Research Article

Habitat Selection of Rocky Mountain Elk in a Nonforested Environment

HALL SAWYER,[1] *Western Ecosystems Technology, Inc., 2003 Central Avenue, Cheyenne, WY 82001, USA*
RYAN M. NIELSON, *Western Ecosystems Technology, Inc., 2003 Central Avenue, Cheyenne, WY 82001, USA*
FRED G. LINDZEY,[2] *United States Geological Survey, Wyoming Cooperative Fish and Wildlife Research Unit, Box 3166, Laramie, WY 82071, USA*
LORRAINE KEITH, *Bureau of Land Management, 280 Highway 191 North, Rock Springs, WY 82901, USA*
JAKE H. POWELL,[3] *United States Geological Survey, Wyoming Cooperative Fish and Wildlife Research Unit, Box 3166, Laramie, WY 82071, USA*
ANU A. ABRAHAM, *Department of Statistics, University of Wyoming, 1000 E. University Avenue, Laramie, WY 82071, USA*

ABSTRACT Recent expansions by Rocky Mountain elk (*Cervus elaphus*) into nonforested habitats across the Intermountain West have required managers to reconsider the traditional paradigms of forage and cover as they relate to managing elk and their habitats. We examined seasonal habitat selection patterns of a hunted elk population in a nonforested high-desert region of southwestern Wyoming, USA. We used 35,246 global positioning system locations collected from 33 adult female elk to model probability of use as a function of 6 habitat variables: slope, aspect, elevation, habitat diversity, distance to shrub cover, and distance to road. We developed resource selection probability functions for individual elk, and then we averaged the coefficients to estimate population-level models for summer and winter periods. We used the population-level models to generate predictive maps by assigning pixels across the study area to 1 of 4 use categories (i.e., high, medium-high, medium-low, or low), based on quartiles of the predictions. Model coefficients and predictive maps indicated that elk selected for summer habitats characterized by higher elevations in areas of high vegetative diversity, close to shrub cover, northerly aspects, moderate slopes, and away from roads. Winter habitat selection patterns were similar, except elk shifted to areas with lower elevations and southerly aspects. We validated predictive maps by using 528 locations collected from an independent sample of radiomarked elk ($n = 55$) and calculating the proportion of locations that occurred in each of the 4 use categories. Together, the high- and medium-high use categories of the summer and winter predictive maps contained 92% and 74% of summer and winter elk locations, respectively. Our population-level models and associated predictive maps were successful in predicting winter and summer habitat use by elk in a nonforested environment. In the absence of forest cover, elk seemed to rely on a combination of shrubs, topography, and low human disturbance to meet their thermal and hiding cover requirements.
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Of the North American ungulates, Rocky Mountain elk (*Cervus elaphus*) are among the most widely distributed and most-studied species. Elk are generally known to avoid roads open to vehicles (Lyon 1983, Witmer and DeCalesta 1985, Grover and Thompson 1986, Rowland et al. 2000), and they prefer areas characterized by edge habitat (Thomas et al. 1979, 1988; Irwin and Peek 1983; Grover and Thompson 1986), where quality forage and forest cover habitats are in proximity. Additionally, topographic features such as slope, elevation, and aspect are known to influence the habitat selection patterns of elk (Edge et al. 1987, Skovlin et al. 2004). This knowledge of elk behavior has been incorporated into numerous habitat suitability and other predictive models (Witmer et al. 1985, Wisdom et al. 1986, Roloff et al. 2001, Benkobi et al. 2004) used to improve elk management and to guide land-use planning in forested regions.

Although considerable data support elk management and habitat preferences in montane and forested environments, our knowledge of elk ecology in nonforested environments is limited. Few studies have focused on elk populations that occupy desert or nonforested environments, and those studies have been restricted to relatively small, nonhunted populations that inhabit land reserves with limited public access in Washington (McCorquodale et al. 1986, 1989; McCorquodale 1991) and Idaho, USA (Strohmeyer and Peek 1996, Strohmeyer et al. 1999). Nonetheless, recent range expansions by elk have demonstrated their ability to readily adapt to open environments (Lindzey et al. 1997), requiring managers to re-evaluate the traditional paradigms of forage (open meadows and clear cuts) and cover (timber) as they relate to managing elk habitat in nonforested areas. Our objective was to identify and describe seasonal habitat selection patterns of a hunted elk population in a non-forested desert region of southwestern Wyoming, USA.

