerance of elk to the well and its associated activities if use changed. (2) Sites were characterized by relatively open, uniform forests that could contain two 100 X 100 m (1 ha) sites, with at least one side of each site ≤20 m from the well pad; (3) Sites had slopes of <35 % in order to reduce soil erosion following cutting, and because elk tend to reduce feeding on slopes of >35 % (Van Dyke and others 1991); (4) Sites did not contain extensive areas of large boulders, bare surface rock or vertical cliffs that would have been considered non-habitat for elk and created potential hazards to the safety of workers removing timber; and (5) The well and its paired sites were >1 km from the nearest neighboring selected sites. Our intention in using this criterion was to achieve as much independence of response as possible among different sites. Elk often move >1 km in the course of individual foraging periods, and we therefore acknowledge that a separation distance of >1 km did not ensure the use of a site by an individual elk would be independent of its use of other sites. We provisionally adopted distances of >1 km as our best feasible separation interval, given the spacing and density of wells meeting criteria 1–4. Sites were used by elk and mule deer (*Odocoileus hemionus)*, but not by cattle. Cattle preferred riparian valleys on the ranch, and were not seen on selected sites, which were on forested ridges, nor were cow feces found on sites.

We recognize that our sampling of paired sites prior to cutting, as well as the sampling of uncut sites after cutting, are pseudo-controls. Before cutting, both sites in each pair were in close proximity to the well and, after cutting, both the cut and uncut site in each pair were in similar close proximity. We intentionally accepted this constraint on our design for three reasons. First, many previous studies have shown that, in unmodified habitats, large herbivores will respond to sites with enhanced foraging opportunities with increased use. Second, in a landscape already experiencing increasing habitat fragmentation from roads and clearings associated with energy development, we considered the additional fragmentation created by adding another level of experimental controls detrimental to elk as well as other wildlife species which require larger blocks of contiguous habitat, and thus counter to our foundational intention of benefitting wildlife through our research. Third, the cost of site modification required to create 10 additional 1-ha cut sites was prohibitive. After considering the ecological and economic cost of such controls and, in our judgment, their limited value relative to what could be learned from previous studies, we chose not to add paired sites located more remotely from operating gas wells.

Once selected, we permanently marked the corners of each site with 1.3 m steel fence posts driven into the ground. After collection of preliminary data in summer 2008, most trees were cut and removed from one (treated) site at each well by chain saw cutting and tree felling machines and then stacked off site. Three to five large seed-producing trees of Ponderosa pine, or other species if present, were left standing on the site to aid in seed dispersal and reforestation following the study. We designated the other site in each pair as the control site and left it untreated. Within each site, we established four 40 m $\times$ 40 m plots and permanently marked their front corners with 1 cm diameter 30 cm rebar rods driven into the ground.

We measured forest stand characteristics on all sites prior to tree removal in 2008 using the point-centered quarter system (Cottam and others 1953) in order to determine if any consistent pre-treatment differences existed between designated control sites and designated treatment sites, such as might obscure the effects of our treatments or bias interpretation of post-treatment responses. We took a diagonal transect between opposite permanently marked corners at each site with center points established at 13 m intervals along the transect and recorded the species, DBH, and distance from the center point of the nearest tree ($\geq$8 cm DBH) in each quarter. No tree was recorded more than once. If no previously unrecorded tree was present $\leq$50 m of the center point in a given quarter, we designated that quarter as non-forest. We corrected density values for non-forest quarters following methods described by Warde and Petranka (1981).

We completed pellet counts on all sites during the first three weeks in June and completed vegetation sampling from late June through late July in 2008, 2009 and 2010. We assessed annual elk use of sites by counting all elk pellet groups within one m on either side of 6 40-m transects perpendicular to the baseline of each plot. In 2008, we considered a pellet group $\leq$1 year in age to be a distinct cluster of $\geq$12 or more predominately black pellets, and counted a pellet group if $\geq$1 pellets in the group lay within 1 m of the transect line. Elk pellets were distinguished from deer pellets, which were also counted, by size and shape. After counting, we scattered pellet groups to prevent double counting in future sampling. Although pellet counts are an indirect measure that should not be used to obtain a quantitative estimate of habitat use or population size (Weckerly and Ricca 2000), they provide a reliable relative index of use in areas accessible to the same population. The technique has been used extensively for this purpose in past studies (e.g., Neff 1968; Edge and others 1987; 1988; Ripple and others 2001) and has continued to provide accurate estimates of relative habitat use in more recent ones (Van Dyke and Darragh 2006a, b, 2007; Acevedo and others 2010). Pellet counts provide estimates of relative habitat use as accurate as those obtained by radio tracking and direct observation (Leopold and others 1984; Loft and Kie 1988; Edge and Marcum 1989), and the most recent comparisons show pellet counts to be as accurate in estimation of relative habitat use as global positioning systems (Månsson and others 2011). Pellet counts were used in our study area prior to our study period to assess elk response to roads, well pads and natural habitat features (Webb and others 2011b), providing results of habitat use and response to human activities similar to those from radio-collared elk monitored by satellite telemetry (Webb and others 2011a, b; Dzialak and others 2011a; Harju and others 2011).

