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SEASONAL HABITAT SELECTION BY ELK IN NORTH CENTRAL UTAH

Jeffrey L. Beck^{1,4}, Kurt T. Smith¹, Jerran T. Flinders², and Craig L. Clyde³

ABSTRACT.—Understanding anthropogenic and environmental factors that influence seasonal habitat selection is critical in establishing conservation objectives for wildlife populations. However, many resource selection studies provide inferences only for single seasons, potentially masking factors essential to populations during other times of the year. Our objective was to model elk (*Cervus elaphus*) habitat selection for 4 seasons to identify factors influencing selection within and across seasons. Using aerial relocation data, we evaluated seasonal habitat selection for 46 radio-marked, migratory adult female elk in a 6123-km² landscape in north central Utah, USA, from 1993 to 1997. We evaluated habitat use and availability within estimated seasonal range boundaries by using binary logistic regression to model habitat selection. Habitat use was measured as a response to predictor variables collected from analysis regions around elk locations. Habitat use was compared to habitat availability by measuring those same variables collected from randomly located analysis regions. Our results showed that roads, topography, and vegetation cover influenced elk habitat selection within and across seasons. Roads did not influence elk habitat selection in spring; rather, elk selected areas with aspen (*Populus tremuloides*) at higher elevations. In summer, elk selected forage-rich habitats, particularly aspen and mountain brush at higher elevations and on cooler aspects. In fall, elk selected sites with steeper slopes at higher elevations in areas with greater cover of aspen and mountain brush than was available in seasonal range boundaries. In winter, elk selected sagebrush (*Artemisia* spp.)-meadow cover on steeper slopes at lower elevations away from major roads. The full array of seasonal habitat selection patterns we found provides managers with greater options for setting conservation objectives for elk on a year-round basis.

RESUMEN.—El comprender los factores antropogénicos y ambientales que influyen en la selección del hábitat según la estación es fundamental para establecer los objetivos de conservación de las poblaciones de vida silvestre. Muchos estudios relacionados con la selección de recursos sólo proporcionan conclusiones para cada una de las estaciones del año por separado, lo que puede enmascarar factores fundamentales para las poblaciones durante otras épocas del año. Nuestro objetivo fue modelar la selección del hábitat del alce (*Cervus elaphus*) durante las cuatro estaciones para identificar los factores que influyen en la selección durante y a lo largo de las estaciones. Evaluamos la selección del hábitat, según la estación, de 46 hembras adultas de hábitos migratorios, en un paisaje de 6123 km² en la zona norte central de Utah, EE. UU., entre los años 1993 y 1997, utilizando la información del traslado obtenida con tomas aéreas. Evaluamos la utilización y disponibilidad del hábitat, dentro de los límites estimados de la zona, según la estación utilizando el método de regresión logística para modelar la selección del hábitat. La utilización del hábitat se midió como respuesta a variables explicativas que se obtuvieron de las regiones que se analizaron en zonas donde se encontraba el alce, en comparación con las regiones que se analizaron al azar para representar la disponibilidad del hábitat. Nuestros resultados demostraron que los caminos, la topografía y la cobertura de vegetación influyeron en la selección del hábitat del alce durante y a lo largo de las estaciones. Los caminos no influyeron en la selección del hábitat del alce durante la primavera, en esa estación, el alce seleccionó áreas en las que había álamo temblón (*Populus tremuloides*) y matorrales montañosos en terrenos elevados. Durante el verano, el alce seleccionó hábitats con abundancia de alimentos, en particular álamo temblón y matorrales montañosos en terrenos más elevados y en áreas más frescas. Durante el otoño, el alce seleccionó lugares con pendientes más empinadas, en terrenos más elevados, en zonas con mayor cobertura de álamo temblón y matorrales montañosos de la que había en los límites de la zona según la estación. Durante el invierno, el alce seleccionó artemisas (especie *Artemisia*) que cubrían las praderas en pendientes más empinadas, en terrenos con menor elevación, alejadas de los caminos principales. La variedad de patrones de selección del hábitat según la estación que reportamos, proporciona mejores opciones para establecer los objetivos de conservación del alce durante todo el año.

Understanding anthropogenic and environmental factors that influence seasonal habitat selection is critical in establishing conservation objectives for wildlife populations. To obtain seasonal resources such as forage and cover, large ungulates, including elk (*Cervus*

elaphus), select numerous habitat features across a large spatial scale during a single annual cycle. Habitat selection by elk has been well studied in both forested and non-forested environments throughout the Intermountain West (McCorquodale et al. 1986,

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Rowland et al. 2000, Beck et al. 2006, Sawyer et al. 2007). Elk tend to avoid anthropogenic features such as roads (Witmer and deCalesta 1985, Rowland et al. 2000) and increase movement and avoidance behaviors in response to off-road recreational activities (Wisdom et al. 2004). Topographic features, including elevation, slope, and aspect, influence elk habitat selection throughout the year (Marcum 1975, Witmer and deCalesta 1985, Edge et al. 1987, Stewart et al. 2002, Sawyer et al. 2007). The gradient of topographic features linked with precipitation and plant phenology provides a diversity of cover and forage availability during different seasonal periods.

Elk populations in mountainous environments move between summer and winter ranges in response to changes in weather conditions, plant phenology, and plant availability (Sweeney and Steinhoff 1976). Spring and fall habitats are used as stopover locations for migratory ungulates. These habitats provide rest, cover, and forage during the transition between summer and winter ranges (Sawyer and Kauffman 2011). Because of the high degree of variability in migrations among separate elk populations (Skovlin et al. 2002), the spatial scale necessary for individuals to meet their seasonal energetic requirements may be largely associated with the juxtaposition of seasonal habitats. Identifying habitat features that may simultaneously influence selection and seasonal habitat use at a yearly temporal scale provides a more holistic approach to elk management and guides land-use practices and conservation efforts.

Although several studies have evaluated elk habitat use during 1 or 2 seasonal periods (e.g., Marcum 1975, Grover and Thompson 1986, Edge et al. 1987, Boyce et al. 2003, Beck et al. 2006, Sawyer et al. 2007), research evaluating seasonal requirements on a year-round basis is scarce (but see Witmer and deCalesta 1983, Unsworth et al. 1998). To date, elk habitat selection studies have not incorporated the variability and spatial distribution of key habitat features that influence selection across seasons, thereby potentially neglecting the suite of habitat characteristics that are selected by elk on a year-round basis. The purpose of our study was to evaluate seasonal habitat selection for migratory elk within a large landscape in north central Utah that encompassed all seasonal habitats (Fig. 1). Our

objective was to model elk habitat selection during spring, summer, fall, and winter to identify factors influencing selection by this population within and across seasons. We predicted elk seasonal habitat selection to reflect road influences, variation in cover, and topographic attributes that maximize the trade-off between forage acquisition and security cover.