STUDY AREA

Our study area was defined by the 2,517-km^2 Jack Morrow Hills Planning Area (JMHPA) located in southwestern Wyoming (Bureau of Land Management [BLM] 2004*a*). Elevations ranged from 2,000 m to 2,650 m. Our study area was generally characterized as a high-elevation cold desert with a variety of sagebrush (*Artemisia* spp.) and mixed shrub–grassland communities. The relative abundance of 8 general land cover types included 5% basin big sagebrush (*A. tridentata tridentata*); 30% Wyoming sagebrush (*A. tridentata wyomingensis*); 14% grassland; 17% greasewood

[1] *E-mail: hsawyer@west-inc.com*
[2] *Present address: 15 Millbrook Road, Laramie, WY 82070, USA*
[3] *Present address: Idaho Department of Fish and Game, Southwest Region, 3101 S. Powerline Road, Nampa, ID 83686, USA*

(*Sarcobatus vermiculatus*); 16% mixed shrub, including saltbush (*Atriplex gardneri*), rabbitbrush (*Chyrsothamnus* spp.), mountain mahogany (*Cercocarpus* spp.), and bitterbrush (*Purshia tridentata*); 14% bare ground or sand dune; 3% riparian grass and shrubs; and 1% tree cover, including aspen (*Populus tremuloides*) and Rocky Mountain juniper (*Juniperus scopulorum*; BLM 2004*b*). The BLM administered 92% of the land surface, including 5 federally designated areas of critical environmental concern and 7 wilderness study areas (BLM 2004*a*). Livestock grazing occurred in 15 allotments of various sizes, and the active permitted use was 26,830 animal unit months, of which approximately 12% were sheep and 88% were cattle (BLM 2004*a*). Approximately 380 km of maintained dirt and 44 km of paved roads occurred in our study area.

Although unregulated hunting extirpated most elk in the region by the early 1900s, the Wyoming Game and Fish Department successfully transplanted 408 elk between 1946 and 1967 (Ryder et al. 1986). Since then, the elk population has steadily increased, and today it is managed for 1,200 animals and provides 350 annual hunting permits (G. Frost, Wyoming Game and Fish Department, unpublished report).

METHODS

Capture and Monitoring

We used helicopter net-gunning to capture and radiomark adult (>1.5-yr-old) female elk across winter ranges in the JMHPA. We blindfolded and hobbled elk to facilitate handling to minimize injuries. Between January 1999 and February 2001, we fitted 55 elk with very high frequency (VHF) radiocollars. Between March and December 2003, we fitted 33 elk with store-on-board Global Positioning System (GPS) radiocollars (TGW 2500, Telonics, Mesa, AZ). We programmed the GPS units to obtain locations every 4 hr. We equipped all collars with mortality sensors that changed pulse rate if the collar remained motionless for >8 hr. We located radiomarked elk from fixed wing aircraft approximately once per month and used helicopter net-gunning to retrieve GPS collars from elk at the end of the study in December 2004. Fix-rate bias was not an issue because of the high fix-rate success (97%), and we did not differentially correct GPS locations because 86% of the locations were 3-dimensional.

Modeling Procedures

We identified 6 variables as potentially important landscape predictors of summer (from 15 Jun to 15 Sep) and winter (from 15 Nov to 15 Mar) elk distribution, including elevation, slope, aspect, distance to road, distance to shrub cover, and habitat diversity. We used the SPATIAL ANALYST extension for ArcView to calculate slope and aspect from a 26 × 26-m digital elevation model (U.S. Geological Survey 1999). We obtained elevation, slope, and aspect (northeast, northwest, southwest, and southeast) values for each of the sampled units. We digitized existing maintained roads from 1:100,000 scale maps and defined them as dirt, gravel, and paved roads actively maintained by the county or state (Powell 2003). We did not include 2-track roads in the analysis because of the relatively low vehicular use they received. We calculated distance to shrub cover and habitat diversity by using a 30-m resolution vegetation map delineated from LandSat thematic mapper data (BLM 2004*b*). We defined cover as any vegetation type with trees or shrubs that could reach 1.5 m in height. Noncover categories included grassland, bare ground, and sand. We calculated a Shannon's diversity index (McGarigal and Marks 1995) for each sampling unit by using a customized FORTRAN routine (T. McDonald, Western Ecosystems Technology, unpublished data) that we based on the 8 land cover types identified under Study Area. We did not include vegetation type as a predictor variable because we wanted to develop a model that could be easily applied or extrapolated to other desert environments where vegetation types may differ from the JMHPA.

