Journal of Wildlife Management 75(1):159–170; 2011; DOI: 10.1002/jwmg.10

Research Article

Validation of Elk Resource Selection Models With Spatially Independent Data

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ABSTRACT Knowledge of how landscape features affect wildlife resource use is essential for informed management. Resource selection functions often are used to make and validate predictions about landscape use; however, resource selection functions are rarely validated with data from landscapes independent of those from which the models were built. This problem has severely limited the application of resource selection functions over larger geographic areas for widely distributed species. North American elk (*Cervus elaphus*) is an example of a widely-distributed species of keen interest to managers and for which validation of resource selection functions over large geographic areas is important. We evaluated the performance of resource selection functions developed for elk on one landscape in northeast Oregon with independent data from a different landscape in the same region. We compared predicted versus observed elk resource use for 9 monthly or seasonal periods across 3 yr. Results showed strong, positive agreement between predicted and observed use for 2 spring and 3 late summer-early fall models (3-yr $r = 0.81$–0.95). Predicted versus observed use was negatively or weakly positively correlated for 3 summer models and 1 mid-fall model (3-yr $r = -0.57$–0.14). Predicted and observed use correlated well when forage was limited (spring and late summer or early fall), corresponding to important biological stages for elk (parturition and breeding seasons). For these seasonal periods, model covariates such as rate of motorized traffic and canopy closure often were effective predictors of elk resource selection. The models we validated for spring and late summer-early fall may be used to evaluate management activities in areas with similar landscape characteristics.

KEY WORDS *Cervus elaphus*, elk, habitat use, model validation, resource selection models.

The use of resource selection functions (RSFs) to estimate and predict spatial distributions and resource use by ungulates and other vertebrates has become routine in recent years (Johnson et al. 2000, Nielsen et al. 2002, Carroll et al. 2003, Hebblewhite et al. 2005, Aldredge and Boyce 2007). This approach, based on deriving RSFs from observed data on animal use of available resources (Manly et al. 2002), provides a rigorous means of identifying environmental variables that best predict choices animals make within large landscapes during different seasons and life history stages.

Despite their popularity and potential utility, resource selection models are rarely validated with data from landscapes independent of those from which models were built (Wiens et al. 2008). This lack of geographic validation poses a formidable obstacle to understanding the spatial as well as temporal repeatability of resource selection patterns for a given species. Knowledge of how well these models can be generalized across space and time is important, given the limited resources available to derive customized resource selection models for each landscape of management interest. For example, can an RSF model developed for one landscape be used to predict elk distribution for other spatially independent landscapes? By validating RSFs in spatially independent areas one can greatly increase the utility of the RSF to land managers.

North American elk (*Cervus elaphus*) is well suited for validation of RSFs because the species is widely distributed, makes resource choices over large landscapes, and is of keen management interest (Wisdom and Cook 2000). Elk populations typically range over large landscapes (e.g., 2,000–5,000 ha) in many areas of the western United States during a given season (Wisdom and Cook 2000, O'Gara and Dundas 2002). In addition, 3rd order elk selection (Johnson 1980) is often detected at relatively course-grained (0.09–225 ha) spatial resolutions (Turner et al. 1997, Rowland et al. 2000, Long et al. 2008). Moreover, both the extent and resolution of elk resource selection are compatible with the diverse spatial data on vegetation, physiography, human activities, and land allocations typically used by agencies that manage elk habitat in the United States (United States Department of Agriculture Forest Service 2010, United States Department of Agriculture Bureau of Land Management 2010). Consequently, elk are well-suited as a species whose patterns of resource use can be evaluated at landscape scales with RSFs (Sawyer et al. 2007).

Our goal was to evaluate the geographic and temporal performance of elk RSFs. We evaluated performance of 9 monthly or seasonal resource selection models for elk on a landscape in northeast Oregon that was independent of the landscape for which the models were developed. Our objectives were to: 1) compare predicted versus observed relative probability of elk resource use for each of the 9 models on the independent landscape; 2) evaluate the degree to which different model covariates were aligned with low or high model performance; and 3) identify the management-based covariates that influenced elk use for models that performed well, as a means of understanding the degree to which management could affect elk distributions and resource selection.

Received: 20 August 2009; Accepted: 23 May 2010

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Table 1. Seasonal precipitation (cm) at Starkey Experimental Forest and Range (Starkey) during years of elk model development (1993–1995) and at Sled Springs (Sled) during years of elk model validation (2003–2005), northeast Oregon, USA. Data are from the National Atmospheric Deposition Program (2008) and Oregon Climate Service (2008).

					1993–1995					2003–2005	
Season	Study area	1993	1994	1995	$\bar{x}$	SD	2003	2004	2005	$\bar{x}$	SD
Mar–May	Starkey	22.1	11.5	19.5	15.3	5.5	19.3	18.4	18.9	18.9	0.4
	Sled	25.0	14.0	25.0	21.3	6.3	31.8	24.6	22.8	26.4	4.8
Jun–Aug	Starkey	20.1	7.0	14.8	14.0	6.6	5.0	12.2	5.2	7.5	4.1
	Sled	19.8	5.6	12.3	12.6	7.1	2.8	12.0	6.0	6.9	4.7
Sep–Nov	Starkey	3.9	16.0	18.4	13.8	7.8	11.4	12.4	10.1	11.3	1.1
	Sled	7.1	24.3	30.5	20.6	12.1	18.7	15.8	14.3	16.3	2.2
Total	Starkey	46.1	34.6	52.7	44.5	9.2	35.4	42.0	34.2	37.2	4.2
	Sled	51.9	43.9	67.8	54.4	12.2	53.3	52.4	43.1	49.6	5.6

ponderosa pine and supported few wet meadows (U.S. Forest Service 2009*a*).

Resource management differed between the 2 areas during the research periods. Timber harvest did not occur during model development at Starkey, but was on-going at Sled Springs during model validation. Cattle were grazed on a rotation system June–October in both study areas. Although hunting occurred at Starkey, seasons were short, and hunting days were censored from the dataset used to construct models. At Sled Springs, 2 rifle hunts for bull elk occurred from mid-October through mid-November during validation years.

Road management at Starkey and Sled Springs provided access for public and administrative use. At Starkey, all-weather roads were open to public use 1 May to early December, and secondary roads were limited to administrative use. At Sled Springs, public access was allowed on all non-barricaded roads from 31 May to 3 days before the start of archery hunting (last Saturday in Aug) and restricted to selected all-weather gravel roads thereafter. Use of roads closed to the public occurred throughout the study periods for timber harvest, livestock management, and administrative uses, and spatial data reflected estimates of level of use for each year and each month.