We assessed grazing intensity by elk and mule deer by constructing a 1.3 m X 1.3 m X 1.3 m exclosure and designating a permanent non-exclosure area of the same size on each plot following tree removal in 2008. Exclosures were made of page wire lined with 0.3 m of chicken wire on the bottom edge to prevent the entrance of smaller herbivores. We clipped live biomass inside exclosures and non-exclosures and sorted it by category, and estimated nutritional content by chemical analysis. Following standard procedures, the Wyoming Department of Agriculture Analytical Services Laboratory (WDAASL) analyzed dried samples to determine dry weight biomass and levels of protein (%) and total digestible nutrients (TDN; %) (AOAC 2000). We considered plant removal by elk and mule deer to be the difference in biomass between exclosure and non-exclosure areas. Due to the synergistic effects of grazing on plant growth, this difference might not represent the exact biomass actually consumed by elk and mule deer because grazing at moderate levels by native ungulates stimulates increased rates of biomass production compared to ungrazed systems (McNaughton and others 1988). We did consider, however, that such a difference would reflect an accurate estimate of the net change in biomass due to grazing.

To determine plant community composition, we estimated the percent cover of each plant species to the nearest 10 % interval in 25.4 cm X 50.8 cm Daubenmire frames. We placed frames at 10 randomly chosen locations along transects in each plot (total 60 samples/plot, 240 samples/site). After recording all species and their percent cover, we clipped and sorted all living plant material in each frame for nutritional analysis by category (graminoid [grass, sedge or rush], forb and shrub). Because WDAASL had difficulty handling and analyzing sample sizes greater than 600 g, we attempted to keep samples under this value by terminating clipping when a sample's biomass approached this amount, and adjusted computations accordingly in such cases. We excluded trees from coverage estimates and nutritional analysis because they are normally not a significant source of elk forage during summer (Hobbs and others 1979).

Numerical and Statistical Analyses

Because our first concern was to determine if paired sites at individual wells were in fact similar in vegetation characteristics prior to treatment, we measured differences in tree density on treatment and control sites prior to timber removal in 2008. We evaluated differences in tree density between treatments prior to timber removal through matched-pairs t tests of treated and control sites paired by location in 2008.

We used generalized linear mixed models to compare counts of elk pellet groups on treatment and control sites. We assumed the count response data (number of pellet groups per transect) followed a Poisson distribution (link = log) and assigned Treatment (control vs. cut), Year, and a Treatment*Year interaction as categorical fixed effects. We included the interaction because we expected the effect of treatment to depend on year; the first year (2008) was the pre-treatment year and no treatment effect was expected. Subsequently, elk response might vary over time as vegetation communities responded to overstory removal. We assigned Transect and Plot as random effects to account for repeated measures among years. We assigned Transect as nested within Plot and Plot as nested within Site to account for autocorrelation arising from the spatial hierarchy of the sampling design. We used SAS 9.2 (SAS Institute, Inc., Cary, NC, USA) and PROC GLIMMIX for the pellet group analyses.

We determined species diversity of understory vegetation on each site using the Shannon Index (H') (Shannon and Weaver 1949), $H' = -\sum (p_i \ln p_i)$, where p_i is the proportion of individuals of the ith species. We compared species richness and plant biomass (kg/ha) through repeated measures multiple ANOVA, with treatment and year as independent variables. To examine similarity of cut and control sites before treatment, and after treatment in cases where interactive effects between time and treatment were detected, we compared species richness and plant biomass on treatments within each year through matched-pairs t tests by location.

We compared all measurements of plant community or nutrition expressed as a percentage (e.g., groundcover, percent of vegetation, and nutritional content) or an index (e.g., Shannon Index) using multivariate randomized block permutation (MRBP) tests (Mielke and Berry 2001). Data expressed as a percent violate assumptions of normality, and are typically arcsine transformed prior to analysis by ANOVA. Such transformation, however, obscures the interpretability of results. To maximize clarity in interpretation, we chose the MRBP test because it makes no assumptions about the distribution of observed values, only that values associated with different groups are independent of one another. Data were grouped by year and treatment. Where groups were dissimilar, we made further pair-wise comparisons of groups using the Peritz closure method (Petrondas and Gabriel 1983). This method allows multiple comparisons among groups by maintaining α at or below specified levels using a specified set of decision rules.

To evaluate the similarity of plant communities, we compared species presence and absence using the Jaccard Index, a measure of similarity between communities, grouping data by year, treatment and location. The Jaccard Index offers an easily interpreted measure of association between communities, but should not be analyzed using standard ANOVA. Therefore, we analyzed whether plant communities in different years or treatments were dissimilar to one another based on a blocked (by plot) permutation test with Bonferroni corrections (Miller 1981; Edgington 1995). $P \leq 0.05$ was considered significant in all cases.

As noted earlier, the uncut site in each pair was not a true control, which would have required cut-uncut juxtapositions at locations remote from gas wells. Nevertheless, our design ensured that cut and uncut sites would be exposed to the same levels of habitat modification and proximity to human activity. Thus, differences in plant and elk responses on cut and uncut sites would be attributable to site treatment and detectable by analyses we employed.