We followed the modeling approach used by Sawyer et al. (2006) that consisted of 4 basic steps: 1) estimate the relative frequency of use (i.e., an empirical estimate of probability of use) for a large number of sampling units for each GPS-collared elk during winter and summer, 2) use the relative frequency as the response variable in a multiple regression analysis to model the probability of use for each elk as a function of predictor variables, 3) develop a population-level model from the individual elk models for each season, and 4) map predictions of population-level models from each season. We treated individual radiomarked elk as the experimental unit to avoid pseudoreplication (i.e., spatial and temporal autocorrelation) and to accommodate population-level inference (Otis and White 1999, Erickson et al. 2001, Millspaugh et al. 2006).

We estimated relative frequency of use for each GPS-collared elk by using a simple technique that involved counting the number of elk locations in each of 10,063 systematically sampled circular sampling units across the study area. We chose circular sampling units that had 250-m (19.6-ha) radii, an area small enough to detect changes in animal movements but large enough to ensure multiple locations could occur in each unit. We measured predictor variables from each of the sampling units and conducted a Pearson's pairwise correlation analysis (PROC CORR, SAS Institute 2000) before modeling to identify multicollinearities and to determine whether we should exclude any variables from the analysis ($|r| > 0.60$).

The relative frequency of locations from a GPS-collared elk found in each sampling unit provided an empirical estimate of the probability of use by that elk, and we used it as a continuous response variable in a generalized linear model (GLM). We used an offset term in the GLM to estimate probability of use for each GPS-collared elk as a function of a linear combination of predictor variables, plus or minus an error term assumed to have a negative binomial distribution (McCullagh and Nelder 1989, White and Bennetts 1996).

We obtained a population-level model for each season by first estimating coefficients for each GPS-collared elk. We used PROC GENMOD (SAS Institute 2000) and the negative binomial distribution to fit the following GLM for each GPS-collared elk during each winter and summer period:

$$\ln(E[r_i]) = \ln(total) + \beta_0 + \beta_1 X_1 + \ldots + \beta p X p, \quad (1)$$

which was equivalent to

$$\ln(E[r_i/total]) = \ln(E[\text{Relative Frequency}_i]) = \beta_0 + \beta_1 X_1 + \ldots + \beta_p X_p, \quad (2)$$

where r_i is the number of locations for a GPS-collared elk within sampling unit i ($i = 1, 2, \ldots, 10{,}063$), *total* is the total number of locations for that elk within the study area, β_0 is an intercept term, $\beta_1, \ldots, \beta_p$ are unknown coefficients for habitat variables $X_1, \ldots, X_p$, and $E[.]$ denotes the expected value. We used the same offset term for all sampled units of a given elk; thus, the term ln(*total*) was absorbed into the estimate of β_0 and ensured we were modeling relative frequency of use (e.g., 0, 0.003, 0.0034, ...) instead of integer counts (e.g., 0, 1, 2, ...). This approach to modeling resource selection estimated the relative frequency or absolute probability of use as a function of predictor variables, so we referred to it as a resource selection probability function (RSPF; Manly et al. 2002).

We assumed GLM coefficients for predictor variable *k* for each elk were a random sample from a normal distribution (Seber 1984), with the mean of the distribution representing the average or population-level effect of predictor variable *k* on probability of use. We estimated coefficients for the population-level model for each winter and summer period by using

$$\hat{\hat{\beta}}_k = \frac{1}{n}\sum_{j=1}^{n} \hat{\beta}_{kj}, \quad (3)$$

where $\hat{\beta}_{kj}$ was the estimate of coefficient *k* for individual *j* ($j = 1, \ldots, n$). We estimated the variance of each population-level model coefficient by using the variation between GPS-collared elk and the equation

$$\text{var}(\hat{\hat{\beta}}_k) = \frac{1}{n-1}\sum_{j=1}^{n}(\hat{\beta}_{kj} - \hat{\hat{\beta}}_k)^2 \quad (4)$$

This method of estimating population-level coefficients has been used to evaluate habitat selection patterns of Stellar's jay (*Cyanocitta stelleri*; Marzluff et al. 2004) and mule deer (*Odocoileus hemionus*; Sawyer et al. 2006). Population-level inferences using equations 3 and 4 are unaffected by potential auto- or spatial correlation, because temporal autocorrelation between locations of an individual elk or spatial autocorrelation between habitat units does not bias model coefficients for the individual radiomarked elk models (McCullagh and Nelder 1989, Neter et al. 1996).

