Management and Conservation Article

Effects of Season and Scale on Response of Elk and Mule Deer to Habitat Manipulation

RYAN A. LONG,[1,2] *Department of Fish and Wildlife Resources, University of Idaho, Moscow, ID 83844, USA*
JANET L. RACHLOW, *Department of Fish and Wildlife Resources, University of Idaho, Moscow, ID 83844, USA*
JOHN G. KIE, *Department of Biological Sciences, Idaho State University, Pocatello, ID 83209, USA, and United States Department of Agriculture Forest Service, Pacific Northwest Research Station, La Grande, OR 97850, USA*

ABSTRACT Manipulation of forest habitat via mechanical thinning or prescribed fire has become increasingly common across western North America. Nevertheless, empirical research on effects of those activities on wildlife is limited, although prescribed fire in particular often is assumed to benefit large herbivores. We evaluated effects of season and spatial scale on response of Rocky Mountain elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*) to experimental habitat manipulation at the Starkey Experimental Forest and Range in northeastern Oregon, USA. From 2001 to 2003, 26 densely stocked stands of true fir (*Abies* spp.) and Douglas-fir (*Pseudotsuga menziesii*) were thinned and burned whereas 27 similar stands were left untreated to serve as experimental controls. We used location data for elk and mule deer collected during spring (1 Apr–14 Jun) and summer (15 Jun–31 Aug) of 1999–2006 to compare use of treated and untreated stands and to model effects of environmental covariates on use of treated stands. In spring, elk selected burned stands and avoided control stands within the study area (second-order selection; large scale). Within home ranges (third-order selection; small scale), however, elk did not exhibit selection. In addition, selection of treatment stands by elk in spring was not strongly related to environmental covariates. Conversely, in summer elk selected control stands and either avoided or used burned stands proportional to their availability at the large scale; patterns of space use within home ranges were similar to those observed in spring. Use of treatment stands by elk in summer was related to topography, proximity to roads, stand size and shape, and presence of cattle, and a model of stand use explained 50% of variation in selection ratios. Patterns of stand use by mule deer did not change following habitat manipulation, and mule deer avoided or used all stand types proportional to their availability across seasons and scales. In systems similar to Starkey, manipulating forest habitat with prescribed fire might be of greater benefit to elk than mule deer where these species are sympatric, and thus maintaining a mixture of burned and unburned (late successional) habitat might provide better long-term foraging opportunities for both species than would burning a large proportion of a landscape. (JOURNAL OF WILDLIFE MANAGEMENT 72(5):1133–1142; 2008)

DOI: 10.2193/2007-337

KEY WORDS *Cervus elaphus*, fuels reduction, manipulative experiment, *Odocoileus hemionus*, Oregon, utilization distribution.

Management-oriented manipulation of forest habitat can affect large herbivores in a variety of ways. Substantial alteration of quality, availability, or distribution of forage is perhaps the most logical of these, and the most frequently studied (Parker and Morton 1978, Carlson et al. 1993, Masters et al. 1993, Perryman et al. 2002). Analysis of forage characteristics alone, however, is insufficient for understanding effects of habitat manipulation on large herbivores. Behavioral responses to manipulation should be considered relative to changes in vegetation and other factors (Van Dyke and Darragh 2007). For example, when manipulated areas are replicated across a landscape, patch characteristics such as distance to cover, proximity to other patches, size, and shape all hold potential to influence patch quality and, therefore, degree of selection or avoidance of a patch by herbivores (Wiens 1976). Reynolds (1966) reported that elk (*Cervus elaphus*) were less likely to use open foraging areas that were >183 m from forested escape cover, and arrangement of habitat patches across a landscape has been shown to affect habitat use and size of the home range in cervids (Leopold et al. 1951, Beier and McCullough 1990, Kie et al. 2002). In addition, habitat manipulation might affect large herbivores by changing the dynamics of interspecific interactions. Preferences for habitat characteristics (as well as adaptations for exploiting habitat) are not uniform across species, and consequently, potential effects of habitat manipulation are not uniform (Collins and Urness 1983). Response of herbivores to habitat manipulation also can vary with season (Rowland et al. 2000, Ager et al. 2003) and scale (Johnson 1980, Wiens 1989, Bowyer et al. 1996, Scott et al. 2002), and failing to account for these sources of variation can lead to misinterpretation of results (Kie et al. 2002, Bowyer and Kie 2006).

Use of mechanical thinning and prescribed fire to restore historic disturbance regimes and reduce fuel loadings in fire-adapted forest ecosystems has become increasingly common across western North America (Dodge 1972, Covington et al. 1997, Weixelman et al. 1998, Tiedemann et al. 2000). Nevertheless, empirical research on effects of those activities on wildlife is limited, although prescribed fire in particular is often assumed to benefit large herbivores such as elk and mule deer (*Odocoileus hemionus*). Few studies of herbivore response to mechanical thinning or prescribed fire, however, have considered >1 of the factors discussed previously, and even fewer have been conducted in an experimental framework with treatments replicated across space and time. We evaluated response of adult (≥2 yr old) female elk and mule deer to an experimental fuels reduction program conducted over a large (78 km^2) geographic area at the Starkey Experimental Forest and Range (hereafter Starkey) in northeastern Oregon, USA.

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[1] *E-mail: longryan@isu.edu*
[2] *Present address: Department of Biological Sciences, Idaho State University, Pocatello, ID 83209, USA*

Patterns of resource selection and spatial distribution of elk and mule deer have been studied extensively at Starkey, providing context for understanding herbivore response to habitat manipulation. Female elk select habitat far from roads, and characterized by gentle slopes and westerly aspects (Johnson et al. 2000, Rowland et al. 2000, Stewart et al. 2002). Foraging strategy has been described as predominately grazing, and diets consist primarily of high-quality forbs, with grasses selected secondarily (Stewart et al. 2003). In contrast, female mule deer select habitat closer to roads, and characterized by steeper slopes, easterly aspects, and more convex topography than do elk (Johnson et al. 2000). Stewart et al. (2003) classified mule deer at Starkey as browsers, with diets consisting largely of sedges but also containing moderate quantities of shrubs and grasses. In addition, Johnson et al. (2000) and Stewart et al. (2002) concluded that habitat selection by mule deer could be explained largely by avoidance of areas used by elk.