Results

Similarity of Sites Before Treatment

Elk pellet groups were present on all sites before treatment, confirming prior elk use of all sites, and followed a Poisson distribution ($\chi2$/d.f. = 1.06). Plant communities and elk use were similar on treated and control sites prior to tree removal (Table 1; Fig. 1). Ponderosa pine accounted for 86.6 % of trees on control sites and 88.2 % of trees on treated sites. Douglas fir, pinyon pine and juniper accounted for the remainder. Treated and control sites were similar in tree density prior to cutting ($t = -0.69$, $d.f. = 9$, $P = 0.51$) (Table 1). Ground cover was predominately bare soil, rock, and pine litter, with vegetation covering on average ≤25 % of the ground ($T = 0.83$, $P = 0.85$). Thirty species of graminoids, 56 species of forbs, and 6 species of shrubs were identified on sites in 2008. Sites were similar in species richness and diversity prior to treatment (Fig. 2; species richness: $t = -0.18$, $d.f. = 9$, $P = 0.85$; Shannon Index: $T = 0.18$, $P = 0.44$). Grass, forb, shrub, and total coverage and biomass were similar between treatments prior to tree removal (Table 1, Fig. 3, Fig. 4). Protein and TDN levels were similar between cut and control sites prior to treatment in grasses and forbs. Shrub protein was higher

Table 1 Elk use, stand density, and vegetative community characteristics on treatment and control sites adjacent to natural gas wells in Raton Basin, Colorado, USA in 2008 prior to tree removal

	Control	Cut	*t*	*P*	*d.f.*
Pellet density (groups/ha)	129.5 (35.0)	149.5 (35.0)	−0.84	0.40	944
Stand density (trees/ha)	251.6 (189.2)	317.1 (201.7)	−0.69	0.51	9
Species richness	33.3 (5.3)	33.6 (9.6)	−0.18	0.85	9
Biomass (kg/ha)					
Total	131.1 (83)	151.8 (102.9)	0.78	0.46	8
Grasses	35.3 (13.3)	30.9 (25.1)	0.14	0.89	8
Forbs	15.3 (9.7)	15.7 (12.2)	0.35	0.73	8
Shrubs	80.6 (76.4)	105.2 (89.2)	0.89	0.4	8

Statistical values represent results of matched-pairs *t*-test. SE in parentheses

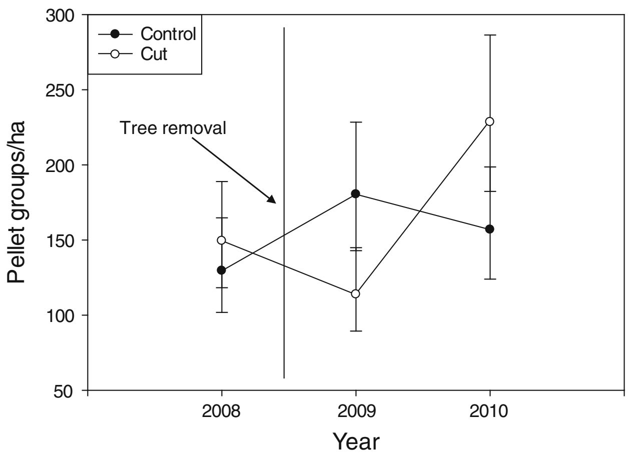

Fig. 1 Average elk use (pellet groups/ha) on cut and control sites adjacent to natural gas wells in Raton Basin, Colorado, USA 2008–2010. *Vertical line* indicates tree removal on cut sites occurred after data collection in 2008. *Error bars* represent 95 % confidence intervals

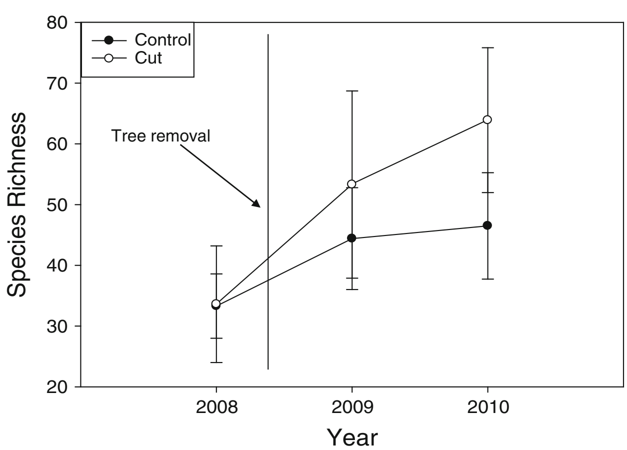

Fig. 2 Average species richness per site on cut and control stands adjacent to natural gas wells in Raton Basin, Colorado USA 2008–2010. *Vertical line* indicates tree removal on cut sites occurred after data collection in 2008. *Error bars* represent standard deviation

on control sites ($\bar{x} = 11.8$ %) than cut sites ($\bar{x} = 10.4$ %, $T = -5.26$, $P < 0.01$) prior to tree removal, as was TDN ($\bar{x} = 61.1$ %, control sites; $\bar{x} = 58.3$ %, cut sites, $T = -3.09$, $P = 0.02$).

Changes in Plant Communities

Treatment produced changes in plant community richness and diversity. In the two years following treatment, 12 additional species of graminoids, 98 additional species of forbs, and 2 additional species of shrubs were identified on sites. Species richness was 29 % higher on cut sites than control sites ($F = 0.41$, *d.f.* $= 18$, $P < 0.02$) and 13 % higher in 2010 than 2009 ($F = 0.81$, *d.f.* $= 18$, $P < 0.01$). Species richness showed year*treatment interactions, the magnitude of difference between treatments increasing 93 % from 2009 to 2010 ($F = 0.35$, *d.f.* $= 18$, $P = 0.03$) (Fig. 2). Plant community diversity (Table 2) was not different between treatments following tree removal in 2009 ($P = 0.15$), but was higher on cut sites than control sites in 2010 ($P < 0.01$). Control sites were similar in diversity between years ($P = 0.57$).