Elk populations varied between study areas. Approximately 450 animals (5–6 elk/km^2, Noyes et al. 1996) were present at Starkey and 2,600 animals in the entire Sled Springs Wildlife Management Unit (1.5 elk/km^2, V. Coggins, Oregon Department of Fish and Wildlife, unpublished data) each spring. The study area boundary at Sled Springs was defined by the 90% kernel density home range estimate of elk locations collected as part of model validation (Coe 2007). Evaluation of models at Sled Springs was limited to timber corporation lands, which composed >98% of the area (Coe 2007).

METHODS

Model Construction at Starkey

Resource selection functions for elk for foraging periods 2 hr before and after sunrise and sunset were constructed at Starkey by Johnson et al. (2000) or Ager et al. (2004) for monthly time steps, beginning the 16th of each month from 16 April to 15 November resulting in 1-month models for 7 seasonal periods. These monthly time steps encompassed the full progression of vegetation growth, development, and senescence on spring, summer, and fall ranges of elk, with time intervals sufficiently narrow to delineate different phases of seasonal vegetation dynamics, and thus captured

Table 2. Environmental data we used to parameterize elk models developed at Starkey Experimental Forest and Range, Oregon, USA, 1993–1995, and validated at Sled Springs 2003–2005, Oregon, USA. Traffic variables are zero = 0, low = 0–1, medium = 1–4, and high ≥ 4 vehicles/day.

	Starkey[a]			Sled Springs		
Variable	$\bar{x}$	Min.	Max.	$\bar{x}$	Min.	Max.
Slope (%)	18.00	0	84	17.50	0	131
Cosine of aspect (northness)	0.07	−1	1	−0.04	−1	1
Sine of aspect (eastness)	0.074	−1	1	−0.02	−1	1
Convexity of topography	500	466	525	500	498	502
Soil depth (cm)	68.07	22	152	111.44	0	152
Traffic, distance to zero (m)	268–280	0	3,182	621–1,924	0	6,228
Traffic, distance to low (m)	869–900	0	3,988	524–714	0	4,725
Traffic, distance to medium (m)	909–1,032	0	3,924	479–1,381	0	5,176
Traffic, distance to high (m)	1,103–1,560	0	3,352	788–2,479	0	7,468
Canopy cover (%)	29	0	85	26	0	65
Cover, distance to >40% (m)	102	0	1,018	316	0	3,152
Edge, distance to (m)	46	0	426	97	0	1,168
Circularity of patch	0.11	0.006	0.917	0.260	0.030	0.850
Forage production (kg/ha)	371	0	2,464	1,079	581	3,454

[a] Johnson et al. (2000).

temporal variation in elk resource selection throughout the grazing season (Ager et al. 2004). In addition, 2-month models for 2 seasonal periods, mid-spring–late spring (16 Apr–15 Jun) and late summer-early fall (16 Aug–15 Oct), also were developed previously at Starkey (Johnson et al. 2000, Coe 2007).

Covariates in Starkey models (Table 2) included physiography (slope, east–west aspect, north–south aspect, convexity), vegetation and forage (canopy closure, distance to cover areas, distance to forage areas, stand shape, and forage production), and roads and associated traffic rates (distances to roads with zero, low, medium, and high rates of traffic). Values of covariates were estimated or summarized to a 30-m × 30-m cell size, with 86,086 cells encompassing Starkey (Starkey Main Study Area, see Wisdom et al. 2005).

Model Validation at Sled Springs

We derived or estimated covariates at Sled Springs (Table 2) at the same scale and with the same methods used to build the models at Starkey (Johnson et al. 2000), with the exception of how traffic covariates were estimated. At Starkey, traffic covariates were developed from traffic counters placed at road intersections throughout the study area (Wisdom et al. 2004). Each road was categorized as 1 of 4 traffic rates (0, 0 to <1, 1 to 4, and >4 vehicles per day), and distances to each traffic rate category road was estimated for all cells in the study area (Wisdom et al. 2004). Because we did not have analogous data across all road systems at Sled Springs, we estimated traffic rates based on road type and management class. We assigned traffic rates of zero, low, moderate, and high to roads classified as closed, conditional, all-weather, and paved, respectively. We then adjusted traffic estimates up or down one category where appropriate according to road management (an annual closure occurred in part of the study area for wildlife security), logging traffic, and research traffic that occurred during each model period (Coe 2007).

We predicted relative probability of elk resource use at Sled Springs using the Starkey models with covariate values from Sled Springs. We made predictions from each Starkey model at Sled Springs for the same seasonal periods for which the Starkey models were built for each of 202,281 30-m × 30-m cells that composed Sled Springs (Coe 2007). We predicted relative probability of use and normalized these predictions across the study area as:

$$\text{Puse}_{isy} = \exp\frac{\beta_0 + \beta_1 x_{1isy} + \beta_2 x_{2isy} + \ldots \beta\text{pxp}_{isy}}{\sum_{sy}(\exp(\beta_0 + \beta_1 x_{1isy} + \beta_2 x_{2isy} + \ldots \beta\text{pxp}_{isy}))} \quad (1)$$

where Puse_{isy} was the proportion of relative probability of elk use at grid cell i during seasonal period s and year y, β_0 was the Starkey model intercept, $\beta_1\ x_{1isy} \ldots \beta\text{pxp}_{isy}$ were non-standardized Starkey model coefficients for each Sled Springs covariate x_1 through x_p model covariates at grid cell i, season s, and year y (Johnson et al. 2000, Table 2; Ager et al. 2004, Table 2; Coe 2007). We scaled the predictions to sum to 1 based on recommendations from Wiens et al. 2008. We predicted elk use for each seasonal period by year (9 seasons × 3 yr). We estimated 3-yr mean predicted use by averaging predictions for each seasonal period across years. To observe use, we captured and radio-collared elk at Sled Springs in March, 2003–2005 (Coe 2007). We placed Lotek 2200L GPS collars (Lotek Wireless, Inc., Newmarket, ON, Canada) on 10 elk in 2003 and Lotek 3300L GPS collars on 17 and 18 elk in 2004 and 2005, respectively. We removed GPS collars from elk each November. All animal handling followed protocols approved by an Institutional Animal Care and Use Committee (IACUC no. 92-F-0004, Wisdom et al. 1993) and complied with American Society of Mammalogists Animal Care and Use Committee Guidelines (Animal Care and Use Committee 1998).