We used a forward-stepwise model-building procedure (Neter et al. 1996) to estimate population-level models for 3 periods: summer 2003, summer 2004, and winter 2003–2004. The forward-stepwise model-building process required fitting the same models to each elk within a season and using equations 3 and 4 to estimate population-level model coefficients. We used a *t*-statistic to determine variable entry ($\alpha \leq 0.15$) and exit ($\alpha > 0.20$; Hosmer and Lemeshow 2000). We considered quadratic terms for distance to road and slope during the model-building process and included the linear form of each variable if the model contained a quadratic form. We used northeasterly aspect as the reference, and if one or more of the other aspect categories (northwest, southeast, and southwest) was significant ($\alpha \leq 0.15$), we elected to include all of the categories rather than define the effects of the nonsignificant categories to be equal.

We mapped predictions of population-level models for each season across 350 × 350-m pixels that covered the study area. We checked predictions to ensure all values were in the [0,1] interval, such that we were not extrapolating outside the range of the model data. We assigned the predictions for each pixel a value of 1 to 4 based on the quartiles of the distribution of predictions for each map. We assigned pixels with the highest 25% of predicted probabilities of use a value of 1 and classified them as high-use areas, assigned pixels in the 51 to 75 percentiles a value of 2 and classified them as medium-high use areas, assigned pixels in the 26 to 50 percentiles a value of 3 and classified them as medium-low use areas, and assigned pixels in the 0 to 25 percentiles a values of 4 and classified them as low-use areas. We then used 528 VHF locations collected between February 1999 and November 2002 from an independent sample ($n = 55$) of radiomarked elk to validate the population-level model predictive maps by calculating the proportion of locations that occurred within each quartile.

RESULTS

Summer 2003

We developed individual RSPFs for 25 GPS-collared elk (13,524 locations) during summer 2003. Most elk had positive coefficients for elevation (22 of 25), habitat diversity (19 of 25), and northerly aspects (15 of 25), and they had negative coefficients for distance to cover (14 of 25). Quadratic terms indicated most elk selected for moderate slopes (24 of 25) and away from roads (24 of 25).

We estimated a population-level model (Table 1) and associated predictive map (Fig. 1) that included all 6 predictor variables, with quadratic terms for slope and distance to road. Elk selected for areas with high elevations, high habitat diversity, close to shrub cover, and northerly aspects. Quadratic terms indicated elk selected areas with moderate slopes and away from roads. Areas with the highest probability of use were 2.78 km (SE = 0.40) away from roads and had slopes of 9° (SE = 0.25).

Summer 2004

We developed individual RSPFs for 20 GPS-collared elk (10,528 locations) during summer 2004. Distance to shrub cover and habitat diversity variables did not enter the models because they were not significant ($\alpha > 0.15$) at the population level. Most elk had positive coefficients for

Table 1. Coefficients for population-level models of Global Positioning System–collared elk during summer 2003, summer 2004, and winter 2003–2004 in the Jack Morrow Hills Planning Area, Wyoming, USA.

Predictor variable	Summer 2003			Summer 2004			Winter 2003–2004		
	β	SE	*P*	β	SE	*P*	β	SE	*P*
Intercept	–34.967	4.021	<0.001	–30.739	6.017	<0.001	–5.663	3.320	0.105
Elevation (m)	0.009	0.002	<0.001	0.008	0.003	0.007	–0.004	0.002	0.038
Slope (°)	0.703	0.065	<0.001	0.584	0.071	<0.001	0.897	0.086	<0.001
Slope^2 (°)	–0.040	0.004	<0.001	–0.032	0.004	<0.001	–0.040	0.005	<0.001
Distance to road (km)	0.927	0.159	<0.001	0.767	0.221	0.003	0.369	0.142	0.018
Distance to road^2 (km)	–0.167	0.027	<0.001	–0.137	0.033	0.001	–0.154	0.025	<0.001
Habitat diversity	0.441	0.222	0.012	N.S.[a]			0.515	0.132	0.001
Distance to cover (m)	–0.002	0.000	0.163	N.S.			–0.006	0.002	0.013
Aspect northwest	0.057	0.118	0.109	0.295	0.169	0.097	–0.212	0.228	0.365
Aspect southeast	–0.199	0.145	0.871	0.287	0.167	0.102	0.384	0.152	0.021
Aspect southwest	–0.622	0.230	0.021	–0.200	0.318	0.537	–0.173	0.297	0.568

[a] Not significant.

elevation (17 of 20) and northerly aspects (14 of 20). Quadratic terms indicated most elk selected for moderate slopes (18 of 20) and away from roads (17 of 20).