Total plant cover (%) did not differ between treatments in 2009 (cut: $\bar{x} = 37$ %, S.E. = 18; control $\bar{x} = 33$ %, S.E. = 10; $P = 0.5$), but was higher on cut sites in 2010 (cut: $\bar{x} = 42$ %, S.E. = 13; control $\bar{x} = 31$ %, S.E. = 9; $P = 0.02$). In 2009, the first season after tree removal, graminoid cover did not vary between treatments ($P = 0.69$), but forb cover was 74 % higher on cut sites ($P = 0.03$) (Fig. 3). The increase in total plant cover on cut sites in 2010 was driven by graminoids and forbs, which were more abundant on cut sites (graminoids: $P = 0.01$; forbs: $P < 0.01$) (Fig. 3). Shrub cover was lower on cut sites than control sites in both years (2009: $P = 0.04$; 2010: $P = 0.03$) (Fig. 3). On control sites, plant cover was higher in 2009 and 2010 than 2008 (2008: $\bar{x} = 24$ %, S.E. = 9; 2009: $\bar{x} = 33$ %, S.E. = 15, $P = 0.02$; 2010: $\bar{x} = 31$ %, S.E. = 12, $P = 0.02$).

Results of the dissimilarity test (Jaccard Index) indicated an average similarity between locations within the same treatment in the same year of 0.47 (baseline similarity) (SE = 0.02). Similarity between the same sites in different years was reduced by an average of 11 % (similarity between years = 0.42, SE = 0.003, $P = 0.0003$). Similarity between the same sites in different treatments was reduced by an average of 6 % (similarity between treatments = 0.44, SE = 0.003, $P = 0.0003$). Dissimilarity

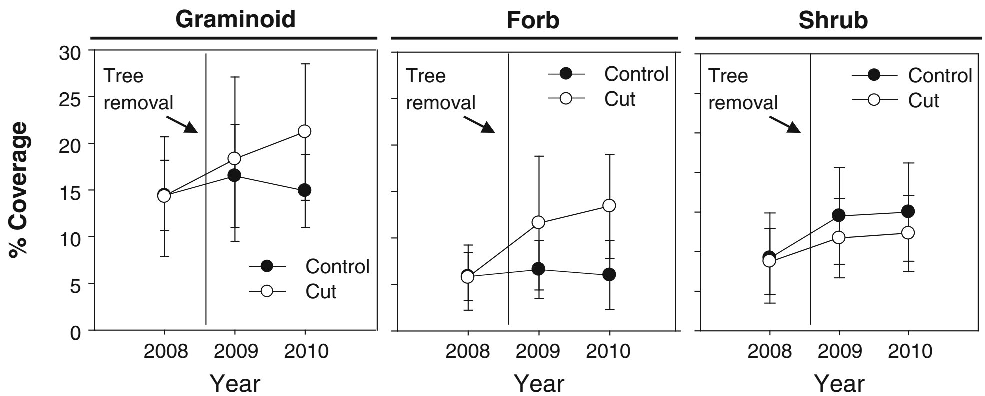

Fig. 3 Average cover (%) of graminoids, forbs and shrubs on cut and control sites near natural gas wells in the Raton Basin, Colorado, USA 2008–2010. *Vertical line* indicates tree removal on cut sites occurred after data collection in 2008. *Error bars* represent standard deviation

Fig. 4 Average biomass (kg/ha) of graminoids, forbs and shrubs on cut and control sites near natural gas wells in the Raton Basin, Colorado, USA 2008–2010. *Vertical line* indicates tree removal on cut sites occurred after data collection in 2008. *Error bars* represent standard deviation

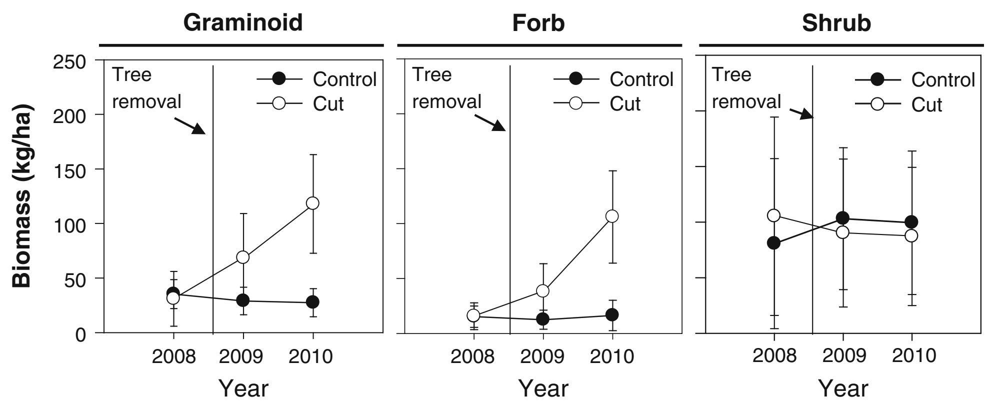

Table 2 Species diversity (Shannon Index) and nutritional content of vegetation on cut and control sites adjacent to natural gas wells, Raton Basin, Colorado, USA 2009–2010