Lotek GPS collars were tested extensively in our study area for precision and accuracy by Hansen and Riggs (2008). Collars were placed at 60 stratified random sites and programmed to collect ≥200 locations at 5–10 min intervals. Hansen and Riggs (2008) measured canopy cover, basal area, tree height, slope, slope position, aspect, and available sky at the sites. Mean horizontal error at these sites varied from 10 m to 50 m, well within resolution requirements for our modeling (Johnson et al. 1998, Hansen and Riggs 2008). Mean observation rate, defined as the mean percentage of scheduled locations successfully obtained by GPS collars for a given seasonal period, varied with canopy cover, and for the collar models used in our study (Lotek 2200L and 3300L), ranged 96–100% across seasonal periods and conditions (Hansen and Riggs 2008, Fig. 5a). Mean observation rate of our collars varied from 92% to 96% by season across the 3 yr of our study. Frair et al. (2004) and Nielson et al. (2009) found that observation rates ≤90% can affect RSF estimates because variation in these lower rates can be biased by environmental conditions. We did not apply corrections for observation rate.

Collars on elk were programmed to obtain 1 location every 15 min or 30 min and we only used locations from 2 hr before and after sunrise and sunset for validation, as was done for Starkey model construction (Johnson et al. 2000). We calculated observed elk use for each cell at Sled Springs by seasonal period for each of the 3 yr. We computed the observed frequency of use for each cell by summing the number of locations for radiocollared elk within each 30-m × 30-m cell for a given seasonal period and year and then dividing by the total number of observed locations in the study area for that period and year (Johnson et al. 2000, Howlin et al. 2004). We estimated 3-yr mean observed use by averaging observed use across years.

We evaluated performance of the 9 seasonal models at Sled Springs based on validation methods recommended by Boyce et al. (2002) and Howlin et al. (2004). For each seasonal period by year and the 3-yr mean, we sorted cells by predicted relative probability of use, from low to high, and we placed the values in 20 equal-area bins. We determined the number of bins by examining the probabilities on a frequency histogram (Boyce et al. 2002, Coe 2007). We then summed the predicted proportion of relative probability of use and observed proportion of use for cells within each bin for each seasonal period by year to obtain overall estimates of predicted and observed use for each period by year. We calculated a Spearman's rank correlation coefficient of predicted versus observed elk use for each period by year (Boyce et al. 2002). We assumed predicted and observed use would be positively correlated (e.g., $r > 0.60$) for better-performing models. To further examine models, we fit a linear regression to the same data and constructed 90% confidence intervals to assess whether the slope of the line included zero or 1 (Johnson et al. 2000, Howlin et al. 2004). We used the Howlin et al. (2004) suggestion to deem models unacceptable if the confidence interval of the slope included zero, acceptable if the slope was positive and the confidence interval excluded zero and 1, and good if the slope was positive and the confidence interval excluded zero and included 1.

We also calculated new RSFs for each of the 9 seasonal periods with elk locations and standardized covariates from Sled Springs. For this analysis, we used the same covariates to build the Sled Springs RSF models as were contained in the Starkey models for each seasonal period. We used a jackknife logistic regression procedure, using each radio-collared animal as the experimental unit, to estimate the coefficients of all standardized covariates for each seasonal period for the Sled Springs models, as was originally done for Starkey model construction (Johnson et al. 2000, Ager et al. 2004). We then compared standardized coefficients and standard errors from these constructed RSFs with those of the same standardized covariates in the analogous Starkey models. Our intent was to gain insight about the degree to which covariates derived at Sled Springs agreed with covariates in the Starkey models for the same seasonal period. This provided a basis for interpreting how well a given covariate or set of covariates contributed to low or high model performance of Starkey models at Sled Springs.

For best-performing (good or acceptable) models we conducted a univariate analysis on observed locations for canopy closure, distance to cover, distance to cover-forage edge, and traffic covariates to further understand how well these management-based covariates contributed to model performance. We divided proportions of observed use by proportions available for categories of each covariate and animal to compute selection ratios (Manly et al. 2002, Rowland et al. 2000). For example, we categorized canopy closure into 6 classes of cover (0–10%, 11–20%, 21–30%, 31–40%, 41–50%, and 51–60%). For each animal and category of canopy closure, we calculated the proportion of grid cells with observed locations within a class divided by the proportion of total grid cells within the class, which yielded selection ratios for the classes of the covariate by seasonal period and year. We then averaged selection ratios for each covariate across animals by seasonal period and year and averaged these ratios across years. We used a log transformation of the mean selection ratio to ensure data were normally distributed (Ramsey and Schafer 2002). For each covariate, we ran a linear regression of the log-transformed use-availability selection ratio (y) and the numerical covariate class (x). For a management covariate to perform well, we expected that regression coefficients would be the same sign as the corresponding model coefficient with model correlations >0.60.

For all analyses, we assumed that the same resources were available to each animal throughout Sled Springs. However, resource availability changed each year because timber harvest was on-going during the 3 yr of study affecting amount and distribution of forage and cover areas and associated covariates (canopy closure, distance to forage areas, distance to cover areas), as well as traffic rates. Consequently, we based all validation analyses conducted at Sled Springs on annual and seasonal estimates of resource use and availability (Coe 2007).

RESULTS

Predicted elk use was positively correlated with observed use for 5 of the 9 models we evaluated (Table 3). The 5 models included 2 for spring and 3 for late summer or early fall. For these 5 models all 3-yr mean correlation coefficients between predicted and observed use were >0.80 (Table 3). Annual correlation coefficients between predicted and observed use for these 5 models also were consistently positive, providing further support for the pattern across years (Table 3). All 5 models rated either acceptable or good based on the slope and 90% confidence intervals of the regression coefficients (Table 3). Landscape patterns of predicted versus observed elk use between the 2 study areas showed high agreement for these 5 model seasonal periods of spring and late summer–early fall (e.g., Fig. 2).

By contrast, predicted use was not strongly positively correlated with observed use for 1 spring model, 2 summer models, and the mid-fall model (Table 3; e.g., Fig. 3). For these 4 models, most annual and 3-yr correlation coefficients were negative or only slightly positive, indicating a lack of agreement between predicted and observed use (Table 3). Most of these models also rated unacceptable based on the slopes and 90% confidence intervals of the regression coefficients (Table 3).