We estimated a population-level model (Table 1) and associated predictive map (Fig. 2) that included 4 of the 6 predictor variables. Elk selected for areas with high elevations and northerly aspects. Quadratic terms indicated elk selected areas with moderate slopes and away from roads. Areas with the highest probability of use were 2.80 km (SE = 0.48) away from roads and had slopes of 9° (SE = 0.54).

Winter 2003–2004

We developed individual models for 19 GPS-collared elk (11,194 locations) during winter 2003–2004. Most elk had negative coefficients for elevation (15 of 19) and distance to cover (13 of 19), and they had positive coefficients for habitat diversity (15 of 19) and southerly aspects (14 of 19). Quadratic terms indicated most elk selected for moderate slopes (18 of 19) and away from roads (16 of 19).

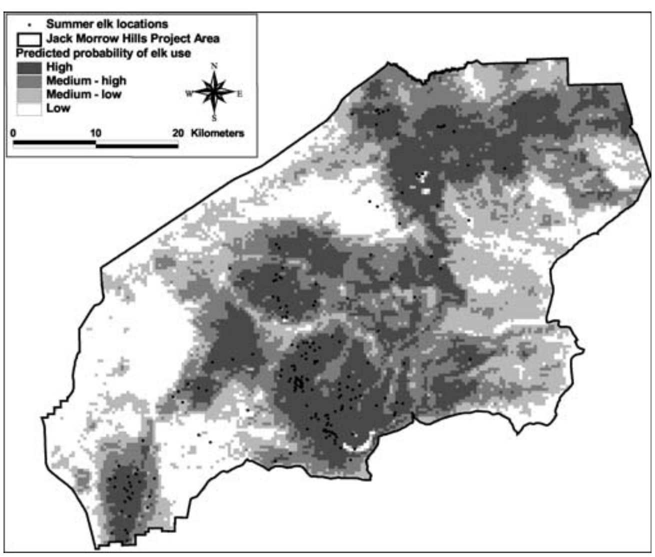

Figure 1. Distribution of 249 radiomarked elk locations collected from an independent sample (n = 55) across the predictive maps and associated categories of elk habitat use during summer 2003 in the Jack Morrow Hills Planning Area, Wyoming, USA.

We estimated a population-level model (Table 1) and associated predictive map (Fig. 3) that included all 6 predictor variables, with quadratic terms for slope and distance to road. Elk selected for areas with low elevations, high habitat diversity, close to shrub cover, and southerly aspects. Quadratic terms indicated elk selected areas with moderate slopes and away from roads. Areas with the highest probability of use were 1.20 km (SE = 0.47) away from roads and had slopes of 11° (SE = 0.73).

Predictive Map Validation

Of the 528 VHF locations we collected from an independent sample of 55 radiomarked elk, 249 locations occurred in summer and 279 in winter. Among the summer elk locations, 81% (n = 201) and 85% (n = 211) occurred in areas categorized as high use by the 2003 (Fig. 1) and 2004 (Fig. 2) summer predictive maps, respectively, whereas 3% (n = 7) occurred in areas classified as low use (Table 2). Areas classified as high or medium-high use by summer 2003 and 2004 predictive maps contained 94% (n = 233) and 93% (n = 232) of the summer elk locations, respectively, whereas areas classified as low or medium-low use contained 6% (n = 16) and 7% (n = 17). Among the winter elk locations, 56% (n = 156) occurred in areas classified as high use by the 2003–2004 winter predictive map (Fig. 3), whereas 10% (n = 28) occurred in areas classified as low use (Table 2). Areas classified as high or medium-high use by the winter predictive map contained 74% (n = 205) of the winter elk locations, whereas areas classified as low or medium-low use contained 26% (n = 74).