METHODS

Study Area

Our study area encompassed 6123 km² (39° 59' N, 110° 47' W) administered by the Bureau of Land Management (992 km², 16.2%), United States Forest Service (2447 km², 40.0%), Utah Division of Wildlife Resources (355 km², 5.8%), private ownership (1645 km², 26.9%), and other ownership (684 km², 11.1%) in Carbon, Duchesne, Utah, and Wasatch counties, Utah, USA (Fig. 1), at elevations ranging from 1400 to 3353 m. Ninety-five percent fixed-kernel ranges (Horne and Garton 2009) computed by season were 4059 km² for spring, 1659 km² for summer, 3541 km² for fall, and 5616 km² for winter (Fig. 1). There were 2 U.S. Natural Resources Conservation Service SNOTEL sites in the summer range portion of our study area. The 19-year (1979–1997) average annual precipitation for the White River 1 SNOTEL site (39° 58' N, 110° 59' W; 2634 m) was 64.4 cm and 85.9 cm at the Strawberry Divide SNOTEL site (40° 11' N, 111° 13' W; 2476 m; NRCS 2011). Most of the moisture precipitated as snow during late fall, winter, and early spring (U.S. Soil Conservation Service 1993). Dominant vegetation communities on the summer range included aspen (*Populus tremuloides*); conifer species including Douglas-fir (*Pseudotsuga menziesii*) and subalpine fir (*Abies lasiocarpa*); sagebrush-grassland consisting of mountain big sagebrush (*Artemisia tridentata vaseyana*), silver sagebrush (*Artemisia cana*), and yellow rabbitbrush (*Chrysothamnus viscidiflorus*); a mountain brush zone including bigtooth maple (*Acer grandidentatum*), Gambel oak (*Quercus gambelii*), and red elderberry (*Sambucus racemosa*); and riparian areas with willows (*Salix* spp.). Winter range vegetation included mountain brush consisting of Gambel oak and bigtooth maple; conifers including Utah Juniper (*Juniperus osteosperma*), two-needle pinyon pine (*Pinus edulis*), and white fir (*Abies concolor*); and

Elk Seasonal Ranges North-Central Utah (1993-1997)

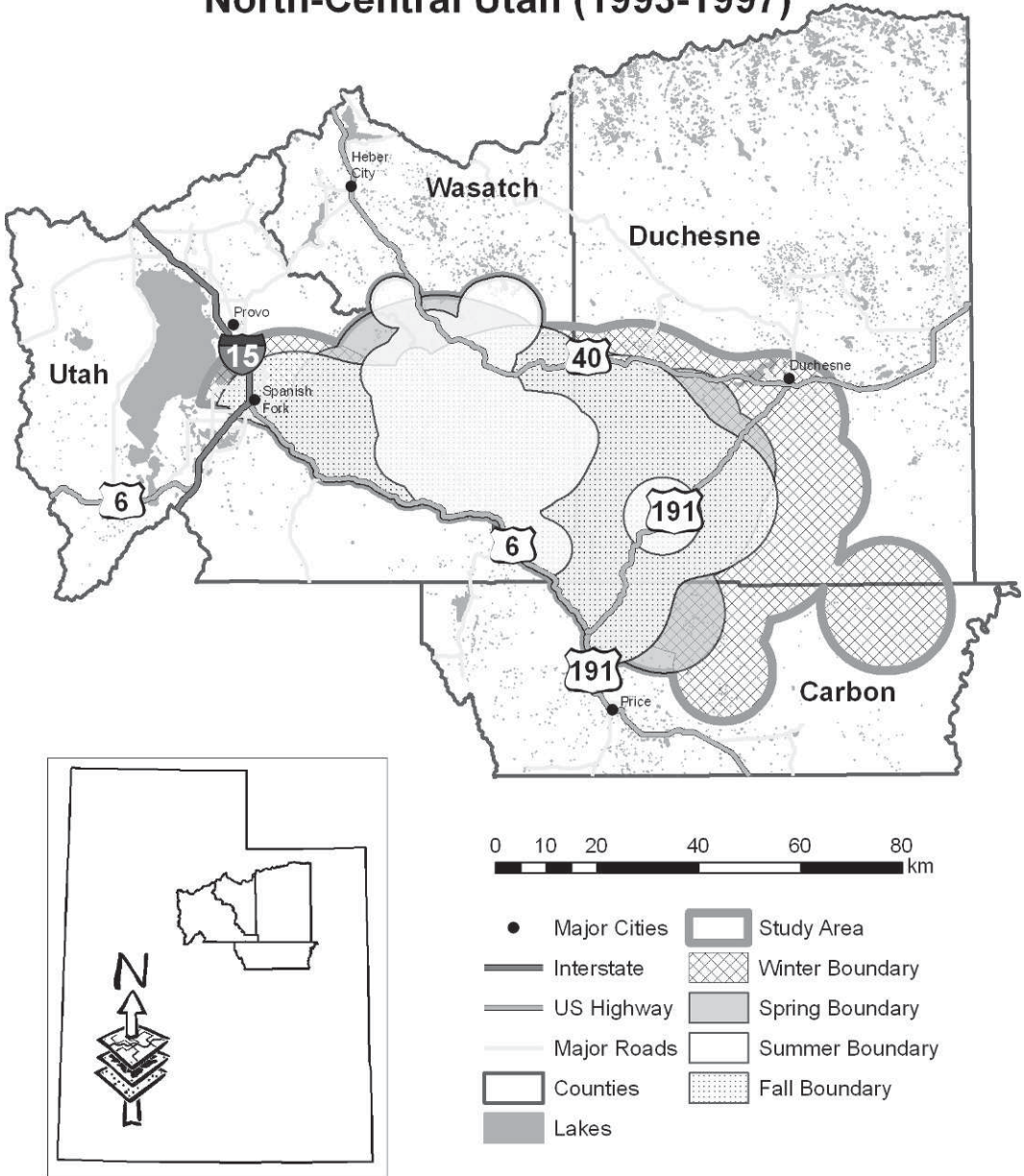


Fig. 1. Map of the study area illustrating elk seasonal ranges in north central Utah, USA, 1993–1997. Ninety-five percent fixed-kernel ranges computed by season were 4059 km² for spring, 1659 km² for summer, 3541 km² for fall, and 5616 km² for winter.

Wyoming big sagebrush (*Artemisia tridentata wyomingensis*). Spring and fall ranges were composed of a mixture of winter and summer plant communities. Grazing of domestic sheep and cattle was common on public and private

lands on spring, summer, and fall ranges. Recreational uses in our study area included camping, fishing, hunting, off-road vehicle touring, and snowmobiling, the last of which primarily occurred on elk summer range.