In addition to previous work at Starkey, Long et al. (2008) conducted a detailed field study following completion of the fuels reduction program to evaluate effects of fuels reduction and season on quantity (% cover) and quality (% in vitro dry-matter digestibility and % nitrogen) of 16 key forage species and genera for elk. Quantity and quality of forage were estimated by Long et al. (2008) for all treatment and control stands during spring and summer of both years. Key results of that study included the following: 1) percent cover of 8 important forage species differed significantly between treatment and control stands, and combined cover of those 8 species was roughly 20% higher in treatment than control stands in spring, but slightly lower in treatment stands in summer; 2) although fuels reduction increased abundance of some herbaceous forage species in spring, abundance of both palatable and unpalatable shrubs was significantly reduced by fuels reduction treatments; 3) nutritional quality of herbaceous forage species in treatment stands did not change significantly in the first few years after treatment, but by the fifth year after treatment had increased above maximum mean values observed in control stands in both seasons; and 4) nutritional quality of all forage species was significantly lower in summer than spring.

We combined results of Long et al. (2008) with general information on foraging behavior of elk and mule deer garnered from previous studies at Starkey to formulate the following hypotheses regarding response of sympatric elk and mule deer to habitat manipulation: 1) as a result of increased quantity and quality of preferred forages in posttreatment years, elk will select treatment stands during peak foraging periods that either were avoided or used proportional to their availability prior to treatment, and use of treatment stands will be consistently greater than use of control stands; 2) positive response of elk to fuels reduction will be strongest in spring as a result of rapid senescence of preferred forage species and the presence of cattle on the study site in summer; 3) the magnitude of selection for treatment stands by elk will increase with increasing distance to roads, westerly aspect, time since treatment, stand area, and proximity to other treatment stands; and decreasing slope; 4) as a result of decreased availability of preferred forages or increased use by elk, mule deer will avoid treatment stands during peak foraging periods that either were selected or used proportional to their availability prior to treatment, and use of control stands will be consistently greater than use of treatment stands; 5) avoidance of treatment stands by mule deer will be less pronounced during summer as a result of decreased use of those stands by elk, but a negative response to fuels reduction will remain evident across seasons and spatial scales; and 6) the magnitude of avoidance of treatment stands by mule deer will increase with increasing distance to roads and selection by elk; and decreasing slope, easterly aspect, and topographical complexity.

STUDY AREA

Site Description

Starkey (45°13′N, 118°31′W) was a 101-km^2 research area managed by the United States Forest Service in the Blue Mountains of northeastern Oregon. A 2.4-m-high fence enclosed Starkey and prevented immigration or emigration of large herbivores (Bryant et al. 1993). This fence also divided Starkey into 5 distinct research areas. We used location data collected in Main Study Area (78 km^2), which is 2–4 times larger than the average home range size reported for elk in the Blue Mountains (Pedersen et al. 1980, Leckenby 1984). Telemetry data for elk and mule deer have been collected annually at Starkey since the early 1990s (Rowland et al. 1997), which provided a unique opportunity to evaluate stand selection by both species before, during, and after a fuels reduction program conducted from 2001 to 2003. Cattle were introduced to Main Study Area each year around 15 June and were moved in a deferred-rotation system among 3 pastures separated by barbed-wire fences, which were not barriers to movements of elk and deer, and an additional pasture outside the study area. The order of cattle rotation was reversed each year. Traffic levels were moderate and recreational activities were similar to patterns of use on nearby public lands (Rowland et al. 1997). Elevations at Starkey ranged from 1,120 m to 1,500 m, and the site supported a mosaic of coniferous forests, shrublands, and grasslands, with moderately sloping uplands dissected by numerous drainages (Johnson et al. 2000, Stewart et al. 2002). Detailed descriptions of Starkey are provided by Skovlin (1991), Wisdom et al. (1993), and Rowland et al. (1997, 1998).

Fuels Reduction Treatments

The fuels reduction program at Starkey took place from 2001 to 2003. During that time, 26 stands of true fir (*Abies* spp.) and Douglas-fir (*Pseudotsuga menziesii*) that experienced high rates of mortality from an outbreak of spruce budworm (*Choristoneura occidentalis*) in the late 1980s were treated to reduce fuel loadings, whereas 27 similar stands were left untreated to serve as experimental controls. Prior to treatment, fuel loadings (both dead and standing and downed fuels) in many stands exceeded 150 tons/ha. In

