

SEX-SPECIFIC RESPONSES OF NORTH AMERICAN ELK TO HABITAT MANIPULATION

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Female and male cervids often use different habitats, and patterns of habitat selection and space use by the sexes may be influenced in part by selection of different forage resources. We tested the hypothesis that female and male ruminants select habitats that differ with respect to quality and abundance of forage by evaluating sex-specific responses of North American elk (*Cervus elaphus*), to an experimental fuels-reduction program at the Starkey Experimental Forest and Range (Starkey) in northeastern Oregon. From 2001 to 2003, 26 stands of true fir (*Abies*) and Douglas-fir (*Pseudotsuga menziesii*) were mechanically thinned and burned, whereas 27 similar stands were left untreated to serve as controls. We used measured differences in forage quality and quantity to predict sex-specific responses to this habitat manipulation. We compared seasonal patterns of habitat selection between the sexes using locations from 48 female and 14 male elk collected during daily periods of peak foraging activity during spring and summer of 2005 and 2006. During spring, females selected 4-year-old burns and used 2- and 3-year-old burns in proportion to their availability, whereas males avoided all fire-treated stands. In addition, control stands were avoided by females but selected by males during spring. During summer, control stands were selected and treatment stands either were avoided or used in proportion to their availability by the sexes. Use of treated stands by female and male elk was influenced by different environmental variables across seasons, but mean overlap of utilization distributions between the sexes was higher in summer than spring. These results indicate that although fuels-reduction treatments at Starkey may have increased foraging opportunities for female elk in spring, those treatments likely were of little benefit to male elk.

Key words: *Cervus elaphus*, habitat manipulation, mechanical thinning, prescribed fire, sexual segregation, utilization distribution

Patterns of habitat selection and space use by female and male cervids often differ throughout much of the year (e.g., Apollonio et al. 2005; Bowyer 1984; Bowyer et al. 2001; Kie and Bowyer 1999; Weckerly et al. 2001). Although a number of broad hypotheses have been forwarded to explain this widespread phenomenon (Barboza and Bowyer 2000; Bleich et al. 1997; Bowyer 2004; Ciuti et al. 2004; Main et al. 1996; Ruckstuhl 1998; Ruckstuhl and Neuhaus 2005; Weckerly 2001), considerable debate exists regarding the ultimate mechanisms underlying spatial segregation of the sexes (Bowyer 2004; Main 2008; Ruckstuhl and Neuhaus 2002). One hypothesis that focuses on forage selection is the

gastrocentric model, which predicts that female and male ruminants will forage differently as a result of sex-specific differences in metabolic requirements, minimal food quality, and digestive retention as they relate to the disparate life-history characteristics of the sexes (Barboza and Bowyer 2000, 2001). Male cervids have larger ruminal volumes than females, which prolongs retention of digesta in the rumen and allows males to minimize their need for dietary protein by urea recycling through ruminal microbes (Barboza and Bowyer 2000). The gastrocentric model predicts that male cervids should consume larger quantities of lower-quality forage than females. Assuming that this type of forage is sufficiently abundant, long retention times of digesta in the rumen combined with acclimation of ruminal microbes to high-fiber diets would cause males to benefit little from switching to very high-quality forages because doing so would reduce efficiency of fiber digestion and urea recycling, and males would risk malabsorption and bloat (Barboza and Bowyer 2000). In contrast, female cervids have smaller ruminal capacities

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and faster passage rates. In addition, reproductive females in particular have higher mass-specific energy and protein requirements as well as increased postnatal development to accommodate demands of late gestation and lactation (Blanchard 2005; Jenks et al. 1994). Consequently, the gastrocentric model predicts that females are probably unable to efficiently use highly fibrous forages of low quality, and therefore should consume lower quantities of higher-quality forage than males.

Given the many complexities associated with the gastrocentric hypothesis, it was not possible to provide a rigorous test of that hypothesis in this study. Instead, we tested the hypothesis that female and male ruminants select habitats that differ with respect to quality and abundance of forage, a test that represents an important step in a more global evaluation of the gastrocentric model. One powerful approach to testing that hypothesis is to evaluate sex-specific responses of cervids to experimental habitat manipulation (Bowyer 2004). However, few studies have been designed to quantify effects of habitat manipulation on female versus male cervids. Two notable exceptions are studies by Bowyer et al. (2001), who reported that mechanical crushing of felleaf willow (*Salix alaxensis*) benefited male but not female Alaskan moose (*Alces alces gigas*), and Stewart et al. (2003), who reported differential use of mechanically or chemically treated plots by sexes of white-tailed deer (*Odocoileus virginianus*).

Large-scale manipulation of habitat in the form of mechanical thinning and prescribed fire is becoming increasingly common in many forests of western North America. Although the primary purpose of those activities typically is fuels reduction or restoration of historical disturbance regimes in fire-adapted forest ecosystems (Covington et al. 1997; Dodge 1972; Tiedemann et al. 2000), fuels-reduction activities provide a unique opportunity to study selection of foraging habitat by female and male herbivores. Habitat manipulation via mechanical thinning or prescribed fire often is assumed to benefit large herbivores. Nevertheless, few studies have considered the potential for fuels reduction to differentially affect the sexes.

We evaluated spatial response of female and male North American elk (*Cervus elaphus*) to an experimental fuels-reduction program, which included replicated treatment stands that were mechanically thinned and burned, and control stands that were unaltered. In addition, Long et al. (2008b) conducted a detailed field study shortly after the fuels-reduction program was completed to evaluate effects of fuels reduction on quantity (percent cover) and quality (percent in vitro dry-matter digestibility and percent nitrogen) of forage for elk during spring and summer. Key results of that study relevant to our investigation of variation in habitat selection between the sexes included that percent cover of 8 key 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 during spring, but slightly lower in treatment than control stands during summer; although fuels reduction increased abundance of some herbaceous forage species during spring, abundance of both palatable and

unpalatable shrubs was significantly reduced by fuels-reduction treatments; nutritional quality of herbaceous forage species in treatment stands did not change significantly in the 1st few years after treatment, but by the 5th year after treatment, quality had increased above maximum mean values observed in control stands during both seasons; and nutritional quality of all forage species was significantly lower during summer than spring.