	2009		2010	
	Control	Cut	Control	Cut
Shannon Index	2.61 (0.24)	2.78 (0.29)	2.58 (0.35)	2.95 (0.26)*
Protein (%)				
Graminoids	10.2 (1.6)	10.7 (1.5)	8.7 (0.6)†	10.4 (1.2)*
Forbs	12.2 (2.7)	14.2 (3.3)	10.3 (1.5)	10.8 (1.3)
Shrubs	12.2 (1.1)	13.5 (1.1)*	11.8 (0.9)	12.7 (0.7)
TDN (%)				
Graminoids	57.3 (1.8)	57.3 (1.6)	59.4 (1.2)†	60.3 (1.7)*
Forbs	63.2 (3.0)	62.2 (5.6)	63.8 (2.5)	61.8 (3.4)
Shrubs	63.7 (2.0)	64.7 (2.0)	62.5 (1.5)	63.0 (0.9)

MRBP test with paired comparison analysis using the Peritz closure method was used to evaluate statistical hypotheses for significance at the 0.05 level. SE in parentheses. Asterisk indicates significant difference between cut and control sites within a year. Dagger indicates significant differences between control sites in different years

arose mainly from small changes in abundance of many species, rather than large changes in abundance of a few species, with no species contributing >4 % of the difference (Table 3). The 20 most common species were all present in both 2009 and 2010, and each was present at ≥60 % of sites each year (Table 3).

Changes in Forage Quantity, Quality, Elk Use and Herbivore Removal

Biomass production of graminoids and forbs showed an immediate increase in response to treatment (Fig. 4). Biomass of graminoids was 232 % higher and forbs 400 %

Table 3 Relative contribution to dissimilarity (%) (Jaccard Index) of the 20 most dissimilar species and the percentage of sites at which each species was present in 2009 and 2010, Raton Basin, Colorado, USA

	Relative contribution to similarity (%)	2009 Site Presence %	2010 Site Presence %
Graminoids			
Schizachyrium scoparium	3.5	100	100
Carex spp.	3.5	100	100
Bouteloua curtipendula	3.5	100	100
Poa fendleriana	3.3	95	100
Muhlenbergia montana	3.3	95	100
Andropogon gerardii	3.3	95	100
Bouteloua gracilis	3.2	90	100
Vulpia octoflora	2.8	90	90
Hordeum jubatum	2.7	90	85
H. pusillum	1.8	60	85
Forbs			
Erigeron flagellaris	3.2	90	100
Artemisia ludoviciana	3.2	95	95
Allium cernuum	2.5	90	80
Senecio integerrimus	2.4	65	100
Arenaria fendleri	2.2	75	85
Antennaria microphylla	2.2	80	80
Solidago spp.	2.1	70	85
Draba sp.	1.8	80	65
Shrubs			
Quercus gambelii	3.5	100	100
Cercocarpus montanus	2.7	90	85
Total	56.7		

higher on treated sites across years (graminoids: $F = 24.4$, $d.f. = 18$, $P < 0.01$; forbs: $F = 42.3$, $d.f. = 18$, $P < 0.01$), and differences increased over time (year*treatment interactions; graminoids: $F = 22.8$, $d.f. = 18$, $P < 0.01$; forbs: $F = 18.5$, $d.f. = 18$, $P < 0.01$) (Fig. 4). Graminoid biomass increased 49 % and forb biomass 142 % from 2009 to 2010 (graminoids: $F = 19.9$, $d.f. = 18$ $P < 0.01$; forbs: $F = 23.3$, $d.f. = 18$, $P < 0.01$), although this difference was due primarily to increases on treatment sites, since control sites were not different between years (matched pairs t-test; graminoids: $t = 1.07$, $d.f. = 9$, $P = 0.31$; forbs: $t = 61.63$; $d.f. = 9$, $P = 0.14$) (Fig. 4). Shrub biomass did not change in response to treatment ($F = 0.23$; $d.f. = 18$, $P = 0.64$), nor did shrub biomass differ between years ($F = 0.10$, $d.f. = 18$, $P = 0.76$) (Fig. 4). Nutrient levels of plants varied with year and treatment. In 2010, graminoid protein and TDN were higher on cut sites, in part because protein declined on control sites in 2010 (Table 2). Although our study was too short to fully examine shrub responses, we did observe some short term responses in this forage category, with shrub protein increasing on cut sites in 2009. This difference did not persist in 2010 (Table 2).

Elk continued to use all sites following treatment, with the effect of treatment varying by year (Fig. 1). In 2009, the first year after tree removal, elk used cut sites 37 % less than control sites ($t = 2.69$, $d.f. = 944$, $P < 0.01$), a difference between treatments of 66 pellet groups/ha. In 2010, this trend reversed, with cut sites receiving more use than control sites at an average difference of 72 pellet groups/ha, 46 % more than control sites ($t = -2.26$, $d.f. = 944$, $P = 0.02$).