For the 5 models that performed well, 29 of 38 (76%) covariate coefficients in the models for Sled Springs agreed in sign with those for the same covariates in the Starkey models for the same seasonal periods (Fig. 4). During mid-spring and mid-spring-late spring periods slope, aspect, soil depth, canopy cover, and distance to cover had the most consistent agreement in coefficient sign between Sled Springs and Starkey. Elk selected areas of flatter topography, south-facing aspects, shallower soils, and lower canopy cover at both Starkey and Sled Springs during these seasonal periods (Fig. 4). During late summer, early fall, and late summer-early fall the most consistent agreement in coefficient signs were cosine of aspect, soil depth, distance to cover, and distance to edge. Elk during these seasonal periods selected for north-facing aspects, deeper soils, closer to or in cover $>40\%$, and farther from cover-forage edges (Fig. 4). For spring periods, slope and canopy cover were the strongest covariates, explaining a significant amount of variation in elk locations (90% CI did not include zero, Fig. 4). In late summer, early fall, and late summer-early fall distance to cover was the strongest covariate (Fig. 4). Agreement in covariate signs between Starkey and Sled Springs models also indicated elk avoided roads of medium traffic in both

Table 3. Spearman rank correlation coefficients and regression results for test of predicted and observed use (summed to 20 bins by equal area across study area) by elk during daily foraging period at Sled Springs, northeast Oregon, USA 2003–2005. We based predicted use on models developed at Starkey Experimental Forest and Range, northeast Oregon, USA 1993–1995.

		Spearman rank correlation		Regression		
Season	Yr	r_s	P	Coeff.	CI	Utility[a]
Mid-spring: 16 Apr–15 May	2003	0.80	<0.001	0.733	$0.654 \le \bar{x} \le 0.812$	A
	2004	0.93	<0.001	0.734	$0.644 \le \bar{x} \le 0.824$	A
	2005	0.98	<0.001	1.088	$1.014 \le \bar{x} \le 1.161$	A
	2003–2005	0.95	<0.001	0.921	$0.843 \le \bar{x} \le 1.000$	G
Late spring: 16 May–15 Jun	2003	0.05	0.825	0.044	$-0.254 \le \bar{x} \le 0.342$	U
	2004	−0.54	0.015	−0.372	$-0.621 \le \bar{x} \le 0.124$	U
	2005	0.13	0.589	0.041	$-0.335 \le \bar{x} \le 0.418$	U
	2003–2005	−0.10	0.650	−0.111	$-0.339 \le \bar{x} \le 0.118$	U
Mid-spring-late spring: 16 Apr–15 Jun	2003	0.96	<0.001	0.996	$0.707 \le \bar{x} \le 1.285$	G
	2004	0.70	<0.001	0.760	$0.539 \le \bar{x} \le 0.981$	A
	2005	0.84	<0.001	0.883	$0.649 \le \bar{x} \le 1.117$	G
	2003–2005	0.91	<0.001	0.878	$0.698 \le \bar{x} \le 1.058$	G
Early summer: 16 Jun–15 Jul	2003	−0.53	0.016	−0.574	$-0.799 \le \bar{x} \le -0.349$	U
	2004	−0.08	0.724	−0.084	$-0.282 \le \bar{x} \le 0.113$	U
	2005	0.65	0.002	0.297	$0.175 \le \bar{x} \le 0.418$	A
	2003–2005	−0.48	0.031	−0.205	$-0.319 \le \bar{x} \le -0.090$	U
Mid-summer: 16 Jul–15 Aug	2003	0.60	0.005	0.173	$0.073 \le \bar{x} \le 0.274$	A
	2004	−0.11	0.643	−0.042	$-0.159 \le \bar{x} \le 0.076$	U
	2005	−0.07	0.745	−0.047	$-0.157 \le \bar{x} \le 0.063$	U
	2003–2005	0.13	0.565	0.037	$-0.056 \le \bar{x} \le 0.131$	U
Late summer: 16 Aug–15 Sep	2003	0.58	0.008	0.144	$0.047 \le \bar{x} \le 0.240$	A
	2004	0.86	<0.001	0.278	$0.192 \le \bar{x} \le 0.364$	A
	2005	0.76	<0.001	0.364	$0.261 \le \bar{x} \le 0.467$	A
	2003–2005	0.91	<0.001	0.279	$0.212 \le \bar{x} \le 0.347$	A
Late summer-early fall: 16 Aug–15 Oct	2003	0.74	<0.001	0.204	$0.135 \le \bar{x} \le 0.274$	A
	2004	0.92	<0.001	0.419	$0.322 \le \bar{x} \le 0.516$	A
	2005	0.87	<0.001	0.285	$0.207 \le \bar{x} \le 0.363$	A
	2003–2005	0.91	<0.001	0.310	$0.241 \le \bar{x} \le 0.379$	A
Early fall: 16 Sep–15 Oct	2003	0.53	0.016	0.297	$0.191 \le \bar{x} \le 0.404$	A
	2004	0.89	<0.001	0.509	$0.390 \le \bar{x} \le 0.627$	A
	2005	0.65	0.002	0.297	$0.175 \le \bar{x} \le 0.418$	A
	2003–2005	0.81	<0.001	0.369	$0.282 \le \bar{x} \le 0.455$	A
Mid-fall: 16 Oct–15 Nov	2003	−0.61	0.005	−0.300	$-0.535 \le \bar{x} \le -0.065$	U
	2004	−0.10	0.677	0.137	$-0.065 \le \bar{x} \le 0.338$	U
	2005	−0.39	0.094	−0.236	$-0.493 \le \bar{x} \le 0.020$	U
	2003–2005	−0.57	0.008	−0.124	$-0.271 \le \bar{x} \le 0.023$	U

[a] Utility: U = unacceptable: coeff. is positive or negative and CI includes 0, A = acceptable: coeff. is >0 and <1 or coeff. is >1 and CI excludes 0 and 1, and G = Good: coeff. > 0 and CI excludes 0 and includes 1 (Howlin et al. 2004).

study areas during mid-spring and roads of low and high traffic during late summer, early fall, and late summer-early fall (the medium traffic covariate did not occur in these models). Use of canopy cover in these models was consistent in all spring periods but opposite in the late summer and late summer-early fall periods (Fig. 4). Whereas elk at Starkey used areas of higher canopy cover during these seasonal periods, elk at Sled Springs continued to use areas of lower canopy cover (Fig. 4).

For the 4 models that did not perform well, 16 of 31 (52%) coefficients did not agree in sign between covariates in Sled Springs and Starkey models (Fig. 5). Only 2 of 5 covariates in the late spring (16 May–15 Jun) model had the same coefficient sign between covariates in the Sled Springs and Starkey models (Fig. 5). Similarly, only 3 of 11 covariates in the early summer model agreed. By mid-summer 7 of the 11 covariates agreed but still resulted in poor performing models in all years except 2003 (Table 3). For these 4 models that did not perform well, coefficient signs still agreed across models for distance to cover and for most traffic covariates (Fig. 5). Elk used more open areas (lower canopy cover) at Sled Springs during mid-summer and mid-fall, contrasting with the same seasonal periods at Starkey, where elk used higher canopy cover areas (Fig. 5).