We hypothesized that female and male elk would respond differently to habitat manipulation during peak foraging periods as a result of the measured effects of habitat manipulation on forage resources. More specifically, we predicted the following sex-specific responses of elk to fuels reduction based on results of Long et al. (2008b), and on previous observations that male cervids often include a larger proportion of woody browse in their diets than females (Beier 1987; Staines et al. 1982): as a result of increased quality of herbaceous forage after fuels reduction, as well as decreased abundance of woody browse, female elk will select treatment stands and avoid control stands during peak foraging periods, whereas male elk will select control stands and avoid treatment stands; positive response of female elk to fuels reduction will be strongest in spring as a result of rapid senescence of preferred forage species during summer; the degree of spatial overlap between females and males during peak foraging periods will be greater during summer than spring, because sex-specific patterns of habitat selection while foraging will be more similar in summer as females begin to increase use of control stands where males are predicted to forage throughout the year; and the relative influence of environmental variables related to topography, proximity to roads, and patch characteristics on use of treated stands by elk will differ between the sexes for a diversity of potential reasons, but will be more similar during summer than spring as females begin to increase use of control stands during summer. We compared use of burned and unburned forest stands by elk during peak foraging periods and modeled sex-specific patterns of stand selection and spatial distribution to evaluate effects of large-scale habitat manipulation on selection of foraging habitat by adult female and male elk.

MATERIALS AND METHODS

Study area.—We conducted research approximately 35 km southwest of La Grande, Oregon, at the Starkey Experimental Forest and Range (hereafter Starkey; 45°13'N, 118°31'W) during spring (1 April–14 June) and summer (15 June–31 August) 2005 and 2006. Starkey is managed by the United States Forest Service and is enclosed by a 2.4-m-high fence that prevents immigration or emigration of large herbivores (Bryant et al. 1993; Rowland et al. 1997). This fence also divides Starkey into 5 distinct research areas. We conducted research in Main Study Area, which encompasses 78 km². Elevations at Starkey range from 1,120 to 1,500 m, and the site supports a mosaic of coniferous forests, shrublands, and grasslands (Johnson et al. 2000; Stewart et al. 2002). Cattle were present in Main Study Area each summer and were

moved in a deferred-rotation system among 3 pastures separated by barbed-wire fence and an additional pasture outside the study area. The order of the cattle rotation was reversed each year. Skovlin (1991), Wisdom et al. (1993), and Rowland et al. (1997, 1998) provide detailed descriptions of Starkey.

A spruce budworm (*Choristoneura occidentalis*), outbreak in the late 1980s led to substantial mortality of true fir (*Abies*) and Douglas-fir (*Pseudotsuga menziesii*), throughout Starkey (Rowland et al. 1997), which in turn resulted in high loads of dead and standing fuels and increased likelihood of high-severity wildfire. As a result, the United States Forest Service initiated a fuels-reduction program at Starkey in 2001. Twenty-six stands (roughly 9% of the study area) were selected for treatment with mechanical thinning followed by prescribed fire over a 3-year period (2001-2003), whereas 27 similar stands were left untreated to serve as controls. Although treatments were assigned randomly to stands to the greatest extent possible within constraints imposed by topography and stand size, control stands were, on average, larger than treatment stands (mean treatment stand area = 26 ha, range = 3-214 ha; mean control stand area = 55 ha, range = 4-168 ha). However, ranges of average slope, aspect, elevation, and distances to roads were comparable between stand types. Treatment stands were mechanically thinned between May and October and were treated with prescribed fire during September or October of either the same year ($n = 13$) or the following year ($n = 13$). From 90% to 100% of the area of each treatment stand was burned in a low- to moderate-intensity ground fire; all treatment stands were broadcast burned, and limited burning of slash piles was conducted in some stands (Walstad et al. 1990). Before fuels reduction, overstory conditions in treatment stands were similar to those in control stands, but after treatment, average tree densities were roughly 2,000 trees/ha lower in treatment than control stands (Long et al. 2008b). Nearly 98% of trees in control stands were <23 cm in diameter at breast height, and 54% were <135 cm tall (Long et al. 2008b). Ten stands initially were treated in 2001 (6 thinned and 4 thinned and burned), 11 in 2002 (7 thinned and 4 thinned and burned), and 5 in 2003 (all thinned and burned; Fig. 1).

Telemetry.—During our study, adult (>2 years old) elk were baited onto a winter feeding pasture with an adjacent handling facility beginning in mid-December, and thereafter were provided a maintenance diet of alfalfa hay until the following spring (Rowland et al. 1997). In early spring (March-April) of each year, elk were herded into a squeeze chute for handling and a subset of animals was fitted with LORAN-C radiocollars (Rowland et al. 1997) before being released back into Main Study Area with the rest of the herd. Radiocollars were placed on 18 females and 5 males in spring 2005, and 30 females and 9 males in spring 2006. Collars were placed on a unique set of individuals in each year. All animal handling procedures were conducted in accordance with protocols approved by an established Institutional Animal Care and Use Committee (Wisdom et al. 1993) and were in compliance with Animal Care and Use Committee guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

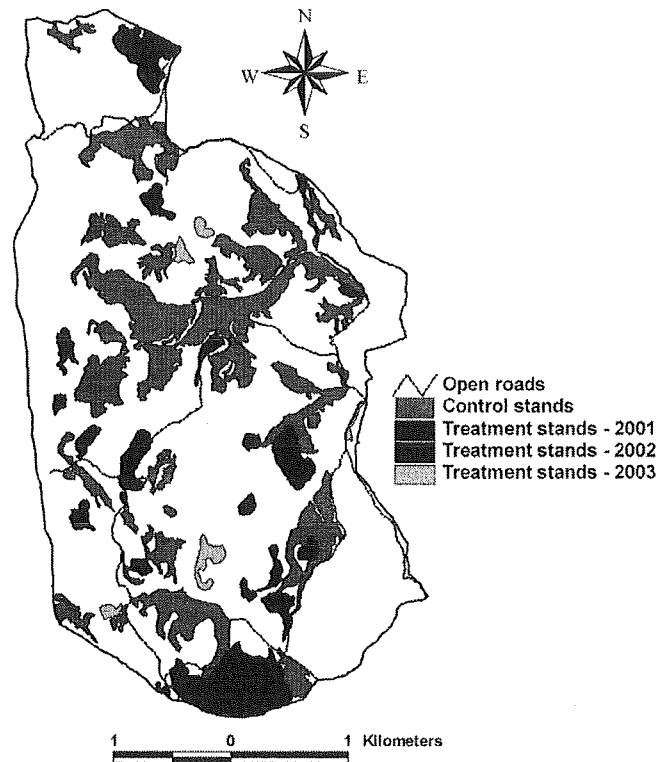


FIG. 1.—Locations of 26 forest stands treated with mechanical thinning and prescribed fire from 2001 to 2003 and 27 untreated control stands at the Starkey Experimental Forest and Range, Oregon. Years associated with treatment stands indicate year of initial treatment (either thinning or thinning and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

Location data were collected using a LORAN-C automated telemetry system (Findholt et al. 1996; Rowland et al. 1997). Mean positional error was $53 \text{ m} \pm 5.9 \text{ SE}$ (Findholt et al. 1996) and we typically obtained a location for each elk every 1-5 h. We only included location data in our analyses that were collected within 1 h of sunrise or sunset because those times represent peak foraging periods for elk (Johnson et al. 2000). In addition, we only included animals with ≥ 30 locations per season, although the mean number of locations per individual in each season was $194 \pm 82 \text{ SD}$. The mid-June cutoff for differentiating between seasons coincided with the introduction of cattle to Main Study Area each year. Finally, to ensure independence of sampling units in subsequent statistical analyses, we evaluated patterns of herd membership and, therefore, spatial independence of elk in our data set using association matrices (Weber et al. 2001).