Within treatments, elk use also varied by year, following a pattern that paralleled differences between treatments over time. From 2008 to 2009, elk pellet density on control sites increased 39 %, from 130 pellet groups/ha to 180 pellet groups/ha ($t = -4.36$, $d.f. = 944$, $P < 0.01$), but decreased to 157 pellet groups/ha in 2010 (13 % lower than 2009) ($t = 1.94$, $d.f. = 944$, $P = 0.05$). A reverse pattern occurred on cut sites, with a 24 % decrease from 150 pellet groups/ha in 2008 to 114 pellet groups/ha in 2009 ($t = 3.32$, $d.f. = 944$, $P < 0.01$), followed by a 101 % increase from 2009 to 229 pellet groups/ha in 2010 ($t = -9.22$, $d.f. = 944$, $P < 0.01$) (Fig. 1).

Elk and mule deer removed negligible and similar amounts of graminoid and forb biomass on cut and control sites in 2009 (graminoids: $P = 0.70$; forbs: $P = 0.09$) (Fig. 5). In 2010, graminoid and forb biomass removal remained low on control sites, but large amounts of biomass in both categories were removed from cut sites (graminoids: $P < 0.01$; forbs: $P < 0.01$) (Fig. 4). There was no difference in removal of shrub biomass between treatments.

Discussion

Responses of Plant Communities

Clarifying elk responses to changes in forage availability in modified landscapes is an important component of understanding current and anticipated future effects of habitat changes on elk, as well as a prerequisite for management action appropriate to such changes. Because responses evident at one scale may be masked at another, predicting ungulate response to habitat alteration is confounded by effects of spatial and temporal boundaries (Vistnes and Nellemann 2008). Our study was constrained by its focus on fine spatial scales as well as a relatively short time span (3 years). These same constraints, however, permit the

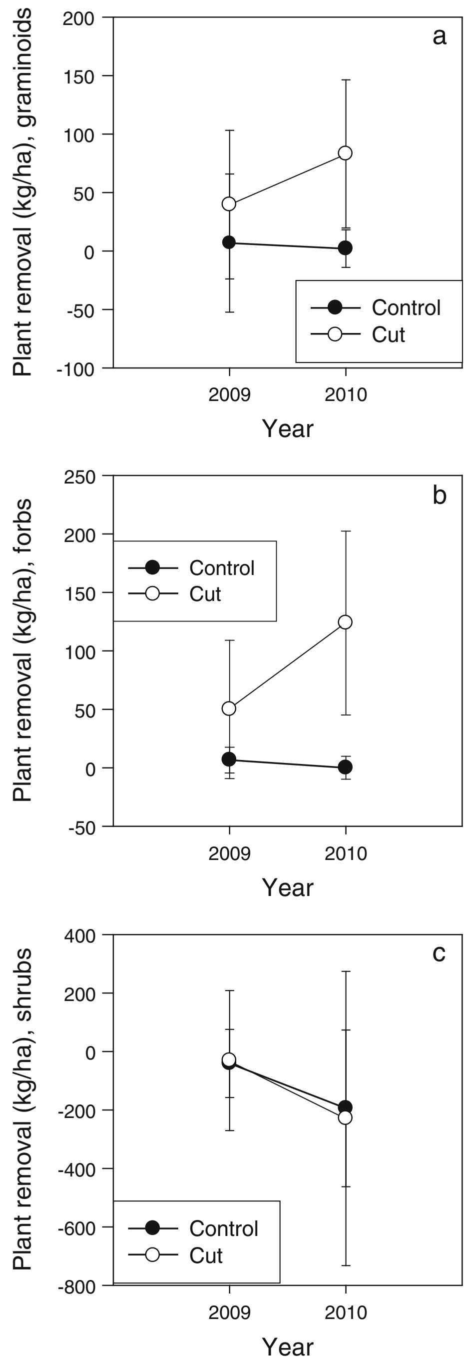

Fig. 5 Average biomass removal (kg/ha) by large herbivores of graminoids (**a**), forbs (**b**), and shrubs (**c**) on cut and control stands near natural gas wells in Raton Basin, Colorado, USA 2009–2010. *Error bars* represent standard deviation

examination of more precise, time-specific behavioral adaptations, including, but not limited to, behaviors difficult to detect or evaluate using larger scale studies covering longer time periods. We examine our findings with awareness of these limitations as well as an understanding of these strengths.

The first fundamental question of our study, how does tree removal affect plant community composition and nutritional quality, was answered with clarity. Within a two-year period following timber removal, plant communities increased in biomass, groundcover, species richness and diversity on cut sites. This effect was detectable in some categories in the first year after tree removal. The response, particularly in biomass production, increased in magnitude in the second year, following a trajectory similar to increases documented on cut sites in lodgepole pine forests (Visscher and Merrill 2009). Increases in biomass and groundcover were driven by increases in graminoids and forbs, the most important components of elk forage.

Plant community composition was affected by year and treatment. Increased numbers of species on both treatments in 2009 and 2010 might have been in slight part attributable to increased rainfall in these years, but the amount of difference from the drier year of 2008 (1.8 cm, 10 % increase) appears too small, both in absolute and proportionate scale, to explain the large changes observed. Different and increased numbers of species were more likely present on cut sites due to changes in light, water, and nutrient availability associated with tree removal. The additive effect of tree removal on the number of species present was apparent in the greater proportion of species unique to cut sites. In the two years following tree removal, one-fifth of all species were present exclusively on cut sites. Only 10 % of species were found exclusively on control sites in 2009, and that proportion was cut in half, to 5 %, in 2010. These differences suggest segregation in plant communities among the two habitat types. Further, the higher Shannon Index values for cut sites in 2010 indicates that not only did cut sites have greater species richness, but that the equitability of species abundance in these plant communities was greater than on control sites. Dissimilarity between years was greater than dissimilarity between treatments, suggesting variables other than treatment might have affected vegetation communities over time, and that secondary succession probably proceeded rapidly on cut sites. The pattern we observed was consistent with a multi-decade study which found that although timber removal associated with logging had long-lasting impacts on community composition, environmental variables also influenced vegetation (Bunn and others 2010).