Several management-based covariates contributed to the effectiveness of the 5 best-performing models. Elk showed strong avoidance of roads with medium traffic rates, based on the univariate selection ratio of observed use versus availability for this covariate in the 1-month mid-spring (16 Apr–15 May) model (Table 4). Similarly, elk avoided roads of medium traffic rates based on selection ratios of these covariates in the 2-month mid-spring-late spring (16 Apr–15 Jun) model (Table 4). Elk also selected areas of lower canopy closure during spring, as shown by selection ratios in the 1- and 2-month spring models (Table 4). Elk avoided roads with low and high traffic rates during late summer based on selection ratios for these covariates in the 1-month late summer (16 Aug–15 Sep) and early fall (16 Sep–15 Oct) models, as well as the 2-month late summer-early fall (16 Aug–15 Oct) model (Table 4). Canopy cover class was not important during the late summer and early fall periods. However, elk selected distance classes closer to or in cover

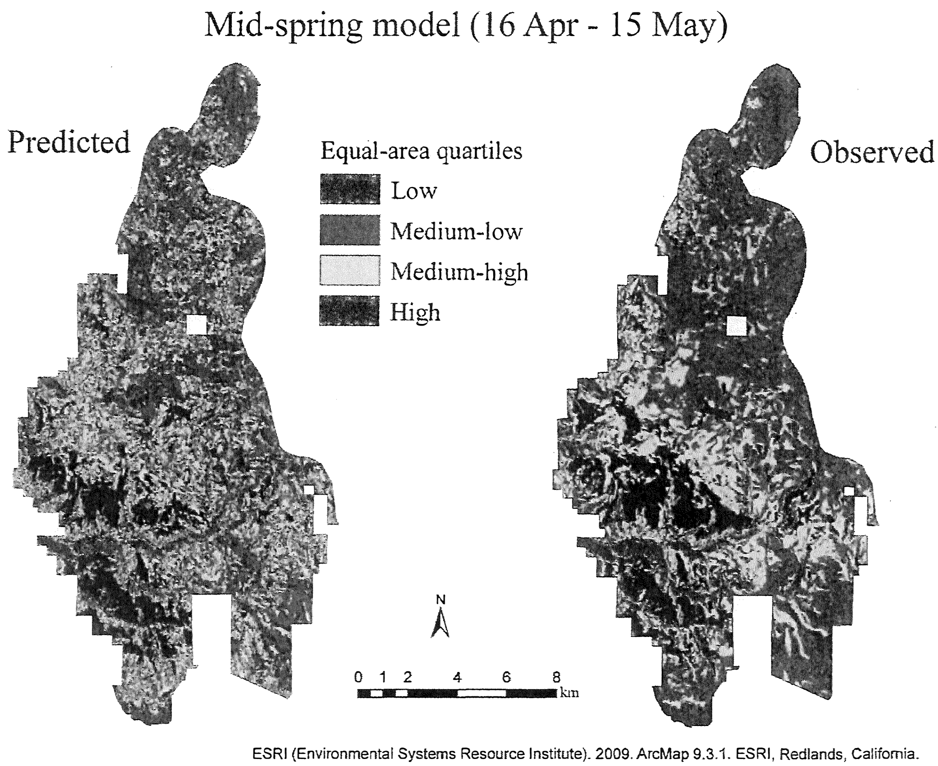

Figure 2. Predicted and observed elk use at Sled Springs, Oregon, USA, 2003–2005 for the 1-month mid-spring (16 Apr–15 May) model, an example of 1 of the 5 best-performing models.

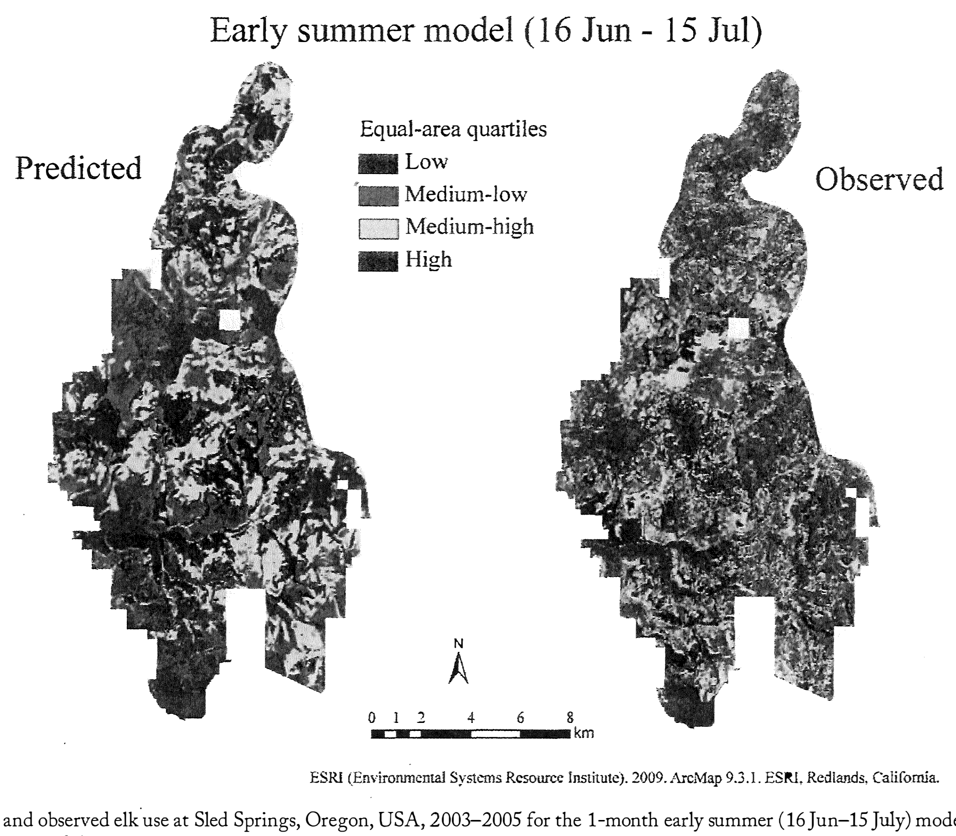

Figure 3. Predicted and observed elk use at Sled Springs, Oregon, USA, 2003–2005 for the 1-month early summer (16 Jun–15 July) model, an example of 1 of the 4 worst-performing models.