Selection ratios and volume of intersection.—To test our first 2 predictions, we calculated stand-specific selection ratios (use/availability-Manly et al. 2002) for individual elk in each season. We quantified use of treatment and control stands by calculating 95% fixed-kernel utilization distributions (UDs) in the program Animal Space Use 1.0 Beta (available at http://www.cnr.uidaho.edu/population_ecology/animal_space_use.htm). We used likelihood cross-validation to select the smoothing parameter for each UD (Horne and Garton 2006) and corrected UD

estimates for spatial bias in the rate at which telemetry locations were obtained across our study area (Home et al. 2007; Johnson et al. 1998). We clipped UD at the Starkey fence boundary, although on average <3.5% of the volume of each UD occurred outside the Starkey boundary. We defined use offorest stands as the proportion of the volume of each elk's UD that overlapped each of the treatment and control stands. The volume of a UD provides a spatially explicit measure of probability of use (Kemohan et al. 2001; Marzluff et al. 2004; Millspaugh et al. 2006), and selection ratios based on the UD (i.e., relative concentration of use-Neatherlin, and Marzluff 2004) improve 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 (Aebischer et al. 1993; Thomas and Taylor 1990), and quantifying use as a continuous random variable (Millspaugh et al. 2006). We defined availability as the proportion of Main Study Area occupied by each treatment and control stand. Consequently, our selection ratios were of the 2nd order (Johnson 1980), and reflected the influence of each stand in determining where elk established home ranges (UDs) within the study area.

We placed each stand into 1 of 5 categories: control, 2-year-old burn, 3-year-old burn, 4-year-old burn, or 5-year-old burn. Although we pooled data across years, 2-year-old burns were only present on the landscape in 2005 and 5-year-old burns were only present in 2006. Therefore, average selection ratios for the population were calculated for those stand types using radiocollared elk from 1 year only. We calculated population average selection ratios for each stand type, sex, and season using the following equation (Manly et al. 2002):

$$\hat{w}_i' = \sum_{j=1}^n \hat{w}_{ij} / n,$$

where w_i' = the average selection ratio for the population, w_{ij} = the selection ratio for the j th animal in the i th combination of stand type, sex, and season, and n = the number of animals sampled in the i th combination of stand type, sex, and season. Values > 1 indicated selection (use > availability), whereas values < 1 indicated avoidance (use < availability). We also used 90% simultaneous Bonferroni confidence intervals around mean selection ratios to evaluate the degree of selection or avoidance of each stand type and around differences between means to assess the significance of pairwise differences in selection ratios (Manly et al. 2002; Neter et al. 1996) for each sex in each season. The difference between 2 average selection ratios within a season was considered statistically significant at the $\alpha = 0.10$ level if the simultaneous confidence interval around the difference did not contain 0.

To test our 3rd prediction, we evaluated similarity in seasonal patterns of space use among individual elk within and between sexes using the volume of intersection (VI) index (Seidel 1992). This index measures the degree of overlap in volume between 2 UD and ranges from 0 to 1, with 0 indicating no overlap and 1 indicating complete overlap (Millspaugh et al. 2000; Seidel 1992). We calculated all pairwise VI index values for elk based on 99% UD in each

season using Animal Space Use 1.0 Beta (VI index analyses using this software automatically utilize the 99% UD). We then divided those values into 3 groups (female-female, male-male, and female-male) and calculated means and 90% confidence intervals for each group and season. We used analysis of variance to test for differences in mean VI index values among the 3 groups in each season. We compared least-squares means in those analyses to account for differential sample sizes among groups. All statistical analyses were performed using Statistical Analysis Systems software (SAS; PROC GLM; SAS Institute Inc. 2002).

Modeling.—To test our final prediction, we evaluated the influence of several environmental variables on use of treatment stands by female and male elk using multiple regression (Neter et al. 1996). We constructed a separate model for each sex and season using average selection ratios (arcsine square-root transformed) as the response variable. The following predictor variables were chosen based on demonstrated potential to influence patterns of habitat selection and space use by elk at Starkey (Ager et al. 2003; Johnson et al. 2000; Rowland et al. 1998; Stewart et al. 2002): slope; convexity (a measure of topographical complexity—Johnson et al. 2000); aspect (transformed with sine and cosine functions to measure east-west and north-south aspects, respectively); distance to open, restricted, and closed roads; distance to permanent water; elevation; stand area; shape index (a measure of shape complexity); canopy closure in a 200-m buffer around each stand; the proportion of a 500-m, 1,000-m, and 2,000-m buffer around each stand consisting of treated habitat; years since burning; cattle presence or absence; and annual precipitation. For continuous variables, we used average values for each stand in our analyses. Additional details on derivation of predictor variables are given by Long et al. (2008a).

We used an information-theoretic approach to model selection (Burnham and Anderson 2002) and placed predictor variables for each combination of sex and season into 1 of 8 effect categories based on their potential to influence space use by elk in similar ways (Long et al. 2008a). For example, slope, convexity, aspect, and elevation all represented topographical effects. Effect categories were topographical, proximity to roads, proximity to permanent water, patch metrics, canopy cover, annual precipitation, time since treatment, and presence or absence of cattle. The number of effect categories considered in each model set after an initial variable-reduction procedure (Long et al. 2008a) ranged from 4 to 6, with 1–3 variables in each category. Before model selection we used the global model for each sex and season to evaluate residual plots for adherence to assumptions of normality and homogeneity of variance (Neter et al. 1996). Both assumptions were met in each case.

We modeled all possible combinations of effect categories for each sex and season, and the total number of models considered in each set ranged from 15 to 63. For each model we recorded R^2_{adj} (to examine model fit), Akaike information criterion adjusted for small sample size (AICc), $\Delta AICc$, and the Akaike weight (w_i —Burnham and Anderson 2002). We identified the 95% confidence set of models from each complete set using w_i values and used models in the confidence

set to calculate weighted model-averaged parameter estimates and unconditional standard errors (*SEs*) for each predictor variable (Burnham and Anderson 2002). We deemed model-averaged parameter estimates to differ significantly from 0 if the 90% confidence interval based on the associated unconditional *SE* did not contain 0. Finally, we calculated Akaike importance weights for each parameter using models in the confidence set.