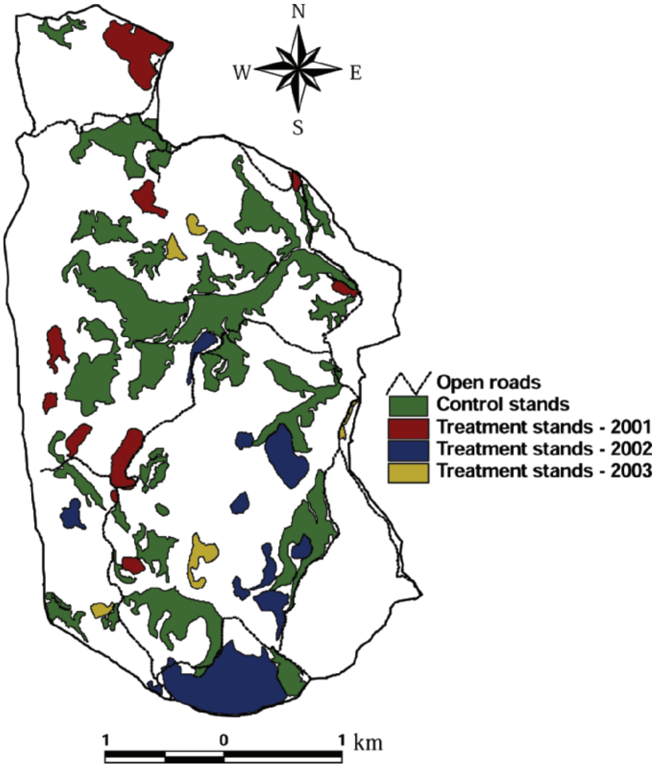

Figure 1. Locations of 26 forest stands treated with mechanical thinning and prescribed fire from 2001 to 2003 and 27 untreated control stands at the Starkey Experimental Forest and Range, Oregon, USA. Years associated with treatment stands indicate year of initial treatment (either thinning or thinning and burning).

addition, although most of the mature conifers in each stand were defoliated following the budworm outbreak, subsequent regeneration resulted in high densities ($\bar{x}$ = approx. 3,000 trees/ha) of young (<23 cm dbh) conifers in each stand by the time of our study (Long et al. 2008). Consequently, mean canopy closure was high in all stands prior to treatment. As a result of logistical constraints imposed by topography and size of some stands, we could not assign treatments in a completely random manner. We made efforts, however, to randomly assign treatments to the greatest extent possible within those constraints. Each treatment stand was mechanically thinned between May and October and was treated with prescribed fire during September or October of either the same year or the following year. All treatment stands were broadcast burned, and limited burning of slash piles was conducted in some stands. Mean flame height was 0.81 m (range = 0.46–1.22 m) and mean rate of spread was 0.07 km/hr (range = 0.02–0.20 km/hr). Following fuels reduction, average tree densities were roughly 2,000 trees/ha lower in treatment than control stands (Long et al. 2008). Ten stands initially were treated in 2001 (6 thinned, 4 thinned and burned), 11 in 2002 (7 thinned, 4 thinned and burned), and 5 in 2003 (all thinned and burned; Fig. 1). We digitized boundaries of all stands in a Geographic Information System (ArcGIS 9.0) from a combination of 28.5-m LANDSAT Thematic Mapper imagery for summers of 2000 (pretreatment), 2003, and 2004, and a 1-m digital orthophoto of Starkey from summer of 2002.

METHODS

Animal Locations and Utilization Distributions

From 1999 to 2006 adult female elk were baited onto a winter feeding pasture with an adjacent handling facility beginning in mid-December and were maintained on a diet of alfalfa hay until the following spring (Rowland et al. 1997). In early spring (Mar–Apr) of each year 20–40 elk were herded into a squeeze chute for handling and were fitted with radiocollars prior to release back into Main Study Area with the rest of the herd. Adult female mule deer were captured throughout the study area in panel traps and fitted with radiocollars during winters of 1999–2004. Collars typically were recovered in the winter following their application and new collars placed on different individuals of each species during the following spring so that each animal generally was monitored for only 1 year. Animal capture and handling procedures at Starkey are described by Rowland et al. (1997). All handling was in accordance with protocols approved by an established Institutional Animal Care and Use Committee and was in compliance with American Society of Mammalogists Animal Care and Use Committee Guidelines (1998; Wisdom et al. 1993). We obtained animal locations using a LORAN-C automated telemetry system with a mean positional error of 53 m (±5.9 SE; Findholt et al. 1996, Rowland et al. 1997). We collected telemetry data 24 hours/day with occasional exceptions resulting from equipment maintenance or repair, and we typically obtained a location for each study animal every 1–5 hours.

We limited our analyses to location data collected during crepuscular hours (±1 hr of sunrise and sunset) when habitat selection was assumed to be strongly influenced by forage distribution (Johnson et al. 2000). In addition, patterns of resource selection and spatial distribution of elk and mule deer have been shown to differ seasonally at Starkey (Rowland et al. 2000, Ager et al. 2003). Therefore, we divided our data set into 2 seasons: spring (1 Apr–14 Jun) and summer (15 Jun–31 Aug). The mid-June cutoff for differentiating between seasons differed only slightly from that suggested by Stewart et al. (2002) based on past precipitation patterns at Starkey, and it coincided with the introduction of cattle to Main Study Area. We only included in our analyses animals with $\geq$30 locations/season, although mean (±SD) number of locations/individual during each season was substantially higher (113 ± 72 for elk, 88 ± 56 for mule deer). Our data set consisted of 267 elk (58,865 locations) and 79 mule deer (13,730 locations). We evaluated spatial independence of individual animals within species and years using association matrices, which indicated within-year independence of all animals in our data set (Weber et al. 2001).

We estimated 95% fixed-kernel utilization distributions (UDs) for each animal in spring and summer using the program Animal Space Use 1.0 Beta (Horne and Garton

2007). We used likelihood cross-validation to select the smoothing parameter (Horne and Garton 2006). In addition, this software allowed us to adjust UD estimates for spatial bias in the rate at which we obtained telemetry locations in our study area by weighting each animal location by the inverse of the observation rate for the pixel in which it occurred (Johnson et al. 1998, Stewart et al. 2002, Horne et al. 2007). Utilization distributions produced in Animal Space Use consisted of a point file with attribute data describing the *x*- and *y*-coordinates of each point and the volume of the UD at that location. We clipped each UD at the Starkey boundary and recorded the volume that remained within the study area. On average, <3.5% of the volume of each UD occurred outside the Starkey boundary.