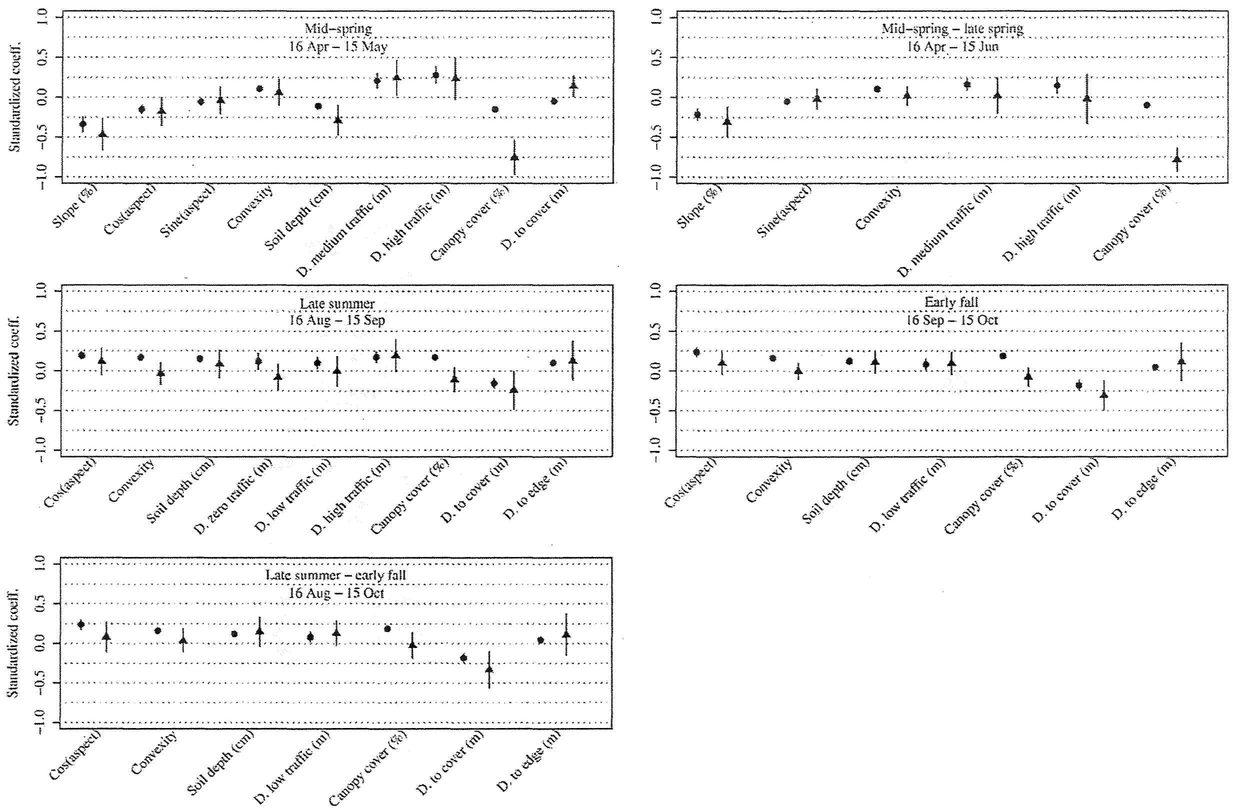

Figure 4. Comparison of elk resource selection function model coefficients from standardized covariates for top performing models developed at Starkey Experimental Forest and Range, Oregon, USA 1993–1996 and validated at Sled Springs, Oregon, USA, 2003–2005. Circles (Starkey) and triangles (Sled Springs) represent model coefficients and error bars represent 90% confidence intervals. Distance is abbreviated as "*D.*" in *x*-axis labels. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com]

>40% during early fall (16 Sep–15 Oct) and late-summer-early fall (16 Aug–15 Oct; Table 4).

DISCUSSION

Our results addressed the concern of extrapolating elk RSFs to areas outside of the study areas where they were developed, a topic that has seldom been addressed in ungulate habitat selection studies (Boyce et al. 2002, Wiens et al. 2008). We identified the seasonal periods during which models performed acceptably (high spatial and temporal repeatability) versus periods associated with poor model performance (low spatial or temporal repeatability). Results were mixed among seasonal models and we discuss possible reasons for model performance and suggest improvements. For models that performed well, correlation of most vegetation and traffic covariates with probability of elk use were consistent with previous studies (Rowland et al. 2000, Ager et al. 2003). Consequently, these models will be useful for management planning in areas with similar landscape characteristics.

Forage Dynamics

Models performed best during seasons when forage for ungulates was limited in northeastern Oregon, including mid-spring, late summer, and early fall (Skovlin 1967, Vavra and Phillips 1980, Miller et al. 1981, Holechek et al. 1982). Models performed poorly during late spring to mid-summer, when forage typically was abundant in many habitat types and when the phenology of most forage species made them highly nutritious across most habitat types in our study areas (Skovlin 1967, Vavra and Phillips 1980). In that regard, poor performance of early and mid-summer models may simply reflect a lack of strong selection patterns by elk during times in which foraging choices were not restricted to a narrow set of habitats.

Availability of nutritious forage at Starkey and Sled Springs during mid-spring was largely associated with south-facing open areas, which composed <20% of landscapes at Starkey and Sled Springs. By contrast, nutritious forage within the larger, forest-dominated areas of these landscapes did not develop until early summer (Skovlin 1967, Miller et al. 1981). Most nutritious forage in forested areas remained available from early summer until senescence in late summer or early fall (Skovlin 1967, Vavra and Phillips 1980). The remaining, nutritious forage was then spatially restricted to mesic sites associated with wet meadows or forests with higher canopy closure (Peek et al. 2001; J. G. Cook, National Council for Air and Stream Improvement, unpublished data). These seasonal forage dynamics largely followed our results that demonstrated high model performance during spring and late summer-early fall (limited habitats with nutritious forage) and low model performance during late spring and mid- and early summer (abundant habitats with nutritious forage).