RESULTS

Use of treatment stands by male elk during peak foraging periods in spring consistently was lower than use of those stands by female elk relative to availability (Fig. 2). Differences in stand use between the sexes were most pronounced for 2- to 4-year-old burns (Fig. 2). Female elk used 2- and 3-year-old burns proportional to their availability, selected 4-year-old burns, and avoided 5-year-old burns, whereas male elk avoided all categories of treatment stands (Fig. 2). Conversely, female elk avoided control stands in spring, whereas male elk selected those stands (Fig. 2). The only statistically significant difference among selection ratios for female elk during spring was between control stands and 4-year-old burns, and in that instance the treatment stands were used significantly more than the control stands relative to their respective availabilities (Fig. 2). In contrast, differences in selection ratios between control stands and both 2- and 4-year-old burns were statistically significant for male elk in spring, and in both instances the control stands were used significantly more than the treatment stands relative to their availabilities (Fig. 2).

The relative influence of environmental variables on use of foraging habitat by elk during spring also differed between the sexes. None of the variables considered in the spring model sets were strongly related to selection of treatment stands by either sex, and the 2 best models accounted for only 37% and 32% of the variance in spring selection ratios for females and males, respectively (Table 1). Nevertheless, model-averaged parameter estimates for at least 1 variable in both models differed significantly from 0. Female elk selected older burns with westerly aspects, and selection ratios decreased with tree canopy closure in a 200-m buffer around each stand (Table 1). Years since treatment was the most important of those effects based on Akaike importance weights, followed by aspect and canopy closure. In contrast, only 1 of those 3 variables (canopy closure) entered the final spring model set for male elk, and the coefficient for that variable did not differ significantly from 0 (Table 1). The only variable in the spring model for males with a coefficient that differed significantly from 0 was elevation, which was negatively related to use of treatment stands (Table 1). Similar to previous results, the most important variable in the spring model for males did not enter the final model set for females.

Patterns of stand use generally were more similar between the sexes during summer than spring, and the direction (+ or -) of differences in selection ratios between females and males was less consistent during summer than spring (Fig. 2). Female elk either avoided treatment stands (3- and 4-year-old

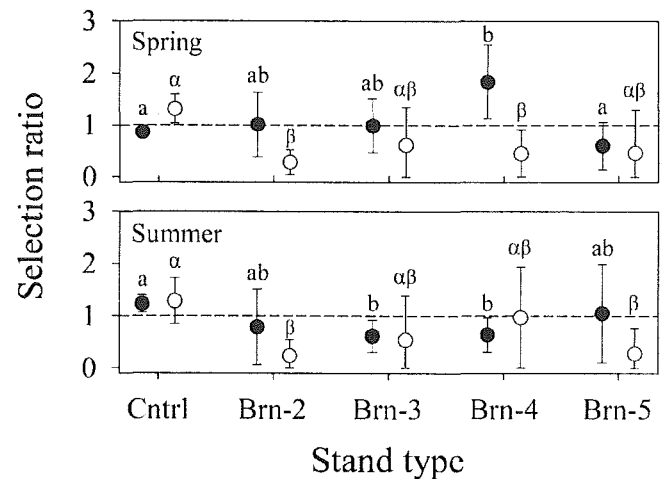


FIG. 2.—A verage selection ratios and 90% simultaneous confidence intervals for female (closed circles; $n_{\text{spring}} = 46$, $n_{\text{summer}} = 38$) and male (open circles; $n_{\text{spring}} = 14$, $n_{\text{summer}} = 8$) elk (*Cervus elaphus*) at the Starkey Experimental Forest and Range, Oregon, during spring (1 April–14 June) and summer (15 June–31 August) 2005 and 2006. Selection ratios reflect the influence of different forest stand types in determining where home ranges were established within the study area (2nd-order selection). Values > 1 indicate selection (use $>$ availability), whereas values < 1 indicate avoidance (use $<$ availability). Unshared letters among selection ratios within seasons (Latin for female elk, Greek for male elk) indicate a significant difference between means. Impossible negative confidence limits were truncated at 0. Stand type abbreviations are defined as follows: Cntrl = control stands, Brn-2 = 2-year-old burn, Brn-3 = 3-year-old burn, Brn-4 = 4-year-old burn, and Brn-5 = 5-year-old burn.

burns) or used them proportional to their availability (2- and 5-year-old burns) during peak foraging periods in summer (Fig. 2). The same general pattern was evident for males, but males avoided 2- and 5-year-old burns and used 3- and 4-year-old burns proportional to their availability (Fig. 2). Mean selection ratios for control stands were nearly equal between the sexes and indicated at least mild selection of those stands by both sexes during summer. Females used control stands significantly more than 3- and 4-year-old burns relative to their availabilities in summer, which was opposite to the pattern of selection by females in spring (Fig. 2). However, males used control stands significantly more than 2- and 5-year-old burns in summer relative to their availabilities, which was similar to patterns of stand use by males during spring (Fig. 2).

Summer models of treatment stand selection by elk differed substantially from spring models for both sexes. Similar to spring, however, modeling results for summer indicated that the relative influence of environmental variables included in our study on use of foraging habitat by elk differed markedly between the sexes. Use of treatment stands by female elk during summer was strongly related to topography, proximity to roads, stand shape, canopy cover, and precipitation, and the best model in the model set accounted for 72% of the variance in summer selection ratios (Table 2). Selection of foraging habitat increased with convexity (topographical complexity),

TABLE 1.-Model-averaged parameter estimates, standard errors (SEs), 90% confidence intervals (90% CIs), and Akaike importance weights for multiple regression models describing the relationship between average selection ratios for female and male elk (*Cervus elaphus*), in spring (1 April-14 June) and 11 variables associated with 26 forest stands treated with mechanical thinning and prescribed fire at the Starkey Experimental Forest and Range, Oregon, 2005-2006.^a

Parameter ^b	Females					Males				
	Estimate	SE	90% CI		Importance weight	Estimate	SE	90% CI		Importance weight
			Lower	Upper				Lower	Upper	
Intercept	4.42	3.74	-1.71	10.54	n/a	-62.37	38.88	-126.14	1.39	n/a
Elevation	n/a	n/a	n/a	n/a	n/a	-4×10^{-3}	1×10^{-3}	-6×10^{-3}	-2×10^{-3}	0.95
Convexity	n/a	n/a	n/a	n/a	n/a	0.13	0.08	-2×10^{-3}	0.25	0.95
Sine of aspect	0.32	0.13	0.10	0.54	0.88	n/a	n/a	n/a	n/a	n/a
Dist_open	1×10^{-4}	9×10^{-5}	-2×10^{-5}	3×10^{-4}	0.55	-1×10^{-4}	1×10^{-4}	-3×10^{-4}	5×10^{-5}	0.42
Dist_restricted	2×10^{-4}	1×10^{-4}	-3×10^{-5}	4×10^{-4}	0.55	n/a	n/a	n/a	n/a	n/a
Dist_water	3×10^{-4}	3×10^{-4}	-1×10^{-4}	7×10^{-4}	0.42	5×10^{-4}	4×10^{-4}	-1×10^{-4}	1×10^{-3}	0.55
Shape index	n/a	n/a	n/a	n/a	n/a	0.12	0.15	-0.13	0.37	0.58
% area treated	n/a	n/a	n/a	n/a	n/a	1.47	0.15	-0.30	3.25	0.58
Canopy closure	-0.01	0.01	-0.03	-2×10^{-3}	0.74	1×10^{-3}	1.08	-4×10^{-3}	6×10^{-3}	0.21
Precipitation	-0.33	0.21	-0.68	0.02	0.64	0.34	0.22	-0.01	0.70	0.66
Yrs since treatment	0.23	0.08	0.09	0.37	0.95	n/a	n/a	n/a	n/a	n/a