Responses of Elk to Changes in Plant Communities

The second question of our investigation was whether elk would tolerate the presence of an operating natural gas well and demonstrate the behavioral capacity to increase use of sites adjacent to such a well with higher levels of forage production. This question also was answered clearly and affirmatively. Increased use of such sites did not occur immediately, but was eventually displayed in a more nuanced behavioral response over a two-year period. In the first year following tree removal (2009), elk used cut sites less than controls. Although this response suggested the possible avoidance of the gas well and its associated activity, it also might have been influenced by the fact that the process of tree removal left little vegetation intact on the site for the winter season immediately following treatment, and therefore provided little standing forage biomass for elk. In addition, contrasts in biomass production between cut and control sites became greater in 2010, which may have strengthened selection preference for cut sites by elk. By the end of the second year following tree removal (2010), new, early successional graminoid and forb communities were well established on cut sites. Associated increases in grass and forb production, along with higher nutritional quality in graminoids, the largest component of elk diets, were probably contributing factors to increases in elk use on cut sites in that year. Increased use was indicated not only by increases in pellet group densities, but by increased removal of graminoid and forb biomass by elk and mule deer. Given that pellet densities of elk on cut sites (229/ha) were nearly three times that of mule deer (86/ha, F. Van Dyke, unpublished data), that elk average approximately three times the weight of mule deer, and that elk typically consume greater proportions of graminoids and forbs in their diet most seasons than mule deer, we believe that a larger proportion of the biomass was probably removed by elk.

Some learned acclimation to the presence of oil well pads may have already taken place in this population before our study began. Pellet densities prior to treatments in 2008 were already at an average density of 139.5 pellet groups/ha, and an earlier study confirmed that the probability of encountering elk increased near well pads in this area (Webb and others 2011b). The overall 53 % increase in pellet densities on cut sites from 2008 to 2010 was statistically and, in our judgment, biologically significant, but not as large as responses to enhanced foraging opportunities in some studies. For example, increases in elk use on sagebrush sites following prescribed burning in Montana ranged from 143 to 492 % (Van Dyke and Darragh 2006a, b, 2007), far greater than what we observed on these sites. Such differences support our suspicion that earlier, learned familiarity of elk with well pads contributed to their ability to exploit better foraging opportunities on cut sites, but also limited the strength of that response in this context.

In evaluating the magnitude of increased use of cut sites, it is also possible that the presence of the well retained a residual depressant effect. If so, the response of elk to enhanced foraging opportunities on cut sites might have been even greater if the same opportunities had been presented in the absence of the well, as they have been in studies noted previously. Our study cannot answer this question because, as noted earlier, we had no experimental paired sites remote from operating wells. Greater use of cut sites, however, was consistent with results of other studies in which elk have selectively increased use of areas of higher grass and forb abundance in undisturbed environments (Creel and others 2005; Frair and others 2005; Proffitt and others 2010), as well as with studies in which elk made greater use of areas in undisturbed environments in which increased forb and grass abundance had been induced by habitat change (Rowland and others 1983; Van Dyke and others 1991; Van Dyke and Darragh 2006a, b, 2007).

In our study, two additional factors might have also contributed to increased use by elk. First, elk might have been attracted to the increasing species richness and diversity of plant communities on cut sites, where a greater diversity of plant species could allow elk to better control the nutritional quality of their diet by selecting species that would optimize nutritional levels (Van Dyke and others 1994; Beck and Peek 2005). Second, protein and TDN levels in graminoids, the most abundant and most important forage component for elk using this area, were higher on cut sites compared to control sites in 2010, the year that elk use shifted strongly in favor of cut sites. Although actual treatment differences were <2 % in both variables and cannot necessarily be assumed to have biological significance, there is evidence that elk can make relatively fine-scale, site-specific discriminations in forage quality (Van Dyke and others 1994; Beck and Peek 2005), and thus might have been able to discern, and actively select for, even slight nutritional advantages in graminoid forage on cut sites.

Consistent with predictions based on the proximity of enhanced forage quantity, elk, in 2010, used artificial forest openings (cut sites) more than forested (control) sites in the presence of operating natural gas wells, suggesting that elk can learn to tolerate the presence of such wells over time and exploit enhanced foraging opportunities in proximity to them. Elk using these sites were $\leq$120 m from well pads which had been in place for $\geq$3 years, and were residing in a landscape where construction and operation of natural gas wells had been an ongoing process for the past 15 years. Female elk in this study area have demonstrated strong fidelity to established home ranges even in the face of increasing development and human activity, although they maintained such fidelity by using range in ways that tended to minimize interaction with development (Webb and others 2011a). Such fidelity would enable elk to discover altered habitats within their home areas quickly, and to make use of such areas if the alterations provided improved foraging opportunities. In this study, elk demonstrated the behavioral capacity to exploit enhanced foraging opportunities in proximity to actively operating gas wells and their associated human activity. Such behavior by elk suggests that these stimuli were not perceived as risks sufficient to forego such opportunities or to deter elk from eventually exploiting areas with enhanced forage production. Our study, however, provides no data on the temporal component of such behavior. Elk in this study area have demonstrated avoidance of roads and natural gas wells during daylight hours, but not during nighttime hours (Dzialak and others 2011a). It is possible that the tolerance apparent in increased use of cut areas during the third year of our study also could have retained a temporal selection component, with use of cut areas occurring primarily at night.