Selection Ratios

We calculated stand-specific selection ratios (use/availability; Manly et al. 2002) for individual elk and mule deer during spring and summer of each year at 2 spatial scales suggested to be most relevant for evaluating animal response to habitat manipulation (Boyce 2006). Second-order selection ratios (Johnson 1980; large scale) reflected the influence of each stand type in determining where elk and mule deer established home ranges within the study area. We defined availability at this scale as the proportion of the study area occupied by each stand type. Third-order selection ratios (Johnson 1980; small scale) reflected the influence of each stand type on space use by elk and mule deer within established home ranges. We defined availability at this scale as the proportion of each animal's home range occupied by each stand type. We quantified use by calculating the proportion of the volume of each animal's UD that overlapped each treatment and control stand on the Starkey landscape. Volume of the UD at any location reflects probability of use of that location, and selection ratios based on the UD (termed Relative Concentration of Use; Neatherlin and Marzluff 2004) offer an improvement upon traditional ratios by accounting for differences in relative intensity of space use within the home range, correctly treating the animal as the sampling unit, and quantifying use as a continuous random variable (Aebischer et al. 1993, Kernohan et al. 2001, Marzluff et al. 2004, Millspaugh et al. 2006, Thomas and Taylor 2006).

For each year of our study, we placed each stand into 1 of 8 categories: control, pretreatment, thinned, or 1-, 2-, 3-, 4-, or 5-year-old burn. We categorized treatment stands as pretreatment until spring of the year following initial treatment (either thinning or thinning and burning). Not all stand types were present on the landscape every year. Therefore, we calculated average selection ratios for each population and stand type within years and seasons using equation 4.29 of Manly et al. (2002:66). Values >1 indicated selection for a stand type whereas values <1 indicated avoidance. We pooled data from the 3 pretreatment years (1999–2001) and calculated one mean selection ratio for both control and pretreatment stands in those years. In addition, we calculated 90% simultaneous Bonferroni confidence intervals around mean selection ratios to evaluate degree of selection or avoidance of each stand type and around differences between means to assess significance of pair-wise differences in selection ratios (Manly et al. 2002). We considered the difference between 2 population selection ratios within a year statistically significant at the $\alpha = 0.10$ level if the simultaneous confidence interval around the difference did not contain zero (Manly et al. 2002). We chose a significance level of 0.10 because we corrected confidence intervals for multiple comparisons and, thus, they were conservative (Manly et al. 2002).

Modeling

We used a series of general linear models to evaluate the influence of several environmental variables on use of treatment stands by elk and mule deer. For both species, we constructed separate models for each combination of season and scale. We included only the 26 treatment stands in this analysis, because our primary interest was in understanding which variables had the greatest influence on use of forest stands subjected to fuels reduction. We used population average selection ratios (arcsine square-root transformed) for each stand in each year as the response variable in our models, with the exception that, consistent with our categorical analyses, we pooled data across the 3 pretreatment years. We included as predictors in our analyses variables with demonstrated potential to influence resource selection and spatial distribution of elk and mule deer (Table 1; Rowland et al. 1998, 2000; Johnson et al. 2000; Kie et al. 2002; Stewart et al. 2002). We obtained values for the following variables on a 30-m^2-pixel basis from the habitat database at Starkey for ungulate research (Rowland et al. 1998): slope; convexity (a measure of topographical complexity; Johnson et al. 2000); aspect (transformed with sine and cosine functions to measure E–W and N–S aspects, respectively); distance to open, restricted, and closed roads; distance to permanent water; and elevation. We used mean values of these variables for each stand in our analyses. We calculated area and a shape index (a measure of shape complexity) for each stand using the program FRAGSTATS (McGarigal and Marks 1995). We derived data on canopy closure on a 30-m^2-pixel basis from photo-interpretation of 1:12,000 color aerial photos, and we included mean canopy closure in a 200-m buffer around each stand as a variable in our analyses. We also calculated the proportion of a 500-, 1,000-, and 2,000-m buffer around each stand that consisted of treated habitat. We incorporated time since treatment (yr) as a continuous variable in our analyses. We also included a categorical variable indicating presence or absence of cattle in summer for both species, and we included stand-specific selection ratios for elk as a predictor variable in models for mule deer. We considered cattle present if a stand was located in a pasture used by cattle during that year, and values changed annually with the deferred rotation system. Finally, we included total precipitation in spring and summer of each year. We obtained data on precipitation from a weather station located on the study site.

We used an information-theoretic approach to model

Table 1. Candidate variables for inclusion in general linear models of stand selection ($n = 26$ treated stands) by elk and mule deer at the Starkey Experimental Forest and Range, Oregon, USA, 1999–2006.

Variable	Effect category[a]	$\bar{x}$	Min.	Max.
Slope (%)	Topographical	10.47	2.38	22.31
Convexity	Topographical	501.38	498.92	503.60
Sine of aspect	Topographical	0.09	−0.86	0.95
Cosine of aspect[b]	Topographical	0.16	−0.52	0.76
Elevation (m)	Topographical	1,403.82	1,175.66	1,470.68
Distance to open road (m)	Proximity to roads	590.01	24.48	1,826.58
Distance to restricted road (m)	Proximity to roads	386.21	51.34	1,047.92
Distance to closed road (m)	Proximity to roads	314.83	62.79	914.90
Distance to permanent water (m)	Proximity to water	314.71	79.19	677.21
Shape index	Patch metric	1.63	1.25	2.44
Stand area (ha)	Patch metric	25.91	2.56	213.97
% of buffered area treated (500-m buffer)	Patch metric	11.00[c]	0.00	46.00
% of buffered area treated (1,000-m buffer)	Patch metric	8.00[c]	0.00	33.00
% of buffered area treated (2,000-m buffer)	Patch metric	7.00[c]	0.00	29.00
Canopy closure (mean % in 200-m buffer)	Canopy cover	18.88	10.71	31.90
Total precipitation (cm)	Annual precipitation	6.89[c]	2.36	14.43
Yr since treatment	Time since treatment	1.79[c]	0.00	5.00
Cattle presence or absence	Interspecific interaction			
Elk selection ratio[b]	Interspecific interaction	1.16[c]	0.00	3.86

[a] Variables categorized for model selection based on potential to influence space use by elk and mule deer in similar ways.