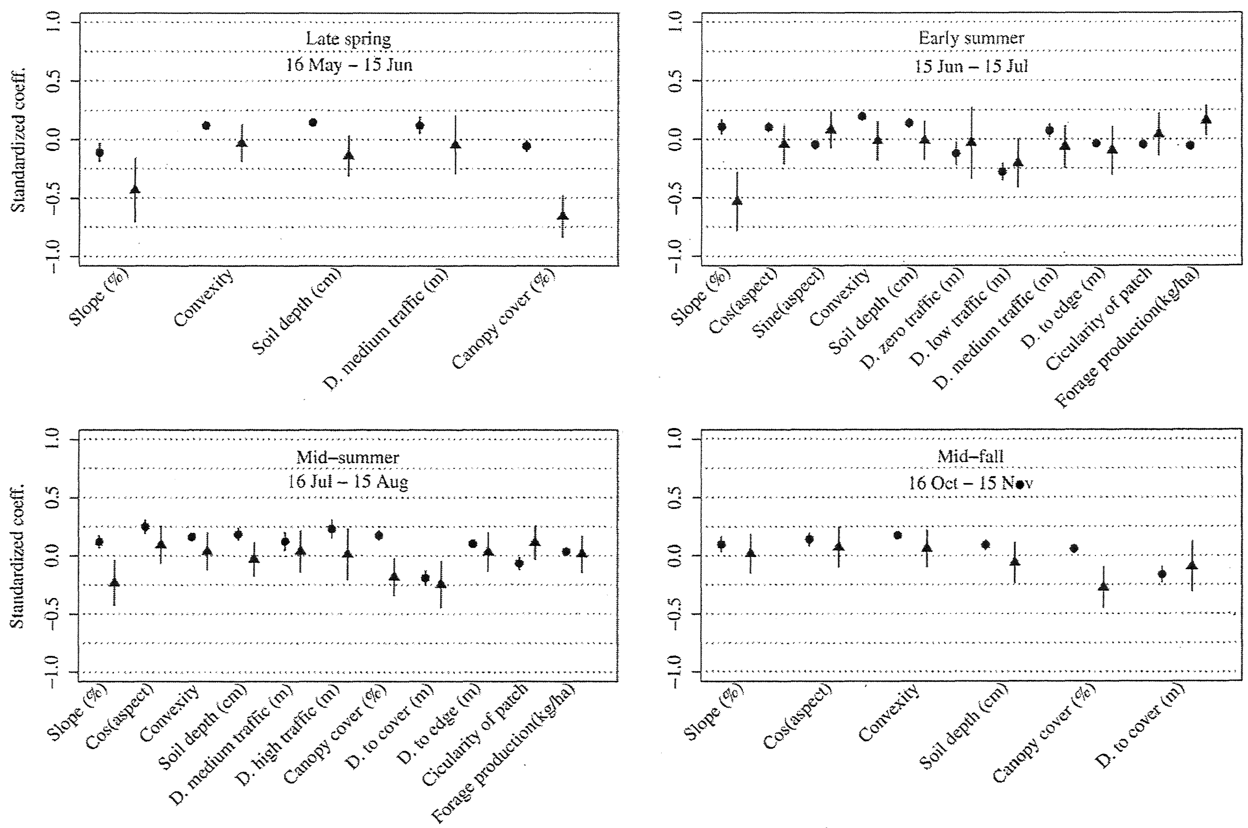

Figure 5. Comparison of elk resource selection function model coefficients from standardized covariates for poor performing models developed at Starkey Experimental Forest and Range, Oregon, USA 1993–1996 and validated at Sled Springs, Oregon, USA, 2003–2005. Circles (Starkey) and triangles (Sled Springs) represent model coefficients and error bars represent 90% confidence intervals. Distance is abbreviated as "*D.*" in *x*-axis labels. Elk were hunted at Sled Springs during the mid-fall observation period. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com]

Precipitation differences between Starkey and Sled Springs appeared to account for differences in phenology between study areas, in turn affecting forage quality and temporal availability during summer months (P. K. Coe, Oregon Department of Fish and Wildlife, unpublished data; T. DelCurto, Oregon State University, unpublished data). Sled Springs was consistently higher in precipitation during March–May and September–November, whereas

Table 4. Univariate regression results of the log-transformed use-availability selection ratios (y) and the numerical covariate classes (x) for each management-based covariate in the 5 best-performing elk resource selection models at Sled Springs, Oregon, USA 2003–2005. Classes for distance covariates were 0–50 m, 51–100 m, 101–250 m, 251–500 m, and 501–1,000 m. Classes for canopy cover were 0–10%, 11–20%, 21–30%, 31–40%, 41–50%, and 51– 60%.

Model	Management covariate	Coeff.	*P*	*r*
Mid-spring: 16 Apr–15 May	Distance to medium traffic	0.0003	0.006	0.97
	Distance to high traffic	−0.0002	0.074	0.84
	Distance to cover	0.0000	0.731	0.11
	Canopy closure	−0.0184	0.005	0.94
Mid-spring-late spring: 16 Apr–15 Jun	Distance medium traffic	0.0001	0.073	0.84
	Distance high traffic	0.0000	0.411	0.42
	Canopy closure	−0.0200	0.005	0.97
Late summer: 16 Aug–15 Sep	Distance to zero traffic	−0.0002	0.024	0.93
	Distance to low traffic	0.0000	0.129	0.69
	Distance to high traffic	0.0000	0.082	0.70
	Distance to cover	−0.0001	0.553	0.31
	Canopy closure	0.0000	0.991	0.01
Late summer-early fall: 16 Aug–15 Oct	Distance to cover-forage edge	0.0004	0.021	0.68
	Distance to low traffic	0.0002	0.003	0.98
	Distance to cover	−0.0004	<0.001	0.93
	Canopy closure	−0.0065	0.047	0.82
Early fall: 16 Sep–15 Oct	Distance to cover-forage edge	0.0002	0.118	0.78
	Distance to low traffic	0.0001	0.017	0.84
	Distance to cover	−0.0001	0.041	0.83
	Canopy closure	−0.0004	0.889	0.07

precipitation in both study areas during July and August was low (Table 1). Higher precipitation during spring at Sled Springs resulted in a longer period of forage growth into mid-summer, a shorter period of summer drought, and delayed forage senescence during late summer and early fall (Skovlin 1967). Similarly, higher precipitation at Sled Springs during fall enhanced forage re-growth during this period (Skovlin 1967, Westenskow et al. 1994). Differences in spring precipitation and forage phenology may have contributed to low performance of the mid-summer (16 Jul–15 Aug) models at Sled Springs because elk at Starkey selected areas of higher canopy closure during summer with earlier onset of forage senescence. During this same seasonal period, elk at Sled Springs continued to select more open canopy areas where forage quality was sustained longer (Fig. 5 and Table 4). Differences in precipitation between the 2 study areas did not appear to be a factor in elk use of areas of low canopy closure during spring. During mid-spring, available forage was concentrated in open, southwest-facing slopes with low or no canopy closure, whereas northern aspects and stands with dense canopy were either covered with snow or the herbaceous vegetation had not started to grow (P. K. Coe, Oregon Department of Fish and Wildlife, unpublished data; T. DelCurto, Oregon State University, unpublished data). Consequently, elk selected areas of <10% canopy closure in open areas with southerly aspects in both study areas during mid-spring, which constituted the largest snow-free areas of nutritious forage.