^a $n_{\text{females}} = 46$; $n_{\text{males}} = 14$; R_{adj}^2 for the best model for females = 0.37; R_{adj}^2 for the best model for males = 0.32. Variables in the model set for only 1 sex are denoted by n/a.
^b Dist_open = distance to open road; Dist_restricted = distance to restricted road; Dist_water = distance to permanent water; % area treated = the proportion of treated habitat within a 2,000-m buffer around each stand; Yrs since treatment = years since treatment.

distance to open roads, canopy closure in a 200-m buffer, and precipitation, and decreased with elevation and shape index (shape complexity; Table 2). Based on Akaike importance weights, each of those variables played a similarly important role in influencing use of treatment stands by female elk (Table 2). Of those 6 variables, however, only convexity and shape index entered the final model set for male elk, and only convexity had a significant (positive) coefficient (Table 2). Percent slope was the only other variable in the summer model for males with a coefficient that differed significantly from 0. Like convexity, the coefficient for percent slope was positive, indicating that male elk increased use of treatment stands

located in areas with relatively complex terrain and steep slopes. Similar to results for spring, though, those relationships were relatively weak for males, because the best model in the model set accounted for only 28% of the variance in summer selection ratios (Table 2).

Overlap in space use between sexes during peak foraging periods was higher in summer than spring (Fig. 3). However, spatial overlap of same-sex groups (female-female and male-male) also increased during summer (Fig. 3). In both seasons, spatial overlap was significantly higher among females than between females and males ($P \leq 0.0002$; Fig. 3). Mean overlap among males was intermediate between means for the other 2

TABLE 2.-Model-averaged parameter estimates, standard errors (SEs), 90% confidence intervals (90% CIs), and Akaike importance weights for multiple regression models describing the relationship between average selection ratios for female and male elk (*Cervus elaphus*) in summer (15 June-31 August) and 11 variables associated with 26 forest stands treated with mechanical thinning and prescribed fire at the Starkey Experimental Forest and Range, Oregon, 2005-2006.^a

Parameter ^b	Females					Males				
	Estimate	SE	90% CI		Importance weight	Estimate	SE	90% CI		Importance weight
			Lower	Upper				Lower	Upper	
Intercept	-68.46	27.21	-113.08	-23.83	n/a	-105.57	41.02	-172.86	-38.29	n/a
Elevation	-2×10^{-3}	7×10^{-4}	-4×10^{-3}	-1×10^{-3}	0.99	n/a	n/a	n/a	n/a	n/a
Convexity	0.14	0.05	0.06	0.23	0.99	0.21	0.08	0.08	0.34	0.99
% slope	n/a	n/a	n/a	n/a	n/a	0.03	0.02	0.01	0.06	0.99
Dist_open	6×10^{-4}	1×10^{-4}	4×10^{-4}	8×10^{-4}	0.99	n/a	n/a	n/a	n/a	n/a
Dist_restricted	n/a	n/a	n/a	n/a	n/a	2×10^{-4}	2×10^{-4}	-7×10^{-5}	6×10^{-4}	0.57
Dist_closed	n/a	n/a	n/a	n/a	n/a	3×10^{-4}	2×10^{-4}	-1×10^{-4}	7×10^{-4}	0.57
Shape index	-0.62	0.17	-0.90	-0.33	0.99	-0.16	0.15	-0.41	0.08	0.47
Stand area	n/a	n/a	n/a	n/a	n/a	1×10^{-3}	1×10^{-3}	-5×10^{-4}	3×10^{-3}	0.47
Canopy closure	0.02	0.01	0.01	0.03	0.87	n/a	n/a	n/a	n/a	n/a
Precipitation	0.21	0.06	0.12	0.30	0.99	n/a	n/a	n/a	n/a	n/a
Yrs since treatment	n/a	n/a	n/a	n/a	n/a	0.10	0.07	-0.02	0.21	0.58

^a $n_{\text{females}} = 38$; $n_{\text{males}} = 8$; R_{adj}^2 for the best model for females = 0.72; R_{adj}^2 for the best model for males = 0.28. Variables in the model set for only 1 sex are denoted by n/a.

^b Dist_open = distance to open road; Dist_restricted = distance to restricted road; Dist_closed = distance to closed road; Yrs since treatment = years since treatment.

groups during both seasons and did not differ significantly from means for those groups in either season ($P \geq 0.14$; Fig. 3).

DISCUSSION

Consistent with our predictions, foraging male elk avoided burned stands, which exhibited increased forage quality after treatment with prescribed fire (Long et al. 2008b). Many other authors have reported increased nutritive value of forage species after fire (Carlson et al. 1993; Cook 2002; Perryman et al. 2002; Schindler et al. 2004), and the gastrocentric model predicts that male cervids would benefit little from switching to high-quality forages because doing so would reduce efficiency of fiber digestion and urea recycling, and males would risk malabsorption and bloat (Barboza and Bowyer 2000). However, how much of an overall increase in forage quality would be necessary to reduce foraging opportunities for males is uncertain. Long et al. (2008b) documented 5-20% increases in digestibility and percent nitrogen of forbs known to be important to female elk at Starkey 5 years after fuels reduction. Although relatively little is known about diet composition of male elk at Starkey, quality of forage species commonly used by males also may have increased, potentially resulting in avoidance of burned habitat by males.

Changes in composition of understory vegetation after fuels reduction also may be related to avoidance of treatment stands by male elk. Although differences in diet composition between female and male elk at Starkey have not been quantified, other studies (Beier 1987; Staines et al. 1982) have documented that male cervids included a larger proportion of woody browse in their diets than females. Total shrub abundance at Starkey was significantly higher in control than treatment stands (mean percent cover of shrubs = 14.67 and 4.85 for control and treatment stands, respectively-Long et al. 2008b), and total abundance of forbs did not differ between stand types (mean percent cover of forbs = 14.03 and 12.41 for control and treatment stands, respectively-Long et al. 2008b). If male elk at Starkey rely heavily on either woody browse or herbaceous species that were not significantly affected by fuels reduction, then males would have little reason to forage in treatment stands regardless of changes in forage quality, and indeed, use of those stands by males might even decline as a result of reduced abundance of preferred forages.