[b] Variables included in models for mule deer only.

[c] We calculated means across all yr and seasons.

selection (Burnham and Anderson 2002). Prior to the formal modeling procedure, however, we conducted an informal variable reduction procedure that included identifying and eliminating highly correlated ($|r| \geq 0.60$) variables (PROC CORR; SAS Institute, Cary, NC) and removing other variables with coefficients of partial determination (partial r^2) < 0.01. In addition, we used residual plots to identify nonlinear relationships or other patterns that might indicate need for a transformation (Neter et al. 1996). With the exception of the initial correlation matrix, which applied to all data sets, we performed the variable reduction procedure separately for each combination of species, seasons, and scales.

Following initial variable reduction, we placed remaining predictor variables for each combination of species, seasons, and scales into 1 of 8 effect categories (Table 1) based on their potential to influence space use by elk and mule deer in similar ways. For example, slope, convexity, aspect, and elevation all represented topographical influences. Actual number of effect categories in each model set ranged from 3 to 6, with 1 to 3 variables in each category. Prior to model selection, we fit the global model for each set and evaluated residual plots for adherence to assumptions of normality and homogeneity of variance (Neter et al. 1996). Both assumptions appeared to be reasonably met for elk across seasons and scales. For mule deer, however, substantial heteroscedasticity was apparent in plots of residuals against predicted values for all 4 combinations of seasons and scales. We resolved this problem by using a weighted least squares procedure to fit models for mule deer.

For each species, season, and scale, we modeled all combinations of effect categories. Total number of models in each set ranged from 7 to 63. For each model we recorded the adjusted multiple coefficient of determination (R^2_{adj}), Akaike's Information Criterion adjusted for small sample size (AIC_c), ΔAIC_c, and the Akaike weight (w_i; Burnham and Anderson 2002). We then selected a 95% confidence set of models from each complete set based on w_i values and used the confidence set to calculate weighted model-averaged parameter estimates and unconditional standard errors for each predictor variable (Burnham and Anderson 2002). We judged model-averaged parameter estimates to differ significantly from zero if the 90% confidence interval based on the associated unconditional standard error did not contain zero. In addition, we calculated Akaike importance weights for each parameter using models in the confidence set.

RESULTS

Stand Use by Elk

Stand use by elk during peak foraging periods varied with season, scale, and stand type. Elk used both pretreatment and thinned stands proportional to their availability within the study area in 2002 and 2003, indicating little or no response by elk to mechanical thinning during spring or summer (Fig. 2). Conversely, in spring elk responded positively to prescribed burning by demonstrating selection for ≥1 category of burned stand in all posttreatment years except 2002 (Fig. 2). In addition, elk consistently used burned stands more than control stands relative to availability within the study area during spring; mean selection ratios for burned stands were, on average, 52% higher than ratios for control stands (Fig. 2). No consistent pattern of selection existed, however, for a particular category of burned stands across years (Fig. 2). In contrast to spring, elk either avoided treatment stands during summer or used them proportional to their availability within the study area, with the possible exception of some

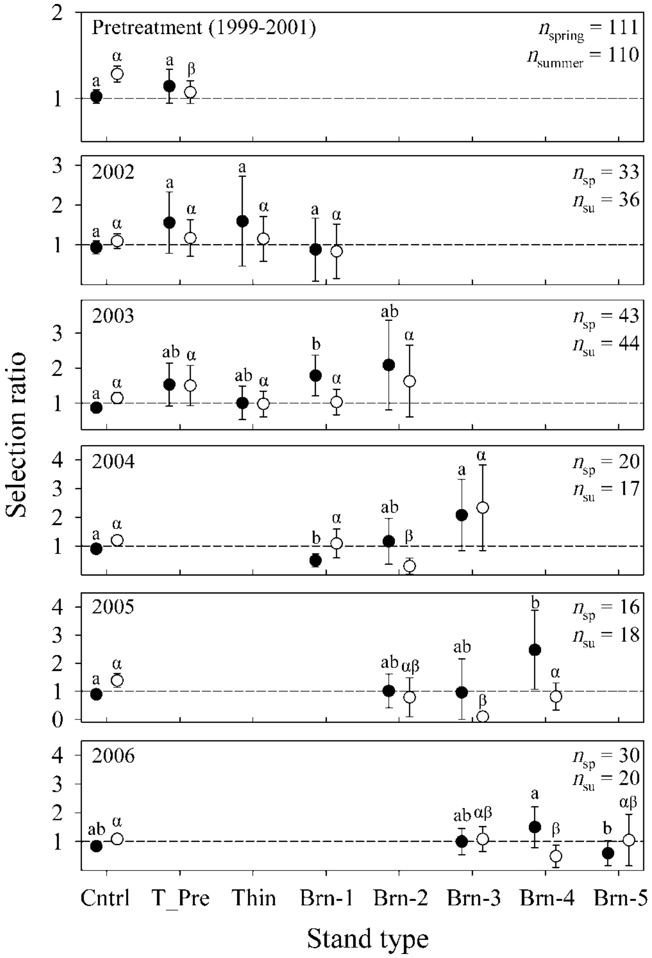

Figure 2. Population average selection ratios and 90% simultaneous confidence intervals for elk at the Starkey Experimental Forest and Range, Oregon, USA, during spring (1 Apr–14 Jun; closed circles) and summer (15 Jun–31 Aug; open circles) 1999–2006. Selection ratios reflect the influence of different forest stand types in determining where home ranges were established within the study area (second-order selection). Unshared letters among selection ratios within years and seasons (Latin for spring ratios, Greek for summer ratios) indicate a significant difference between means. We truncated impossible negative confidence limits at zero. Stand type abbreviations are defined as follows: Cntrl = control stands, T_Pre = pretreatment, Thin = thinned, and Brn-1, Brn-2, Brn-3, Brn-4, and Brn-5 = 1-, 2-, 3-, 4-, and 5-year-old burn, respectively.

selection for 3-year-old burns in 2004. Moreover, elk selected control stands during summer in both pre- and posttreatment years (Fig. 2). Use of treatment and control stands by elk within established home ranges did not differ in either season, and nearly all stands were avoided or used proportional to their availability at that scale. Our results indicate that stand selection by elk during peak foraging periods occurred primarily at the scale of the study area, and, consequently, we present modeling results for that scale only.