Capture and Relocation

We used helicopter net gunning (Helicopter Wildlife Management, Salt Lake City, UT) to capture 40 adult female elk on 22 and 23 July 1993 on lands administered by the USDA–Uinta National Forest. Thirty elk were captured within the 100-km² Willow Creek drainage and 10 elk along Strawberry Ridge, immediately adjacent to the west of Willow Creek. Each elk was equipped with a very high frequency (VHF) radio-collar (Lotek, Newmarket, Ontario, Canada). Seven of the 40 cows were harvested during the fall 1993 hunting season; 6 of these collars were reattached to adult female elk in the Willow Creek drainage on 11 July 1994. We located collared elk from the air with a Cessna 185 aircraft equipped with telemetry receivers at approximately 1-month intervals to facilitate systematic sampling (Scheaffer et al. 1996). Latitude and longitude of elk locations were recorded with the Loran-C navigation system (accuracy 174.3 m ± 99.5 m; Leptich et al. 1994) for 51 flights from 23 July 1993 to 23 June 1997 during morning hours and across spring, summer, fall, and winter. Data from 8 flights were omitted from our analysis due to inaccuracy.

Habitat Measurements

We identified habitat variables that were predictive of elk habitat selection in other studies, including vegetation characteristics, topography, and anthropogenic features (Witmer and deCalesta 1985, Edge et al. 1987, Rowland et al. 2000, Stewart et al. 2002, Beck et al. 2006, Sawyer et al. 2007). We obtained a 30 × 30-m resolution Landsat 5 Thematic Mapper image from the U.S. Geological Survey to classify cover in the study area as aspen, conifer, mountain brush, sagebrush-meadow, and perennial water. We grouped sagebrush and herbaceous meadows into a single cover type because we often observed elk foraging in these open communities near woody cover and because sagebrush often grew in meadows. We used ERDAS IMAGINE 9.3 (ERDAS®, Inc., Atlanta, GA) and ArcMap 9.3 (Environmental Systems Research Institute, Redlands, CA) to cluster pixels into spectrally similar cover features. Then we converted these pixels to a polygon database and dissolved the classified polygons into the 4 vegetation cover classes and perennial water sources. Cover classification accuracy was

assessed by comparing 597 elk locations with habitat classifications recorded during flights. Classifications were considered correct if aerial habitat classifications were recognized within the region of error for projected elk locations. We evaluated agreement between aerial classifications and map predictions with Cohen's Kappa Coefficient (Cohen 1960; Cohen's $k = 0.896$). We calculated the proportion of each cover class within the circular analysis region around each used and randomly available location and also calculated the distance from each used and available location to the nearest perennial water source by using the Nearest Neighbor extension for ArcMap 9.3.

The Spatial Analyst extension for ArcMap was used to calculate aspect and mean elevation and slope within each circular analysis region from a 30 × 30-m digital elevation model (USGS 1999). The dominant aspect in the grid cells forming each circular analysis region were classified as warm (136–314°) or cool (315–135°). We used the Vector Ruggedness Measure (VRM), which is the difference in radians between the cells formed from a digital elevation model grid cell and its immediately surrounding cells, to measure average terrain ruggedness within each circular analysis region. The VRM ranges from 0 (no terrain variation) to 1 (complete terrain variation), with typical values for natural terrain ranging between 0 and approximately 0.4 (Sappington et al. 2007). VRM values were calculated using a 3 × 3 cell format (Sappington et al. 2007) and then rescaled by multiplying the original values by 1000 for interpretation. We obtained a road dataset (Utah Automated Geographic Reference Center) and classified roads as either minor (low-maintenance gravel or 2-track) or major (well-maintained and paved surfaces). The Nearest Neighbor extension was used to measure the distance from the center of each analysis region to the nearest minor and major road.

Study Design

We employed a use-availability design to evaluate elk seasonal habitat selection (Boyce et al. 2002, Manly et al. 2002, Johnson et al. 2006), where we identified resource use as locations obtained from fixed-wing aircraft of radio-collared elk during 1993–1997. Locations were pooled across individual elk to represent a population-level habitat selection

response (a Type 1 Design; Manly et al. 2002, Thomas and Taylor 2006). It is important to consider annual variation in habitat selection models if resource use varies between years (Schooley 1994). However, we observed no indication of behavioral differences in elk within seasons across the 4 years of our study. Therefore, to increase sample size and account for seasonal selection patterns that may be observed in the same areas across years, we included elk locations from all 4 years in the same seasonal models (Carpenter et al. 2010). Furthermore, we focused our analysis on habitat components within a home range (i.e., Johnson's [1980] third-selection order), whereby we constrained habitat availability within seasonal home-range boundaries. When multiple elk were located within a 300-m radius during a single flight, we randomly removed locations until no locations were within 300 m of one another to ensure that locations were selected independently. We based our removal distance on field observation of elk herd behavior, which resulted in <1% of locations removed. Numbers of locations per elk in a given season were equalized to avoid overrepresentation of the selection response of individuals. We randomly selected 1000 locations within each seasonal boundary, excluding locations in bodies of water, to represent available habitat.

We defined seasons by changes in elk behavior, summarized by distance moved from locations collected during previous fixed-wing aircraft flights, as winter, 9 December–7 March; spring, 8 March–3 June; summer, 4 June–28 September; and fall, 29 September–8 December (Fig. 1). We calculated 100% fixed-kernel home ranges for each independent flight and used smoothing factors (H values) for these home ranges based on the elk locations from each flight, with likelihood cross-validation (Horne and Garton 2006, 2009). To define seasonal boundaries, we generated a 95% fixed-kernel area around individual home ranges from each flight that occurred within a season. Our seasonal home-range boundaries were truncated along U.S. Highway 6 on the south and near Spanish Fork on the west, because elk locations did not occur past these landmarks and because our observations indicated they likely formed barriers to movement (Fig. 1). For each season, we estimated daily movement of elk by dividing the average distance moved between locations by the number of days

between subsequent flights. We used estimated daily movements to create circular analysis regions around used and available locations. These regions accounted for the area that was hypothetically available to elk on a daily basis, but also exceeded flight location error.

Data Analysis

We used 95% Bailey's simultaneous confidence intervals (Bailey 1980) in Resource Selection Version 1.0 (Leban 1999) to assess elk preference and avoidance of vegetation cover types for each season. Independent sample *t* tests were used to assess differences in continuous explanatory variables between used and available locations in each season. A Fisher's exact test was used to assess the proportion of cool and warm aspects between elk and available locations.