Management Implications

Previously completed analyses of elk movements and landscape-level habitat selection in this study area have demonstrated that elk show aversion to roads and natural gas wells during daylight hours (Dzialak and others 2011a; Harju and others 2011), and that individual elk showed more constrained selection of landscape features inside this natural gas field than outside of it (Harju and others 2011). Such findings suggest that natural gas development limits habitat and resource selectivity in elk when it occurs in proximity to other, naturally occurring landscape features because elk not only avoid roads and gas wells, but the habitats adjacent to them, even if such habitats otherwise offer elk advantages in resource availability, including forage availability. Learned tolerance to roads and gas wells, however, is one means through which elk could recover some measure of habitat and resource selectivity, and its associated advantages to their health and survivorship. Managers facing energy development and its associated habitat modifications in areas used by elk should expect that elk are likely to show reduced habitat and resource selectivity in the face of such development, and predict and plan accordingly for such changes and the implications they are likely to have for elk behavior, vulnerability and survival.

Our findings indicate that managed forage and habitat availability can affect the responses of large herbivores like elk to activities associated with energy development. Although managers should recognize that some elk in our study area might be utilizing modified habitats in close proximity to energy development, our results do not demonstrate that all individuals responded similarly, nor do they demonstrate that a similar response would be seen during different stages of well development. Levels of human activity differ with different types and phases of energy development, and are likely to generate differing responses in large herbivores. For example, in oil development, mitigation measures such as directional drilling, seasonally-limited human occupancy and use of drilling sites and removal of visual evidence of drilling during non-drilling periods have been effective in minimizing changes in home range and movement patterns of elk in the drilling area (Van Dyke and Klein 1996). Likewise, in areas developed as gas fields, herbivores such as elk show differing responses to different densities of gas wells and different phases of development, with aversive behaviors becoming stronger at higher well densities established later in the development period (Webb and others 2011a).

The treatment approach we employed using one ha square cuts immediately proximate to operating gas wells was employed primarily for its experimental clarity, not necessarily because such specifications would represent the best option in all circumstances. In efforts to maximize actual benefit for elk, smaller cuts might be used more if they reduced flight distance to adjacent habitat providing concealment. Circular cuts would reduce the ratio of edge to interior area in a cut of any given size. Sites burned following cutting would likely demonstrate a stronger, albeit short term, increase in nutrient levels, especially protein levels, in forage plants (Van Dyke and others 1991; Van Dyke and Darragh 2006a, b, 2007). Similarly, sites subjected to hydro-ax mulching, chaining, or roller choppers would like produce different responses in their patterns of plant regeneration than our removal of trees by chain saw cutting and tree felling machines.

Assertion that elk can learn to exploit enhanced foraging opportunities in the proximity of environmental changes like the construction of wells and roads associated with natural gas development at a time when there is increasing concern regarding possible negative effects of human presence on wildlife, may be perceived as counterintuitive by the public, potentially posing a ‘credibility challenge’ for scientists (Thompson and Henderson 1998). In interpreting and communicating results of studies of this nature, it will not only be important to understand elk responses to habitat alterations, but also to consider how to create effective communication with the general public such that findings like this will be perceived as credible and trustworthy.

Managers should recognize that, although the increased use of cut sites near natural gas wells suggests that at least some individual elk in our study area may be learning to tolerate the presence of such wells and associated human activity, it does not prove that all individuals have developed this capacity (Whittaker and Knight 1998), or that such tolerance would have long term benefits for elk at individual or population levels. In our study, the increased use of cut sites adjacent to wells may represent a systemic learning behavior acquired by most individuals in this population. It also is possible that the results we observed were generated by a subset of the population previously habituated to wells, and even that timber cutting near wells may have reduced overall use of areas near these well pads by elk that were not so habituated.

With these considerations in mind, we note that an opposite response, that of increasing avoidance to a change-related stimulus over time, has been documented in mule deer (Sawyer and others 2006), and the possibility of the presence or development of a similar response in elk in this population should not be prematurely dismissed. Neither the effects of long term tolerance nor avoidance can be definitively assessed without further monitoring to determine if the behaviors we observed would become a stable and consistent pattern in this population, or if it would be beneficial or detrimental in the long run. Managers should therefore recognize the appropriate and considerable value and applications of short-term, highly time specific studies like this one which can pinpoint more precisely when vegetation changes occur relative to habitat alteration, and are then accompanied or followed by elk response, as well as appreciating the value of continuing longer-term monitoring of elk response to this and other types of environmental modification whenever the opportunity exists to do so. Although studies with short time frames permit precise examination of plant and animal responses within a limited time period, questions involving long-term response of elk to energy development and the adaptive and evolutionary value of avoidance or toleration of such development can only be answered by longer-term studies of elk population dynamics in modified landscapes.

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