Use of treatment stands by elk within the study area was not strongly related to any of the environmental variables we considered during spring, and the best model accounted for only 24% of the variance in spring selection ratios (Table 2). Nonetheless, model-averaged parameter estimates for several variables differed from zero (Table 2). Elk made greater use of treatment stands with westerly aspects and use increased with distance to open and closed roads, stand area, and years since treatment. Use of treatment stands decreased with greater shape complexity, canopy closure in a 200-m buffer, and proportion of treated habitat within a 2,000-m buffer (Table 2). The most important effect category in the model set based on Akaike importance weights was canopy cover, followed by patch metrics and proximity to roads (Table 2). Models of stand use by elk during summer performed notably better, and the best model in the set explained 50% of variance in summer selection ratios (Table 2). Although fewer environmental variables were included in the model set for summer as a result of preliminary variable reduction, parameter estimates for all variables differed from zero. Elk made greater use of treatment stands where cattle were absent and use increased with increasing slope, convexity (topographical complexity), distance to open roads and water, stand area, and canopy closure in a 200-m buffer and with decreasing shape complexity (Table 2). The most important effect categories in the model set were topography, proximity to roads, and presence of cattle, followed by the patch metrics (Table 2).

Stand Use by Mule Deer

In contrast to elk, mule deer either avoided treatment stands or used them proportional to their availability within the study area during peak foraging periods in spring (Fig. 3). Mule deer also avoided control stands in spring of posttreatment years, and there were no significant differences in selection ratios between treatment stands and control or pretreatment stands (Fig. 3). In addition, patterns of stand use by mule deer generally were consistent across seasons and spatial scales. Together these results indicate little or no response by mule deer to fuels reduction treatments.

Also in contrast to elk, models of stand use by mule deer within the study area performed relatively well in spring, and the best model in the set explained 69% of the variance in spring selection ratios (Table 3). Use of treatment stands by mule deer in spring was most strongly related to topography and proximity to roads and increased with decreasing elevation and distance to open, restricted, and closed roads (Table 3). Summer models of stand use by mule deer had less predictive strength than models for spring. The best model in the set for summer explained 41% of variance in summer selection ratios (Table 3). Similar to spring results, however, use of treatment stands by mule deer in summer was most strongly related to topography and proximity to roads and increased with decreasing elevation and distance to open roads (Table 3).

DISCUSSION

Elk selected burned stands primarily at the larger spatial scale, indicating that fuels reduction significantly affected where elk established home ranges but had little effect on space use within home ranges. Similar patterns have been reported elsewhere (Bowyer and Kie 2006). For example, Kie et al. (2002) demonstrated that strength of the

Table 2. Model-averaged parameter estimates, standard errors, 90% confidence intervals, and Akaike importance weights for general linear models describing the relationship between second-order population average selection ratios for elk in spring (1 Apr–14 Jun) and summer (15 Jun–31 Aug) and 14 variables associated with 26 forest stands treated with mechanical thinning and prescribed fire at the Starkey Experimental Forest and Range, Oregon, USA, 1999–2006.[a]

	Spring					Summer				
			90% CI					90% CI		
Parameter[b]	Estimate	SE	Lower	Upper	Importance wt	Estimate	SE	Lower	Upper	Importance wt
Intercept	26.56	21.04	−7.95	61.07	na	−56.28	20.16	−89.34	−23.22	na
% slope	na	na	na	na	na	0.04	0.01	0.02	0.05	0.98
Convexity	−0.05	0.03	−0.11	0.01	0.78	0.11	0.04	0.05	0.18	0.98
Sine of aspect	0.12	0.07	0.01	0.23	0.78	na	na	na	na	na
Dist_open	2e − 4	9e − 5	7e − 5	4e − 4	0.93	4e − 4	1e − 4	2e − 4	5e − 4	0.98
Dist_closed	4e − 4	2e − 4	8e − 5	6e − 4	0.93	na	na	na	na	na
Dist_water	na	na	na	na	na	6e − 4	3e − 4	1e − 4	1e − 3	0.78
Shape index	−0.26	0.12	−0.46	−0.06	0.94	−0.39	0.13	−0.61	−0.17	0.92
Log(stand area)	0.07	0.03	0.02	0.12	0.94	0.06	0.03	7e − 4	0.11	0.92
(% area treated)^{2c}	−4.77	2.11	−8.23	−1.31	0.94	na	na	na	na	na
Canopy closure	−0.02	0.01	−0.03	−0.01	0.95	0.01	0.01	1e − 3	0.02	0.79
Precipitation	−0.02	0.01	−0.03	2e − 3	0.63	na	na	na	na	na
Yrs since treatment	0.05	0.03	3e − 3	0.09	0.73	na	na	na	na	na
Cattle	na	na	na	na	na	−0.28	0.08	−0.41	−0.14	0.98

[a] $n_{\mathrm{spring}} = 131$, $n_{\mathrm{summer}} = 133$, R^2_{adj} for the best model in spring = 0.24, R^2_{adj} for the best model in summer = 0.50; na = not applicable.

[b] Variables in the model set for only one season are denoted by an na (see text for a description of preliminary variable reduction).

[c] (% area treated)^2 = the square of the proportion of treated habitat within a 2,000-m buffer around each stand.