We employed binary logistic regression with used and available locations for model selection. For each season, we determined the probability of use within seasonal range boundaries where used and available locations were the dependent variables and a suite of habitat characteristics formed our set of predictor variables for each season (Johnson et al. 2006). We conducted statistical analyses with Statistical Analysis Software (SAS) version 9.2 (SAS Institute, Inc. 2009). We removed non-predictive variables to prevent model overfitting (Burnham and Anderson 2002). We tested each predictive variable individually and removed it if the 95% confidence interval (CI) for the odds ratio overlapped 1.0 (Arnold 2010). We computed a Pearson's correlation matrix to test for multicollinearity among the variables and eliminated one of each correlated variable when correlation coefficients (*r*) were $\geq |0.6|$ by retaining the variable with the lowest log-likelihood value (Doherty et al. 2010). We further tested multicollinearity with the collinearity tolerance option in PROC REG (SAS Institute, Inc. 2009). Variables with low tolerance ($t \leq 0.4$) were removed from further analysis. Finally, we did not allow variables to compete in the same model when the signs of coefficients switched in the presence of another variable. Instability in the signs of coefficients can be a sign of moderate correlation and can lead to inflated standard errors (Doherty 2008). We evaluated all possible combinations of remaining variables in logistic regression models (Carpenter et al. 2010).

We used 2nd-order Akaike's information criterion corrected for small sample sizes (AIC_c ; Burnham and Anderson 2002) to rank all candidate models for each season by degrees of support. We computed cumulative Akaike weights (w_i) for all candidate models to provide weights of evidence in support of each seasonal model being the most parsimonious compared to the other models under consideration (Burnham and Anderson 2002). We followed the convention that models with weights of evidence (w_i) within 90% of the best model were competitive (Burnham and Anderson 2002, Arnold 2010). When a single top model was not evident based on the weight of evidence (w_i), we performed a model-averaging procedure to calculate mean coefficients, standard errors, confidence intervals, and odds ratios for each variable in the model-averaged set. We quantified the relative importance (RI) for each variable by summing the Akaike weights for each variable across all the models it occurred in (Burnham and Anderson 2002).

Lastly, we performed a 5-fold cross-validation procedure to evaluate goodness-of-fit for our best elk habitat selection model for each season (Boyce et al. 2002, Beck et al. 2006). We followed the approach of Sawyer et al. (2007) to map model predictions for each season across 30×30 -m pixels in our study area to provide a depiction of the spatial array of selection probabilities. We report all estimates as means with one standard error (SE), and we set statistical significance at $\alpha = 0.05$.

RESULTS

From July 1993 to June 1997, we obtained 1063 elk locations from 43 aerial flights (spring, 8 flights; summer, 15 flights; fall, 9 flights; winter, 11 flights). Of these locations, we used 150 from 25 elk in spring, 240 from 30 elk in summer, 145 from 29 elk in fall, and 168 from 28 elk in winter. Circular analysis regions located based on daily movement radii around elk-used and randomly available locations were 0.554 km^2 in spring, 0.126 km^2 in summer, 0.528 km^2 in fall, and 0.166 km^2 in winter.

Spring Habitat Selection

In spring, elk preferred aspen ($P < 0.001$), avoided sagebrush-meadow ($P < 0.05$), and

used conifer and mountain brush in proportion to their availability (Fig. 2). Distance to minor roads, major roads, and water, as well as percent conifer, percent slope, aspect, and topographic ruggedness (VRM), did not differ among elk-used and available locations (Appendix 1). In spring, elk selected higher elevations (used = 2471 m, SE 19; available = 2352 m, SE 8; $t_{1148} = 5.25$, $P < 0.001$) in areas with higher aspen cover (used = 25.0%, SE 1.9; available = 17.1%, SE 0.6; $t_{1148} = 4.63$, $P < 0.001$) and lower sagebrush-meadow cover (used = 42.8%, SE 2.5; available = 52.3%, SE 1.1; $t_{1148} = 3.14$, $P = 0.002$) compared to available locations (Appendix 1).

The logistic regression model that best explained elk habitat selection in spring included elevation and percent aspen (Appendix 2). The global model was competitive with the top model ($\Delta AIC_c = 1.35$) and included percent aspen, percent mountain brush, and elevation. Model averaging indicated that the 95% confidence interval for the odds ratio estimate of mountain brush overlapped 1 (Appendix 3); therefore, we considered mountain brush to be an uninformative predictor and limited our top spring model to include aspen and elevation. Relative importance weights for variables in the top models ranged from 0.99 to 1.0; relative importance for mountain brush was 0.34. For every 10% increase in aspen cover, the likelihood of elk use increased by approximately 4.3% (Fig. 3). With an increase of 100 m elevation, the likelihood of elk use increased by approximately 3.5% (Fig. 3). Our cross-validation analysis indicated that our best model was a strong, positive predictor of elk habitat use in spring ($r_s = 0.87$, $P = 0.001$, $n = 10$).

Summer Habitat Selection

During summer, aspen ($P < 0.001$) and mountain brush ($P < 0.001$) were preferred, sagebrush-meadow ($P < 0.001$) was avoided, and conifer was used in proportion to its availability (Fig. 2). Distance to major roads and water, as well as percent conifer, percent slope, and topographic ruggedness (VRM), did not differ among elk-used and available locations (Appendix 1). In summer, elk selected habitats at higher elevations (used = 2610 m, SE 10; available = 2482 m, SE 7; $t_{1238} = 8.27$, $P < 0.001$); closer to minor roads (used = 0.5 km, SE 0.03; available = 0.6 km, SE 0.02;