Hunting Effects

Our results showed poor model performance at Sled Springs during rifle hunting seasons in mid-fall. Starkey models developed for mid-fall purposely excluded hunting seasons. Performance of this non-hunting Starkey model at Sled Springs during hunting seasons suggested that elk resource selection patterns can be strikingly different for hunting versus non-hunting periods during equivalent times of year. This inference is supported by previous research on behavioral responses of elk to hunting at Starkey, which showed that movement rates and distances moved increase dramatically with the onset of rifle hunting (Johnson et al. 2004). The mid-fall, non-hunting Starkey model performed poorly when tested at Starkey during an elk hunting season (Johnson et al. 2004). Pre-hunt resource selection patterns are likely to change with onset of hunting, with increased and longer movements of elk in response to avoidance of hunters (Johnson et al. 2004). Conner et al. (2001) documented rapid, long-distance movements of elk in response to hunting. This type of response was evident in our GPS elk location data at Sled Springs, which showed that several radiocollared elk moved long distances and some left the study area during rifle hunts (Coe 2007).

Potential Model Improvements

The predictive ability of our resource selection models for elk might be improved with the addition of an explicit nutrition covariate. Our forage production covariate was based on a course-grained plant community type and was not explicitly related to changing forage dynamics (Johnson et al. 2000). A nutrition covariate would more directly account for differences in precipitation and associated forage conditions between the 2 study areas and in other areas where our models might be applied and validated. Development of a nutrition covariate requires data on biomass and digestible energy of elk forage species and groups of species by season. Such data are costly and time-consuming to collect and analyze, but once collected, could be linked to remotely-sensed classified vegetation data and used to build and evaluate different nutrition covariates in relation to predicted and observed use of landscapes by elk. Alternatively, site-specific differences in nutritional resources could be accounted for by incorporating a greenness covariate into models. Greenness indices, such as the Normalized Difference Vegetation Index (NDVI) or the Enhanced Vegetation Index (EVI), are less costly and time-consuming for indexing forage dynamics between different study areas but do not directly measure forage quality (Burgan et al. 1996, Huete et al. 2002). Data for bi-weekly periods are widely available at a resolution of 1 km^2 (USDA Forest Service 2009*b*) and somewhat less available at higher resolutions of 0.02–0.80 km^2 (U.S. Geological Survey 2009).

Greenness indices have been used in resource selection studies for large vertebrates (Carroll et al. 2003, Nielsen et al. 2003, Marshal et al. 2006) as important predictors of spatial distribution. Moreover, it is likely that greenness covariates would be positively correlated with more explicit nutrition covariates. Hamel et al. (2009) found that NDVI accounted for most variation in fecal crude protein levels for mountain goat (*Oreamnos americanus*) and bighorn sheep (*Ovis canadensis*) populations in Canada. Results of Hamel et al. (2009) were compelling, given that NDVI remained highly correlated with fecal crude protein throughout all phases of seasonal forage dynamics. These results suggest that additional research to understand the potential utility of greenness covariates as predictors of forage conditions could be productive. If such a relationship was documented for elk and other ungulates, the use of a greenness covariate in resource selection models could potentially account for differences in seasonal forage dynamics, such as at Starkey and Sled Springs.

MANAGEMENT IMPLICATIONS

On a local level, validation of these models may be useful to land managers in the Blue Mountains of northeast Oregon because the validation extends the inference space to a different landscape (spatial validation) and to different years (temporal validation). In addition, we validated the models on private industrial lands as opposed to public lands, where the models were developed. Models that performed well can be expected to perform well across land ownerships in the Blue Mountains, which is helpful in assessing cumulative impacts of management activities associated with timber and road management on a landscape level.

Our 2-month models for mid-spring-late spring and late summer-early fall performed well, suggesting that these models would be effective for management applications. Covariates in these models are readily available and routinely used by most resource management agencies. The 2-month mid-spring–late spring (16 Apr–15 Jun) model encompassed an important life stage (late gestation and parturition) for elk (Thorne et al. 1976). Similarly, the 2-month late summer-early fall (16 Aug–15 Oct) model encompassed a critical period for elk nutrition and reproduction (Cook et al. 2004). Consequently, these 2-month models are arguably the most useful to land managers interested in mitigating effects of management activities on elk. Management-based covariates that influenced elk use independently of other variables in these 2-month models included roads of different traffic rates, canopy cover, distance to cover-forage edge, and distance to cover. Manipulation of these covariates by managers would help facilitate desired changes in elk distributions to meet elk objectives for a given landscape.

On a regional level our results indicate that elk RSFs may be transferable to other large landscapes of public and private lands in the Blue Mountains ecoregion, as well as to large landscapes with similar environmental conditions in other ecoregions. The best performing models may be useful in other heterogeneous, forested landscapes of the intermountain west with similar climate patterns and rural character in forest planning and travel management plans.

Our results illustrated the importance of validating resource selection models on landscapes and over time periods independent of those from which the models were built and across a variety of seasonal periods. Without evaluating how generalizable resource selection models are, management applications beyond areas of model development are difficult to justify. Increased emphasis on validating elk resource selection patterns across different landscapes would further strengthen management use of resource selection models.

ACKNOWLEDGMENTS

We thank the Associate Editor, 2 anonymous reviewers L. McDonald and H. Sawyer for their helpful reviews, and R. Riggs, B. Kernohan, S. Dodson, D. Damarin, E. Darambazar, and D. Motanic for geographic information system and data support. Assistance with data analysis and analytical methods were provided by H. Beyer, N. Cimon, C. Erickson, M. Hansen, B. Huber, A. Rodgers, and G. Roloff. Financial and logistical support was provided by Federal Aid in Wildlife Restoration Project W-87-R, Oregon Department of Fish and Wildlife, USDA Forest Service Pacific Northwest Research Station, National Council for Air and Stream Improvement, Rocky Mountain Elk Foundation, Eastern Oregon Agricultural Research Station, Oregon State University Research Foundation, Boise Cascade Corporation, and Forest Capital Partners, Inc.

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Associate Editor: Scott M. McCorquodale.