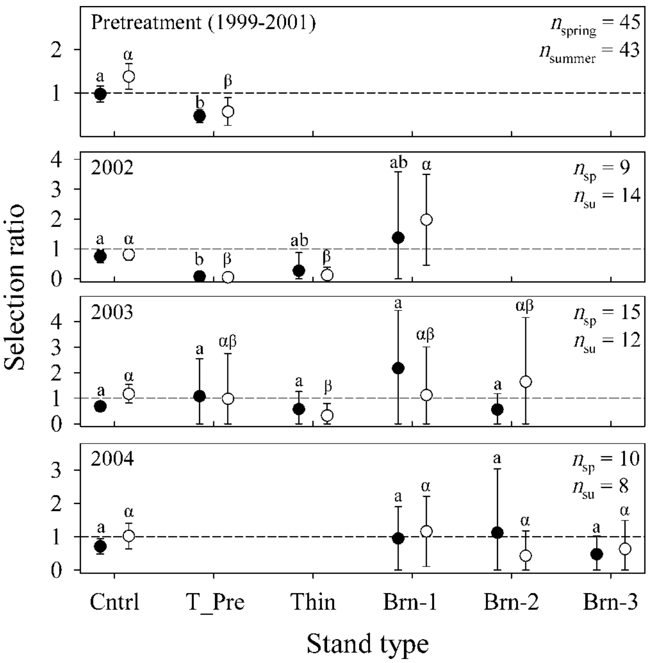

Figure 3. Population average selection ratios and 90% simultaneous confidence intervals for mule deer at the Starkey Experimental Forest and Range, Oregon, USA, during spring (1 Apr–14 Jun; closed circles) and summer (15 Jun–31 Aug; open circles) 1999–2004. Selection ratios reflect the influence of different forest stand types in determining where home ranges were established within the study area (second-order selection). Unshared letters among selection ratios within years and seasons (Latin for spring ratios, Greek for summer ratios) indicate a significant difference between means. We truncated impossible negative confidence limits at zero. Stand type abbreviations are defined as follows: Cntrl = control stands, T_Pre = pretreatment, Thin = thinned, and Brn-1, Brn-2, and Brn-3 = 1-, 2-, and 3-year-old burn, respectively.

relationship between home range size and measures of habitat heterogeneity in mule deer increased with increasing scale. The largest spatial scale Kie et al. (2002) considered was notably larger than home ranges of most mule deer, indicating that mule deer assessed areas well outside their home ranges in making decisions about where to establish home ranges (Kie et al. 2002). Similarly, elk at Starkey may have had close access to burned stands throughout their home ranges once those stands were selected at the larger scale, thereby eliminating the need to use burned stands in greater proportion than their availability while foraging within home ranges; this is consistent with the suggestion of Boyce (2006) that landscape patterns affect habitat selection primarily through their influence on establishment of home ranges.

Our hypothesis that elk would respond positively to fuels reduction primarily in spring was supported. At the larger spatial scale, elk selected burned stands and avoided control stands in spring of nearly all posttreatment years, but the opposite was true during summer. We hypothesize that this effect resulted from a combination of seasonal changes in phenology of forage species and presence of cattle at Starkey during summer. Average summer temperatures at Starkey are substantially higher than temperatures in spring (Stewart et al. 2002). Consequently, in areas with relatively open canopy cover most grass species and many forbs have cured or senesced by about mid-July as a result of increased exposure to direct sunlight. Conversely, in areas with denser canopy cover those species often persist for several weeks longer. As a result, control stands might actually provide better foraging opportunities than burned stands during hotter summer months. This hypothesis is supported by selection ratios for control stands in summer being consistently higher than selection ratios for those stands in

Table 3. Model-averaged parameter estimates, standard errors, 90% confidence intervals, and Akaike importance weights for general linear models describing the relationship between second-order population average selection ratios for mule deer in spring (1 Apr–14 Jun) and summer (15 Jun–31 Aug) and 15 variables associated with 26 forest stands treated with mechanical thinning and prescribed fire at the Starkey Experimental Forest and Range, Oregon, USA, 1999–2006.[a]

	Spring					Summer				
			90% CI					90% CI		
Parameter[b]	Estimate	SE	Lower	Upper	Importance wt	Estimate	SE	Lower	Upper	Importance wt
Intercept	−50.32	46.27	−126.20	25.57	na	9.76	1.44	7.40	12.11	na
Elevation	−4e − 3	1e − 3	−0.01	−2e − 3	0.87	−0.01	1e − 3	−0.01	−5e − 3	0.96
Convexity	0.11	0.09	−0.03	0.25	0.87	na	na	na	na	na
Sine of aspect	na	na	na	na	na	0.22	0.24	−0.17	0.61	0.96
Cosine of aspect	0.03	0.14	−0.19	0.26	0.87	na	na	na	na	na
Dist_open	−4e − 4	2e − 4	−8e − 4	−1e − 4	0.60	0.00	2e − 4	−6e − 4	−1e − 5	0.44
Dist_restricted	−3e − 4	1e − 4	−5e − 4	−3e − 5	0.60	−3e − 4	2e − 4	−5e − 4	7e − 6	0.44
Dist_closed	−6e − 4	3e − 4	−1e − 3	−1e − 4	0.60	na	na	na	na	na
Dist_water	2e − 4	2e − 4	−1e − 4	6e − 4	0.33	na	na	na	na	na
Shape index	0.02	0.03	−0.03	0.07	0.10	na	na	na	na	na
Log(stand area)	−1e − 3	0.01	−0.01	0.01	0.10	na	na	na	na	na
% area treated[c]	−0.08	0.09	−0.23	0.06	0.10	na	na	na	na	na
Canopy closure	na	na	na	na	na	−0.01	0.01	−0.02	2e − 3	0.32
Precipitation	0.02	0.01	−2e − 3	0.03	0.44	0.01	0.01	−0.01	0.03	0.31
Yrs since treatment	na	na	na	na	na	−0.01	0.02	−0.05	0.03	0.22

[a] $n_{\text{spring}} = 82$, $n_{\text{summer}} = 82$, R^2_{adj} for the best model in spring = 0.69, R^2_{adj} for the best model in summer = 0.41; na = not applicable.