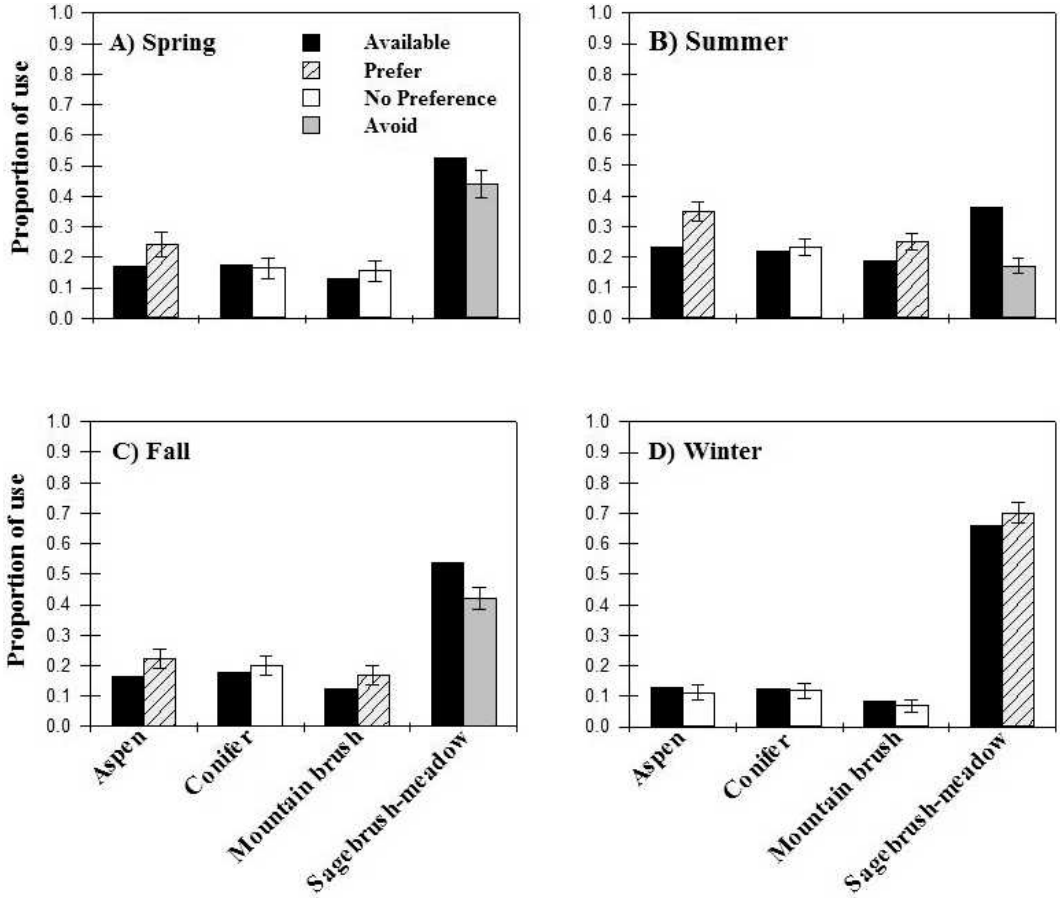


Fig. 2. Proportions of aspen, conifer, mountain brush, and sagebrush-meadow cover types at elk-used and available locations during spring (A), summer (B), fall (C), and winter (D) in north central Utah, USA, 1993–1997. Error bars depict Bailey’s 95% confidence intervals estimating preference, use proportional to availability, and avoidance of different habitat types by season.

$t_{1238} = 3.04, P = 0.002$); with higher cover of aspen (used = 34.7%, SE 1.6; available = 22.5%, SE 0.7; $t_{1238} = 7.51, P < 0.001$) and mountain brush (used = 25.1%, SE 1.4; available = 18.3%, SE 0.6; $t_{1238} = 4.56, P < 0.001$) and lower cover of sagebrush-meadow (used = 17.0%, SE 1.6; available = 35.2%, SE 1.1; $t_{1238} = 7.58, P < 0.001$); and on cooler aspects ($P = 0.008$; Appendix 1).

Our top 5 logistic regression models were competitive in explaining elk summer habitat selection ($\Delta AIC_c \leq 3.94$; Appendix 2). Potential explanatory variables included minor roads, aspect, elevation, and percent cover of aspen, mountain brush, and sagebrush-meadow (Appendix 3). Model-averaged 95% confidence intervals around the odds ratios for minor

roads and sagebrush-meadow overlapped 1 (Appendix 3); therefore, we considered our most competitive summer model to include aspect, elevation, and percent cover of aspen and mountain brush. Weights for the most explanatory variables supporting our model were 0.88 for aspect, 1.00 for aspen, 0.99 for mountain brush, and 1.0 for elevation. For every 10% increase in aspen and mountain brush cover, the likelihood of elk use increased by approximately 10.1% and 8.7%, respectively (Fig. 3). With an increase of 100 m elevation, the likelihood of elk use increased by approximately 11.0% (Fig. 3). Cross-validation indicated that the best model was a very strong, positive predictor of elk habitat use in summer ($r_s = 0.97, P < 0.001, n = 10$).

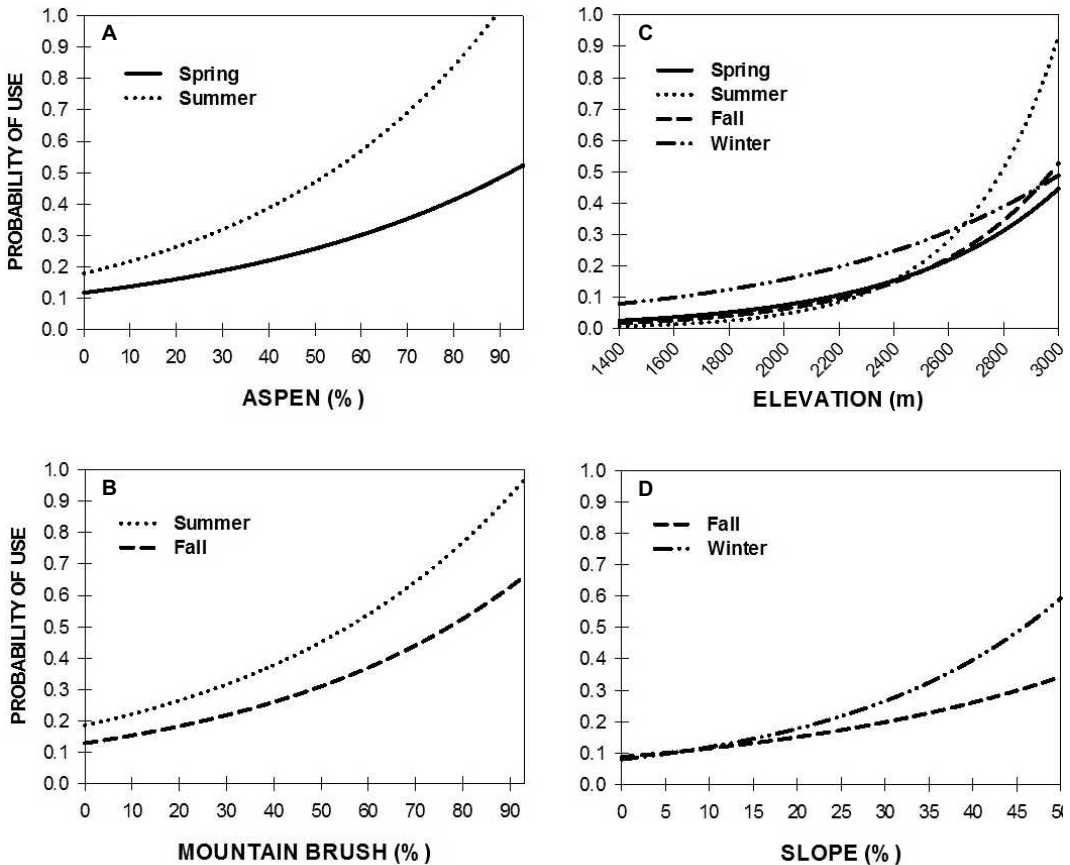


Fig. 3. Probability of elk use of spring, summer, fall, and winter habitats as a function of percent aspen (A), percent mountain brush (B), elevation (C), and slope (D) in north central, Utah, USA, 1993–1997. Probability graphs were derived from final models for each season. Variables of interest were free to vary, whereas other variables in each model were held at their mean values. Upper limits of variables were truncated based on the maximum values within circular analysis regions recorded for use locations within respective seasons.