Use of treatment stands by female and male elk was influenced by different variables in both seasons, and modeling results were more similar between the sexes in summer than spring. In addition, however, there were marked differences between the sexes in predictive power of spring versus summer models. For females, selection of treatment stands during summer was more strongly related to environmental variables than during spring, even though use of treatment stands by female elk was lower in summer than spring. Therefore, although use of treatment stands was lower in general during summer, female elk appeared to discriminate among those stands based on landscape characteristics (Long et al. 2008a). However, results for male elk were reversed. Use of treatment stands by males was only weakly related to environmental variables

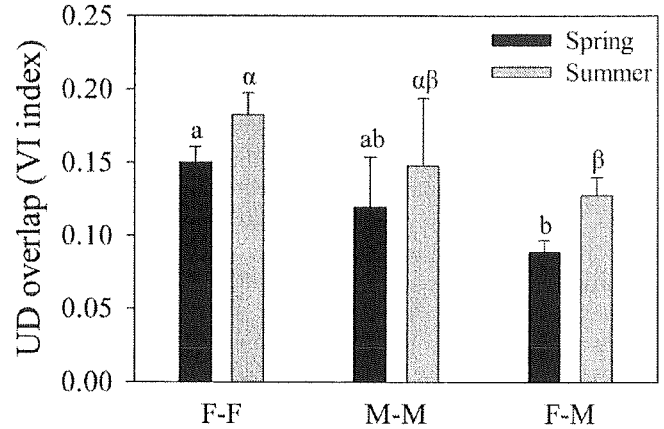


FIG. 3.—Mean volume of intersection (VI) index values and 90% confidence intervals within and between sexes of elk (*Cervus elaphus*, in spring (1 April–14 June) and summer (15 June–31 August) of 2005 and 2006 at the Starkey Experimental Forest and Range, Oregon. VI index values indicate the degree of overlap in the volumes of two 99% fixed-kernel utilization distributions (UDs) and range from 0 to 1, with 0 indicating no overlap and 1 indicating complete overlap. Means were calculated from all possible pairwise comparisons of UD within groups and seasons. Unshared letters among groups within each season (Latin for spring, Greek for summer) indicate a significant difference between means. Group abbreviations are as follows: F-F = female-female comparisons, M-M = male-male comparisons, and F-M = female-male comparisons.

(primarily topography) in both seasons, and predictive power of the best model in summer was lower than the best model for spring. These results indicate that, unlike females, male elk used treatment stands both rarely and relatively indiscriminately during foraging periods in both spring and summer.

We predicted that because the positive response of female elk to fuels reduction likely would occur primarily during spring, the degree of spatial overlap between females and males during peak foraging periods would be greater in summer than spring as females begin to increase use of control stands during summer. Our results are consistent with that prediction; mean overlap of UD between sexes was higher in summer than spring. In addition, however, spatial overlap of same-sex groups also increased during summer. We hypothesize that overlap of foraging habitat was higher in summer than spring across groups for the same reason that selection of treatment stands by female elk was more strongly related to specific environmental variables in summer than spring. Average summer temperatures at Starkey often are $\geq 10^{\circ}\text{C}$ higher than temperatures in spring (Stewart et al. 2002). As a result, most grass species and many forbs in foraging areas with relatively open canopy cover have cured or senesced by about mid-July as a result of increased exposure to direct sunlight. We hypothesize that this reduction in forage availability focuses foraging activities of elk at Starkey onto a smaller absolute area (or smaller number of patches) during summer, which in turn increases shared space use and UD overlap. In addition, although increased spatial overlap during summer was evident both within and between sexes and likely occurred before

habitat manipulation, fuels reduction may have intensified this effect by simultaneously increasing abundance of open-canopy foraging areas and decreasing the number of closed-canopy stands on the landscape. Examination of pretreatment data for female elk supports this hypothesis (Long et al. 2008a), and although no pretreatment data were available for males, perhaps an ecological consequence of fuels reduction at Starkey was increased spatial segregation of the sexes during spring and decreased segregation during summer.

Results of our study could reflect continued use of traditional feeding areas by elk after fuels reduction. Indeed, site fidelity has been demonstrated to influence habitat selection by cervids (Garrot et al. 1987; Kie and Bowyer 1999; Main and Coblentz 1996). Nevertheless, site fidelity among elk typically occurs at a relatively broad spatial scale (Craighead et al. 1973; Edge et al. 1985; Irwin and Peek 1983; Knight 1970), and we are unaware of any studies that have documented continued use of specific foraging locations by elk within their home ranges after substantial habitat disturbance. In addition, Long et al. (2008a) evaluated stand selection by female elk from 3 years before to 3 years after completion of the fuels-reduction program at Starkey. Results of that study indicated that female elk increased use of fir stands during spring after the application of prescribed fire (Long et al. 2008a). Although no pretreatment data were available for male elk, males are even less likely than females to show strong site fidelity (Main and Coblentz 1996), especially at small spatial scales.

Experimental research represents one of the most powerful tools in science for identifying causal relationships (Campbell 1957; Cook and Campbell 1979; Garton et al. 2005; Stouffer 1950). The fuels-reduction program at Starkey provided a unique opportunity to obtain a post hoc test of hypotheses related to sex-specific responses of elk to habitat manipulation over a relatively large geographic area. Results of our study indicate that habitat manipulation at Starkey influenced patterns of space use by female and male elk, and that fuels reduction may have affected the degree of sexual segregation of elk. Other studies have documented differential effects of habitat manipulation on female and male cervids (Bowyer et al. 2001; Stewart et al. 2003), and our results add support to the hypothesis that differential selection of foraging habitat by the sexes plays an important role in influencing sexual segregation in cervids. Our results also have important implications for forest and wildlife managers. Long et al. (2008a) concluded that, as a result of the interaction between fuels reduction and seasonal changes in plant phenology at Starkey, a mixture of burned and unburned forest habitat might provide better long-term foraging opportunities for female elk than burning a large proportion of a landscape. We support that conclusion, but add that such a strategy also may be important for minimizing negative impacts of fuels reduction on male elk. However, we note that this conclusion applies only to relatively short-term responses of elk to fuels reduction, because the oldest burns in our study were only 5 years old. As succession continues to progress in burned stands, responses of both sexes might change. For example, Peck and Peek (1991) reported that use of burned areas by elk in British Columbia, Canada, declined

10 years after burning. Similarly, as densities of shrubs and trees increase in burned stands, use of those stands by male elk also might increase.