[b] Variables in the model set for only one season are denoted by an na (see text for a description of preliminary variable reduction).

[c] % area treated = the proportion of treated habitat within a 500-m buffer around each stand.

spring. Results of Long et al. (2008) provide additional support for this hypothesis by demonstrating that percent cover of key forage species was higher in treatment than control stands during spring, whereas the opposite was true during summer. In addition, presence of cattle was negatively associated with use of treatment stands by elk in summer.

Although use of burned stands by elk was lower in summer than spring, summer selection ratios were more strongly related to environmental variables considered in our modeling analyses than were spring selection ratios, which may indicate that although they foraged less in burned stands during summer, elk discriminated more among those stands. Results of previous research on resource selection by elk at Starkey have been reported primarily for spring and, thus, further research will be necessary to determine whether elk generally exhibit stronger patterns of selection in summer than spring apart from effects of habitat manipulation. Regardless, the influence of specific variables on selection of treatment stands by elk in summer was consistent with our hypotheses and with results of past research at Starkey (Johnson et al. 2000, Rowland et al. 2000, Coe et al. 2001, Stewart et al. 2002). Elk avoided cattle and roads and used stands with steeper average slopes, greater topographical complexity, larger areas, and simpler shapes.

Fuels reduction at Starkey had little influence on short-term patterns of resource selection and space use by mule deer. We hypothesized that avoidance of treatment stands by mule deer would result from selection of those stands by elk, decreased availability of preferred forages, or both. If increased use of forest stands by elk following treatment was the primary cause of avoidance of those stands, then mule deer should have made greater use of treatment stands in summer than spring. This did not occur, however, and stand-specific selection ratios for elk were not a significant predictor of mule deer selection ratios at any scale or season. Decreased availability of preferred forages also may have caused mule deer to avoid treatment stands, because Long et al. (2008) demonstrated decreased abundance of woody browse following fuels reduction. If this were the case, however, use of pretreatment stands should have been consistently greater than use of treatment stands. Once again though, our results were not consistent with this prediction, indicating that foraging by mule deer was not greatly affected by the fuels reduction program at Starkey.

Our hypothesis that use of control stands by mule deer would be consistently greater than use of treatment stands was supported only during summer. During spring, use of control stands by mule deer rarely differed from use of treatment stands at either spatial scale. In summer, however, selection ratios for control stands increased and often were higher than selection ratios for treatment stands. Our results, combined with those of Long et al. (2008), support the hypothesis that control stands might provide better foraging opportunities than burned stands during hotter summer months as a result of rapid senescence of understory vegetation in areas with open canopy cover.

Modeling results for mule deer were consistent with our hypotheses, although not all variables predicted to influence use of treatment stands by mule deer were statistically significant. Treatment stands generally were avoided by mule deer across scales and seasons, however, which likely influenced our models. Nevertheless, mule deer made greater use of treatment stands located at low elevations near roads in both spring and summer. Because habitat manipulation at Starkey did not elicit a significant response in foraging by mule deer, these results likely reflect general patterns of habitat selection, and they are consistent with results of past research on mule deer at Starkey (Johnson et al. 2000). Unlike elk, mule deer did not appear to benefit from the fuels reduction program.

MANAGEMENT IMPLICATIONS

Large-scale habitat manipulations are being conducted with increasing frequency in western forests, often in an attempt to reduce fuel loadings and, therefore, risk of high-severity wildfires. Understanding ecological consequences of fuels reduction is critical for sound management of wildlife habitat in forest ecosystems. Prescribed fire in particular often is assumed to benefit large herbivores. In areas with seasonal climatic patterns and vegetation associations similar to those at Starkey, maintaining a mixture of burned and unburned (e.g., late successional) forest habitat might provide the best long-term foraging opportunities for large herbivores as a result of rapidly declining forage abundance in burned stands between spring and summer. Seasonal differences in energetic requirements, however, also should be considered. For example, spring often represents a critical period for both elk and mule deer because of the need to recover from the physiological stresses of winter and meet energetic demands of reproduction (Johnson et al. 2000, Cook 2002). As a result, the positive response of elk to prescribed fire that we documented in spring might be more energetically significant than the apparent avoidance of treatment stands during summer. In addition, presence of cattle might substantially reduce benefits of prescribed fire to elk, because elk often demonstrate strong avoidance of cattle, which would be particularly pronounced if cattle were attracted to treated areas, a question not addressed in our study (Coe et al. 2001, Stewart et al. 2002). Finally, in systems similar to Starkey, habitat manipulation via prescribed fire might be more beneficial to elk than mule deer, which is an important consideration for managers, because mule deer are declining throughout much of their range whereas elk populations are stable or increasing. If improving habitat for elk is the primary goal, our results indicate that within ranges we considered, larger burns located far from roads might provide the greatest benefit to elk.

ACKNOWLEDGMENTS

Our research was supported by the Joint Fire Science Program, the Rocky Mountain Elk Foundation, and the United States Department of Agriculture Forest Service Pacific Northwest Research Station. We thank M. Vavra for facilitating funding and assisting with project logistics, and we appreciated the assistance of Starkey Project personnel, including B. Dick, R. Kennedy, J. Nothwang, and M. Wisdom. We also thank R. Bowyer, E. Garton, P. Morgan, A. Alldredge, and 2 anonymous reviewers for helpful comments on earlier drafts of this manuscript; N. Cimon, C. Borum, and J. Boyd for database support; and K. Long for assistance with data entry and preparation.

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Associate Editor: Euler.