Fall Habitat Selection

In fall, aspen ($P < 0.05$) and mountain brush ($P < 0.05$) were preferred, sagebrush-meadow was avoided ($P < 0.001$), and conifer was used equal to availability (Fig. 2). Aspect and distance to water were the only explanatory variables that did not differ among elk-used and available locations (Appendix 1). In fall, elk selected habitats farther from minor (used = 0.9 km, SE 0.07; available = 0.7 km, SE 0.02; $t_{1143} = 2.86$, $P = 0.004$) and major (used = 5.4 km, SE 0.30, available = 4.5 km, SE 0.12, $t_{1143} = 2.67$, $P = 0.008$) roads, as well as areas with greater aspen (used = 22.2%, SE 1.7; available = 16.5%, SE 0.6; $t_{1143} = 3.19$, $P = 0.001$), conifer (used = 20.8%, SE 1.4; available = 17.5%, SE 0.6;

$t_{1143} = 2.02$, $P = 0.044$), and mountain brush (used = 16.8%, SE 1.4; available = 12.2%, SE 0.5; $t_{1143} = 3.32$, $P < 0.001$). Habitat selected by elk in fall also included less sagebrush-meadow (used = 40.2%, SE 2.5; available = 53.6%, SE 1.1; $t_{1143} = 4.38$, $P < 0.001$), steeper slopes (used = 25.0%, SE 0.9; available = 21.6%, SE 0.4; $t_{1143} = 3.38$, $P < 0.001$), higher elevation (used = 2477 m, SE 20; available = 2357 m, SE 8; $t_{1143} = 5.27$, $P < 0.001$), and higher VRM (used = 8.2, SE 0.5; available = 6.2, SE 0.2; $t_{1143} = 4.49$, $P < 0.001$) compared to available locations.

The logistic regression model best explaining fall elk habitat selection included percent mountain brush, slope, and elevation (Appendix 2). The global model was competitive with

the top model ($\Delta AIC_c = 0.84$) and included elevation, slope, and percent cover of aspen and mountain brush. Model-averaged 95% confidence intervals around the odds ratio for aspen cover overlapped 1 (Appendix 3); therefore, we considered our most competitive fall model to include elevation, slope, and percent mountain brush. Weights for the most explanatory variables supporting our model were 0.98 for mountain brush, 0.99 for slope, and 0.99 for elevation. For every 10% increase in mountain brush cover, the likelihood of elk use increased by approximately 5.9% (Fig. 3). With an increase of 100 m elevation, the likelihood of elk use increased by approximately 4.7% (Fig. 3). The likelihood of elk use increased by approximately 5% with every 10% increase in slope (Fig. 3). Cross-validation indicated that our best model was a very strong, positive predictor of elk habitat use during fall ($r_s = 0.96$, $P < 0.001$, $n = 10$).

Winter Habitat Selection

During winter, sagebrush-meadow was preferred ($P < 0.05$), whereas aspen, conifer, and mountain brush were used in proportion to their availability (Fig. 2). Aspect and percent cover of aspen, conifer, mountain brush, and sagebrush-meadow did not differ among elk-used and available locations (Appendix 1). In winter, elk selected habitats farther from minor (used = 0.9 km, SE 0.06; available = 0.6 km, SE 0.02; $t_{1166} = 4.45$, $P < 0.001$) and major (used = 6.5 km, SE 0.3; available = 4.9 km, SE 0.1; $t_{1166} = 4.81$, $P < 0.001$) roads. Elk selected habitat farther from water (used = 1.6 km, SE 0.1; available = 1.4 km, SE 0.03; $t_{1166} = 2.03$, $P = 0.042$), on steeper slopes (used = 26.8%, SE 1.1; available = 18.9%, SE 0.4; $t_{1166} = 6.82$, $P < 0.001$), at higher elevations (used = 2348 m, SE 21; available = 2269 m, SE 9; $t_{1166} = 3.42$, $P < 0.001$), and at sites with greater VRM (used = 8.4, SE 0.5; available = 5.6, SE 0.2; $t_{1166} = 5.53$, $P < 0.001$) than at random sites.

We considered our top 2 logistic regression models to be competitive in explaining elk habitat selection in winter ($\Delta AIC_c \leq 4.35$; Appendix 2). Potential explanatory variables included distance to minor roads, percent sagebrush-meadow, percent slope, and elevation (Appendix 3). Model-averaged 95% confidence intervals for the odds ratios for all explanatory variables did not include 1; therefore, we

retained all variables in our top model. Weights for the most explanatory variables were 0.89 for minor roads, 0.99 for percent sagebrush-meadow, 0.99 for percent slope, and 0.99 for elevation. For every 10% increase in slope, the likelihood of elk use increased by approximately 10.8% (Fig. 3). With an increase of 100 m elevation, the likelihood of elk use increased by approximately 5.8% (Fig. 3). Cross-validation indicated that the best model was a strong, positive predictor of elk habitat use in winter ($r_s = 0.83$, $P = 0.003$, $n = 10$).

DISCUSSION

Studies aimed at identifying factors that influence habitat selection during a single season may not incorporate the temporal scale necessary to prioritize habitats on a year-round basis. Our study design allowed us to evaluate the relative effect of several habitat variables that influence elk habitat selection across seasons. Our results demonstrated that female elk in north central Utah showed strong selection for a suite of vegetation cover types and topographical characteristics during each season. In spring, elk disproportionately used habitats with greater aspen cover, less sagebrush-meadow, and greater elevation compared to available habitats. The variables that best predicted elk use in spring were aspen and elevation. In summer, elk selected locations in cooler aspects with greater cover of aspen and mountain brush, as well as lower sagebrush-meadow cover at higher elevations closer to minor roads. Distance to minor roads, however, was not predictive of selection, but was probably indicative of elk using flatter terrain near areas where minor roads tended to be located, as well as less human activity on these roads in summer. Fall habitats consisted of greater slope and elevation in areas with greater aspen, conifer, and mountain brush cover. During fall, elk used areas with less sagebrush-meadow cover farther from roads. During winter, elk selected locations in lower-elevation sagebrush habitats on steeper slopes far from major roads.

Our results support the notion that animals select habitats to maximize fitness on a seasonal basis. Vegetation provides food resources and structural cover for elk on a year-long basis. We found strong selection for aspen, mountain brush, and sagebrush-meadow cover.

We found no support for selection of coniferous habitats in any season. However, locations of elk were in areas with equal availability of conifer compared to available points. The importance of conifer stands as security cover to elk is well known (Irwin and Peek 1983, Rowland et al. 1984, Skovlin et al. 2002). Use of conifer habitat by elk in our study in proportion to its availability in all seasons may reflect the relatively homogenous distribution of this cover type. Stands of mixed aspen and conifer provide areas of security cover during periods of inactivity between foraging bouts (Irwin and Peek 1983, Anderson et al. 2005) and when human activity is high (Millspaugh et al. 2000). Cover requirements have been studied extensively (Thomas et al. 1979, Edge et al. 1990) and vary with seasonal temperature and precipitation regimes. We suspect that selection of conifer stands implies the presence of a mixture of vegetation and complex topography that creates suitable security cover, especially during fall (Thomas et al. 1979, Skovlin et al. 2002).