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LITERATURE CITED

- AEBISCHER, P. A., ROBERTSON, AND R. E. KENWOOD. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74:1313-1325.
- AGER, A. A., B. K. JOHNSON, J. W. KERN, AND J. G. KIE. 2003. Daily and seasonal movements and habitat use by female Rocky Mountain elk and mule deer. *Journal of Mammalogy* 84:1076-1088.
- APOLLONIO, S., CIUTI, AND S. LUCCARINI. 2005. Long-term influence of human presence on spatial sexual segregation in fallow deer (*Dama dama*). *Journal of Mammalogy* 86:937-946.
- BARBOZAP, S., AND R. T. BOWYER. 2000. Sexual segregation in dimorphic deer: a new gastrocentric hypothesis. *Journal of Mammalogy* 81:473-489.
- BARBOZAP, S., AND R. T. BOWYER. 2001. Seasonality of sexual segregation in dimorphic deer: extending the gastrocentric model. *Alces* 37:275-292.
- BEIER, P. 1987. Sex differences in quality of white-tailed deer diets. *Journal of Mammalogy* 68:323-329.
- BLANCHARD, P. 2005. On lactation and rumination in bighorn ewes (*Ovis canadensis*). *Journal of Zoology (London)* 265:107-112.
- BLEICH, V. C., R. T. BOWYER, AND D. D. WEHAUSEN. 1997. Sexual segregation in mountain sheep: resources or predation? *Wildlife Monographs* 134:1-50.
- BOWYER, R. T. 1984. Sexual segregation in southern mule deer. *Journal of Mammalogy* 65:410-417.
- BOWYER, R. T. 2004. Sexual segregation in ruminants: definitions, hypotheses, and implications for conservation and management. *Journal of Mammalogy* 85:1039-1052.
- BOWYER, R. T., B. M. PIERCE, K. DUFFY, AND D. A. HAGGSTROM. 2001. Sexual segregation in moose: effects of habitat manipulation. *Alces* 37:109-122.
- BRYANT, L. D., J. W. THOMAS, AND M. M. ROWLAND. 1993. Techniques to construct New Zealand elk-proof fence. United States Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, General Technical Report PNW-GTR-313:1-17.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York.
- CAMPBELL, D. T. 1957. Factors relevant to the validity of experiments in social settings. *Psychological Bulletin* 54:297-312.

- CARLSON, P. C., G. W. TANNER, J. M. WOOD, AND S. R. HUMPHREY. 1993. Fire in key deer habitat improves browse, prevents succession, and preserves endemic herbs. *Journal of Wildlife Management* 57:914-928.
- CIUTI, S., S. DAVINI, S. LUCCARINI, AND M. APOLLONIO. 2004. Could the predation risk hypothesis explain large-scale spatial sexual segregation in fallow deer (*Dama dama*)? *Behavioral Ecology and Sociobiology* 56:552-564.
- COOK, J. G. 2002. Nutrition and food. Pp. 259-349 in *North American elk: ecology and management* (D. E. Toweill and J. W. Thomas, eds.). Smithsonian Institution Press, Washington D.C.
- COOK, T. D., AND D. T. CAMPBELL. 1979. Causal inference and the language of experimentation. Pp. 1-36 in *Quasi-experimentation: design and analysis issues for field settings* (T. D. Cook and D. T. Campbell, eds.). Houghton Mifflin, Boston, Massachusetts.
- COVINGTON, W. W., ET AL. 1997. Restoring ecosystem health in *Pinus ponderosa* forests of the Southwest. *Journal of Forestry* 95:23-29.
- CRAIGHEAD, J. J., F. C. CRAIGHEAD, JR., R. L. RUFF, AND B. W. O'GARA. 1973. Home ranges and activity patterns of nonmigratory elk of the Madison drainage herd as determined by biotelemetry. *Wildlife Monographs* 33:1-50.
- DODGE, M. 1972. Forest fuel accumulation—a growing problem. *Science* 177:139-142.
- EDGE, W. D., C. L. MARCUM, AND S. L. OLSON. 1985. Effects of logging activities on home-range fidelity of elk. *Journal of Wildlife Management* 49:741-744.
- FINDHOLT, S. L., B. K. JOHNSON, L. D. BRYANT, AND J. W. THOMAS. 1996. Corrections for position bias of a LORAN-C radio-telemetry system using DGPS. *Northwest Science* 70:273-280.
- GANNON, W. L., R. S. SIKES, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 88:809-823.
- GARROT, R. A., G. C. WHITE, R. M. BARTMANN, L. H. CARPENTER, AND A. W. ALLDREDGE. 1987. Movements of female mule deer in northwest Colorado. *Journal of Wildlife Management* 51:634-643.
- GARTON, E. O., J. T. RATTI, AND J. H. GIUDICE. 2005. Research and experimental design. Pp. 43-71 in *Techniques for wildlife investigations and management* (C. Braun, ed.). Wildlife Society, Bethesda, Maryland.
- HORNE, J. S., AND E. O. GARTON. 2006. Likelihood cross-validation versus least squares cross-validation for choosing the smoothing parameter in kernel home-range analysis. *Journal of Wildlife Management* 70:641-648.
- HORNE, J. S., E. O. GARTON, AND K. A. SAGER-FRADKIN. 2007. Correcting home-range models for observation bias. *Journal of Wildlife Management* 71:996-1001.
- IRWIN, L. L., AND J. M. PEEK. 1983. Elk habitat use relative to forest succession in Idaho. *Journal of Wildlife Management* 47:664-672.
- JENKS, J. A., D. M. LESLIE, JR., R. L. LOCHMILLER, AND M. A. MELCHORS. 1994. Variation in gastrointestinal characteristics of male and female white-tailed deer: implications for resource partitioning. *Journal of Mammalogy* 75:1045-1053.
- JOHNSON, B. K., ET AL. 1998. Mitigating spatial differences in observation rate of automated telemetry systems. *Journal of Wildlife Management* 62:958-967.
- JOHNSON, B. K., J. W. KERN, M. J. WISDOM, S. L. FINDHOLT, AND J. G. KIE. 2000. Resource selection and spatial separation of mule deer and elk during spring. *Journal of Wildlife Management* 64:685-697.
- JOHNSON, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65-71.
- KERNOHAN, B. J., R. A. GRIZZEN, AND J. J. MILLSPAUGH. 2001. Analysis of animal space use and movements. Pp. 126-166 in *Radio tracking and animal populations* (J. J. Millspaugh and J. M. Marzluff, eds.). Academic Press, San Diego, California.
- KIE, J. G., AND R. T. BOWYER. 1999. Sexual segregation in white-tailed deer: density-dependent changes in use of space, habitat selection and dietary niche. *Journal of Mammalogy* 80:1004-1020.
- KNIGHT, R. R. 1970. The Sun River elk herd. *Wildlife Monographs* 23:1-66.
- LONG, R. A., J. L. RACHLOW, AND J. G. KIE. 2008a. Effects of season and scale on response of elk and mule deer to habitat manipulation. *Journal of Wildlife Management* 72:1133-1142.
- LONG, R. A., J. L. RACHLOW, J. G. KIE, AND M. VAVRA. 2008b. Fuels reduction in a western coniferous forest: effects on quantity and quality of forage for elk. *Rangeland Ecology and Management* 61:302-313.
- MAIN, M. B. 2008. Reconciling competing ecological explanations for sexual segregation in ungulates. *Ecology* 89:693-704.
- MAIN, M. B., AND B. E. COBLENTZ. 1996. Sexual segregation in Rocky Mountain mule deer. *Journal of Wildlife Management* 60:497-507.
- MAIN, M. B., F. W. WECKERLY, AND V. C. BLEICH. 1996. Sexual segregation in ungulates: new directions for research. *Journal of Mammalogy* 77:449-461.
- MANLY, B. F. J., L. L. McDONALD, D. L. THOMAS, T. L. McDONALD, AND W. P. ERICKSON. 2002. *Resource selection by animals: statistical design and analysis for field studies*. 2nd ed. Kluwer Press, Boston, Massachusetts.
- MARZLUFF, J. M., J. J. MILLSPAUGH, P. HURVITZ, AND M. S. HANDCOCK. 2004. Relating resources to a probabilistic measure of space use: forest fragments and Steller's jays. *Ecology* 85:1411-1427.
- MILLSPAUGH, J. J., G. C. BRUNDIGE, R. A. GITZEN, AND K. J. RAEDEKE. 2000. Elk and hunter space use sharing in South Dakota. *Journal of Wildlife Management* 64:994-1003.
- MILLSPAUGH, J. J., ET AL. 2006. Analysis of resource selection using utilization distributions. *Journal of Wildlife Management* 70:384-395.
- NEATHERLIN, E. A., AND J. M. MARZLUFF. 2004. Campgrounds enable American crows to colonize remote native forests. *Journal of Wildlife Management* 68:708-718.
- NETER, J., M. H. KUTNER, C. J. NACHTSHEIM, AND W. WASSERMAN. 1996. *Applied linear statistical models*. 4th ed. WCB McGraw-Hill, Boston, Massachusetts.
- PECK, V. R., AND J. M. PEEK. 1991. Elk, *Cervus elaphus*, habitat use related to prescribed fire, Tschudi River, British Columbia. *Canadian Field-Naturalist* 105:354-362.
- PERRYMAN, B. L., R. A. OLSON, S. PETERSBURG, AND T. NAUMANN. 2002. Vegetation response to prescribed fire in Dinosaur National Monument. *Western North American Naturalist* 62:414-422.
- ROWLAND, M. M., L. D. BRYANT, B. K. JOHNSON, J. H. NOYES, M. J. WISDOM, AND J. W. THOMAS. 1997. The Starkey Project: history, facilities, and data collection methods for ungulate research. United States Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, General Technical Report PNW-GTR-296:1-62.
- ROWLAND, M. M., ET AL. 1998. The Starkey habitat database for ungulate research: construction, documentation, and use. United States Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, General Technical Report PNW-GTR-430:1-48.
- RUCKSTUHL, K. E. 1998. Foraging behaviour and sexual segregation in bighorn sheep. *Animal Behaviour* 56:99-106.