Aspen typically occurs at intermediate elevations in areas where high snowpack provides moisture for growth of shrubs, grasses, and succulent forbs (Mueggler 1988) that are typical of elk diets during spring, summer, fall, and winter (Kufeld 1973, DeByle 1985, Beck et al. 1996, Beck and Peek 2005a). Aspen has considerable value as forage for elk during all seasons (Kufeld 1973, DeByle 1985). The adjacency of forage to the dense canopy cover of mature timber stands creates edge habitats characteristically used by elk (Witmer and deCalesta 1983, Grover and Thompson 1986, McCorquodale 2003). The selection of mountain brush during summer and fall may have been associated with a shift in forage availability. We found a preference for aspen cover in fall, but aspen was not considered an influential variable in the fall model. Two of the most common mountain brush species in our study area were red elderberry and Gambel oak. Both species occur in a variety of subalpine vegetation zones in Utah (Conrad and McDonough 1972) and are highly palatable to elk during late summer, fall, and winter when other forage is less available (Conrad and McDonough 1972, Mower and Smith 1989, Beck et al. 1996). Elk shifted to sagebrush-dominated landscapes at the onset of winter when habitat availability was restricted to lower

elevations. This shift is common for many elk populations (Irwin and Peek 1983, Unsworth et al. 1998, Mao et al. 2005).

We found that topographic features influence habitat selection during all seasons. The elevational range (~1400–3350 m) in our study area provided elk with a variety of topographic features to choose from in their seasonal habitat selection. During winter, elk typically select areas of lower elevation where navigation through snow is more manageable and forage is more available. Steeper windswept slopes in areas of deep snow allow for greater access to available food sources. In spring, elk occupied areas of mid-elevation, likely following a nutritional gradient of plant phenology associated with snow retreat (Sawyer and Kauffman 2011). Crude protein declines in plants over time, suggesting that forage quality for elk is at an optimum during periods of new growth (Beck and Peek 2005b). In our study, the average distance elk moved between summer and winter ranges was 33.1 km (range 17.5–57.8 km, $n = 28$). In summer, elk selected cooler aspects at higher elevations in areas containing aspen and mountain brush, suggesting a movement response to areas of higher forage quality and also avoidance of harassment from tabanid (blood-sucking) flies (Beck et al. 1996). During summer, north-facing slopes at higher elevations in more mesic environments provide higher-quality forage while simultaneously affording thermal escape from elevated temperatures (Witmer and deCalesta 1983). Edge et al. (1987) found a similar preference for higher elevations as summer progressed in western Montana. Although elk used moderate slopes ($18.7 \pm 0.6\%$), we found no evidence for selection of slope during summer. In fall, elk occupied areas with complex topography of moderate elevation and steeper slopes, offering greater security and escape cover from hunters. By comparison, Edge and Marcum (1991) found that probability of elk use was greatest when topographic relief afforded visual separation from roads, and Webb et al. (2011) reported that a mix of vegetative cover and topographical features may minimize disturbance to elk by reducing visual detection from nearby human disturbances.

Elk in our study area used locations farther from roads only in fall and winter, and selection away from minor roads was documented only in winter. Other factors besides human

activity, including topography, cover, and climatic conditions, may have also influenced selection of habitat away from roads in these seasons; however, the tendency of elk to avoid areas near roads has been well documented (Lyon 1983, Witmer and deCalesta 1985, Rowland et al. 2000, Wisdom et al. 2004). Roads were generally located in areas of less complex topography relative to areas of higher elevation used by elk in spring and summer. In addition, many minor roads in our study area were inaccessible in spring due to snow drifts, fallen trees, and mud, thereby reducing their use by motorists and concomitantly reducing avoidance by elk. Although we have no supportive data, we found that vehicular traffic in summer was primarily limited to activities associated with livestock management but greatly increased in fall during hunting seasons. We assume that an increase in vehicular traffic during fall hunting seasons, as well as increased recreational activities in winter, caused elk to utilize areas farther from roads.

Recommendations

Roads, topography (aspect, slope, elevation), and cover types (aspen, mountain brush, and sagebrush-meadow) were selected by elk within and across seasons. Our results indicate that elk spring and summer habitat management should focus efforts on conserving aspen and mountain brush communities at higher elevations. Fall habitat management should consider actions that maintain a diversity of mountain brush and aspen cover in areas with complex topography and few roads. Managers should target lower-elevation sagebrush habitats on steeper slopes far from roads for winter habitat security. The variation in seasonal habitats, coupled with the relative isolation of habitats from each other, suggests that evaluation of single-season resource selection for elk is insufficient to explain the variation in factors that influence selection on a larger temporal scale. The full array of seasonal habitat selection patterns we found provides managers with greater options for setting conservation objectives for elk on a year-round basis.

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APPENDIX 1. Habitat characteristics of elk-used and available locations for each season in north central Utah, USA, 1993–1997. Numbers in parentheses for each seasonal designation represent the area (km²) of circular analysis regions. *P* values were obtained from independent 2-sample *t* tests for all variables except aspect, where *P* values were obtained from a Fisher's exact test. Degrees of freedom were 1148 for spring, 1238 for summer, 1143 for fall, and 1166 for winter.

Habitat characteristic	Elk-used		Available		<i>t</i>	<i>P</i>
	Mean	SE	Mean	SE		
Spring (0.554 km ²)						
Minor roads (km)	0.6	0.1	0.7	0.02	0.51	0.612
Major roads (km)	4.5	0.3	4.3	0.1	0.59	0.553
Water (km)	1.1	0.1	1.3	0.03	1.72	0.086
Aspen (%)	25.0	1.9	17.1	0.6	4.63	<0.001
Conifer (%)	16.3	1.1	17.4	0.6	0.72	0.471
Mountain brush (%)	15.9	1.2	12.9	0.5	2.20	0.028
Sagebrush-meadow (%)	42.8	2.5	52.3	1.1	3.14	0.002
Slope (%)	20.2	0.8	20.4	0.3	0.15	0.881
Elevation (m)	2471	19	2352	8	5.25	<0.001
VRM ^a	5.8	0.03	5.9	0.2	0.10	0.919
Aspect-warm ^b	54.7		49.2			
Aspect-cool ^c	45.3		50.8			0.221 ^d
Summer (0.126 km ²)						
Minor roads (km)	0.5	0.03	0.6	0.02	3.04	0.002
Major roads (km)	4.1	0.2	3.9	0.1	0.77	0.440
Water (km)	1.0	0.04	1.0	0.02	0.20	0.840
Aspen (%)	34.7	1.6	22.5	0.7	7.51	<0.001
Conifer (%)	23.1	1.4	21.4	0.7	1.08	0.281
Mountain brush (%)	25.1	1.4	18.3	0.6	4.56	<0.001
Sagebrush-meadow (%)	17.0	1.6	35.2	1.1	7.58	<.001
Slope (%)	18.7	0.6	19.2	0.4	0.53	0.594
Elevation (m)	2610	9	2482	7	8.62	<0.001
VRM ^a	4.8	0.3	5.2	0.2	1.24	0.215
Aspect-warm ^b	40.0		49.6			
Aspect-cool ^c	60.0		50.4			0.008 ^d
Fall (0.528 km ²)						
Minor roads (km)	0.9	0.1	0.7	0.02	2.86	0.004
Major roads (km)	5.4	0.3	4.5	0.1	2.67	0.008
Water (km)	1.4	0.1	1.3	0.03	1.37	0.172
Aspen (%)	22.2	1.7	16.5	0.6	3.19	0.001
Conifer (%)	20.8	1.4	17.5	0.6	2.02	0.044
Mountain brush (%)	16.8	1.4	12.2	0.5	3.32	<0.001
Sagebrush-meadow (%)	40.2	2.5	53.6	1.1	4.38	<0.001
Slope (%)	25.0	0.9	21.6	0.4	3.38	<0.001
Elevation (m)	2477	20	2357	8	5.27	<0.001
VRM ^a	8.2	0.5	6.2	0.2	4.49	<0.001
Aspect-warm ^b	44.1		49.2			
Aspect-cool ^c	55.9		50.8			0.286 ^d
Winter (0.166 km ²)						
Minor roads (km)	0.9	0.1	0.6	0.02	4.45	<0.001
Major roads (km)	6.5	0.3	4.9	0.1	4.81	<0.001
Water (m)	1.6	0.1	1.4	0.03	2.03	0.042
Aspen (%)	10.7	1.4	12.9	0.7	1.28	0.202
Conifer (%)	11.3	1.2	12.5	0.6	0.78	0.433
Mountain brush (%)	6.6	1.0	8.4	0.5	1.44	0.152
Sagebrush-meadow (%)	71.3	2.4	66.0	1.2	1.76	0.079
Slope (%)	26.8	1.1	18.9	0.4	6.82	<0.001
Elevation (m)	2348	21	2269	9	3.42	<0.001
VRM ^a	8.4	0.5	5.6	0.2	5.53	<0.001
Aspect-warm ^b	51.8		48.4			
Aspect-cool ^c	48.2		51.6			0.453 ^d

^aUnless

^bPercent circular buffers containing majority warm (136–314°) aspect

^cPercent circular buffers containing majority cool (135–315°) aspect

^dFrom Fisher's exact test

APPENDIX 2. Top and competitive ($w_i \geq 10\%$ of top model w_i) models best explaining seasonal habitat selection by female elk in north central Utah, USA, 1993–1997. Null and global models are also reported for comparison.

Season	Model	K ^a	AIC _c	w_i	Rank ^b
Spring	Aspen + Elevation	3	0.00	0.66	1
	Aspen + Mountain brush + Elevation [Global]	4	1.35	0.34	2
	Null	1	39.65	0.00	8
Summer	Aspect + Aspen + Mountain brush + Elevation	5	0.00	0.41	1
	Minor roads + Aspect + Aspen + Mountain brush + Elevation	6	1.11	0.23	2
	Aspect + Aspen + Mountain brush + Sagebrush-meadow + Elevation	6	1.95	0.15	3
	Minor roads + Aspect + Aspen + Mountain brush + Sagebrush-meadow + Elevation [Global]	7	3.10	0.09	4
	Aspen + Mountain brush + Elevation	4	3.94	0.06	5
	Null	1	131.23	0.00	64
	Mountain brush + Slope + Elevation	4	0.00	0.59	1
Fall	Aspen + Mountain brush + Slope + Elevation [Global]	5	0.84	0.38	2
	Null	1	46.63	0.00	16
	Minor roads + Sagebrush-meadow + Slope + Elevation [Global]	5	0.00	0.89	1
Winter	Sagebrush-meadow + Slope + Elevation	4	4.35	0.10	2
	Null	1	70.37	0.00	16

^aNumber of parameters (K)

^bWithin seasonal model ranking based on AIC_c

APPENDIX 3. Parameter estimates, variable importance, and odds ratios for habitat variables that were included in top models depicting seasonal habitat selection by female elk in spring, summer, fall, and winter in north central Utah, USA, 1993–1997.

Parameter	Estimate	95% CI		P^c	Relative importance ^d	Odds ratio	95% CI	
		Lower	Upper				Lower	Upper
Spring ^a								
Intercept	-6.553	-8.377	-4.729	<0.001				
Elevation (m)	0.002	0.001	0.003	<0.001	1.00	1.002	1.001	1.003
Aspen (%)	0.016	0.008	0.024	<0.001	0.99	1.016	1.008	1.024
Mountain brush (%) ^b	0.005	-0.007	0.017	0.411	0.34	1.005	0.993	1.017
Summer ^a								
Intercept	-9.821	-12.185	-7.457	<0.001				
Aspect (warm)	-0.401	-0.726	-0.077	0.017	0.88	0.669	0.484	0.926
Elevation (m)	0.003	0.002	0.004	<0.001	1.00	1.003	1.002	1.004
Aspen (%)	0.019	0.012	0.027	<0.001	1.00	1.019	1.012	1.027
Mountain brush (%)	0.018	0.010	0.025	<0.001	0.99	1.018	1.010	1.026
Sagebrush-meadow (%) ^b	-0.0004	-0.009	0.008	0.937	0.28	0.999	0.991	1.008
Minor roads (km) ^b	-0.158	-0.499	0.183	0.364	0.36	0.854	0.607	1.201
Fall ^a								
Intercept	-8.017	-10.050	-5.983	<0.001				
Elevation (m)	0.002	0.001	0.003	<0.001	1.00	1.002	1.001	1.003
Slope (%)	0.027	0.011	0.043	0.001	0.99	1.028	1.012	1.044
Aspen (%) ^b	0.005	-0.004	0.014	0.271	0.40	1.005	0.996	1.014
Mountain brush (%)	0.018	0.007	0.028	0.002	0.98	1.018	1.007	1.028
Winter ^a								
Intercept	-6.426	-8.163	-4.689	<0.001				
Elevation (m)	0.001	0.001	0.002	<0.001	0.99	1.001	1.001	1.002
Slope (%)	0.040	0.028	0.053	<0.001	1.00	1.041	1.028	1.054
Sagebrush-meadow (%)	0.013	0.008	0.019	<0.001	1.00	1.013	1.008	1.019
Minor roads (km)	0.340	0.082	0.599	0.010	0.90	1.405	1.085	1.820

^aIncludes model-averaged parameter estimates

^bParameters that have no predictive power because the 95% confidence intervals of the odds ratios include 1

^c P values from model containing all variables in top models

^dCalculated by adding Akaike weights for all models within a season that a variable was present in