- RUCKSTUHL, K. E., AND P. NEUHAUS. 2002. Sexual segregation in ungulates: a comparative test of three hypotheses. *Biological Reviews* 77:77-96.
- RUCKSTUHL, K. E., AND P. NEUHAUS (EDS.). 2005. Sexual segregation in vertebrates—ecology of the sexes. Cambridge University Press, Cambridge, United Kingdom.
- SAS INSTITUTE INC. 2002. SAS OnlineDoc®, version 9.1.3, SAS Institute Inc., Cary, North Carolina.
- SCHINDLER, J. R., T. E. FULBRIGHT, AND D. A. FORBES. 2004. Shrub regrowth, antiherbivore defenses, and nutritional value following fire. *Journal of Range Management* 57:178-186.
- SEIDEL, K. S. 1992. Statistical properties and applications of a new measure of joint space use for wildlife. M.S. Thesis, University of Washington, Seattle.
- SKOVLIN, J. M. 1991. Fifty years of research progress: a historical document on the Starkey Experimental Forest and Range. United States Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, General Technical Report PNW-GTR-266: 1-58.
- STAINES, B. W., J. M. CRISP, AND T. PARISH. 1982. Differences in the quality of food eaten by red deer (*Cervus elaphus*) stags and hinds in winter. *Journal of Applied Ecology* 19:65-77.
- STEWART, K. M., R. T. BOWYER, J. G. KIE, N. J. CIMON, AND B. K. JOHNSON. 2002. Temporospatial distributions of elk, mule deer, and cattle: resource partitioning and competitive displacement. *Journal of Mammalogy* 83:229-244.
- STEWART, K. M., T. E. FULBRIGHT, D. L. DRAWE, AND R. T. BOWYER. 2003. Sexual segregation in white-tailed deer: responses to habitat manipulations. *Wildlife Society Bulletin* 31:1210-1217.
- STOUFFER, S. A. 1950. Some observations on study design. *American Journal of Sociology* 55:355-361.
- THOMAS, D. L., AND E. J. TAYLOR. 1990. Study designs and tests for comparing resource use and availability. *Journal of Wildlife Management* 54:322-330.
- TIEDEMANN, A. R., J. O. KLEMMEDSON, AND E. L. BULL. 2000. Solution of forest health problems with prescribed fire: are forest productivity and wildlife at risk? *Forest Ecology and Management* 127:1-18.
- WALSTAD, J. D., S. R. RADOSEVICH, AND D. V. SANDBERG (EDS.). 1990. Natural and prescribed fire in Pacific Northwest forests. Oregon State University Press, Corvallis.
- WEBER, K. T., M. BURCHAM, AND C. L. MARCUM. 2001. Assessing independence of animal locations with association matrices. *Journal of Range Management* 54:21-24.
- WECKERLY, F. W. 2001. Are large male Roosevelt elk less social because of aggression? *Journal of Mammalogy* 82:414-421.
- WECKERLY, F. W., M. A. RICCA, AND K. P. MEYER. 2001. Sexual segregation in Roosevelt elk: cropping rates and aggression in same-sex groups. *Journal of Mammalogy* 82:825-835.
- WISDOM, M. J., J. G. COOK, M. M. ROWLAND, AND J. H. NOYES. 1993. Protocols for care and handling of deer and elk at the Starkey Experimental Forest and Range. United States Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, General Technical Report PNW-GTR-311:1-49.

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