DISCUSSION

Given that most elk management guidelines and knowledge of habitat preferences were developed in montane and forested regions, the recent range expansions by elk into nonforested and desert habitats across the Intermountain West have required that important elk habitat characteristics also be identified in these areas. Our results suggested that large (>1,000) hunted elk populations can meet their year-round forage and cover requirements in nonforested regions,

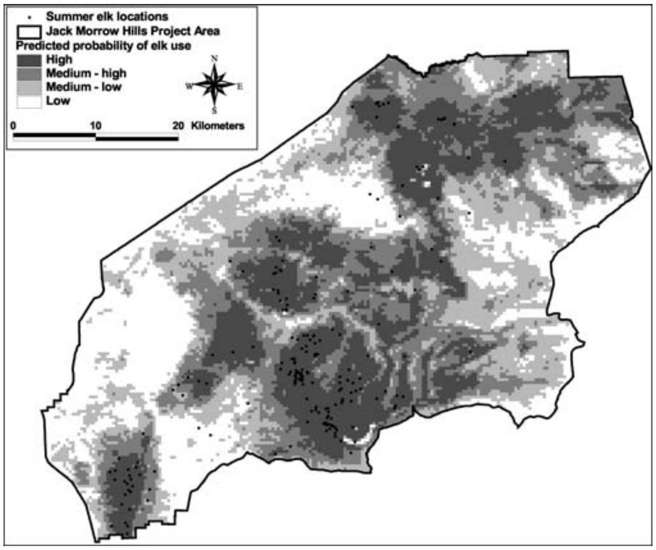

Figure 2. Distribution of 249 radiomarked elk locations collected from an independent sample ($n = 55$) across the predictive maps and associated categories of elk habitat use during the summer of 2004 in the Jack Morrow Hills Planning Area, Wyoming, USA.

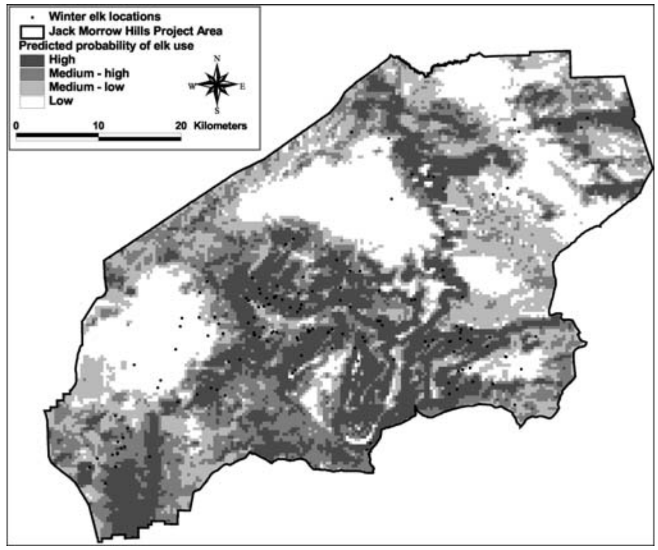

Figure 3. Distribution of 279 radiomarked elk locations collected from an independent sample ($n = 55$) across the predictive maps and associated categories of elk habitat use during winter 2003–2004 in the Jack Morrow Hills Planning Area, Wyoming, USA.

provided there is limited vehicular traffic, a range of elevations available, and dominant shrub communities. Specifically, our population-level models and associated predictive maps indicated that elk in the JMHPA selected for summer habitats characterized by higher elevations in areas of high vegetative diversity, close to shrub cover, northerly aspects, moderate slopes, and away from roads. Distance to shrub cover and habitat diversity did not enter the summer 2004 model; however, the predictions and validation for both the summer 2003 and 2004 models were similar. Winter habitat selection patterns were similar, except elk shifted to areas with lower elevations and southerly aspects. We attributed these seasonal differences to increased winter forage availability at lower elevations and south-facing slopes. The range of elevation (2,000–2,650 m) available across the JMHPA seemed to be important for providing elk with a variety of elevation, slope, and aspect options, such that they could make appropriate seasonal shifts in their habitat selection patterns.

The proximity of high-use elk habitats to roads during the winter versus the summer probably reflected the decrease in human activity that occurs in the winter when roads in the JMHPA become less accessible to vehicles and recreational use declines (L. Keith, BLM, unpublished report). If human activity were to increase during the winter because of land-use changes, such as off-road vehicle use, energy development, or mineral extraction, we would expect elk to distance themselves from roads in a manner similar to summer, altering the amount of winter habitat available to them. Generally, the effectiveness of elk habitat in forested regions declines when road densities exceed 0.62 km/km^2 (1 mi/mi^2; Lyon 1983, Wisdom et al. 1986, Thomas et al. 1988). Road density in the JMHPA (0.17 km/km^2) was much lower than 0.62 km/km^2, yet roads significantly influenced both summer and winter habitat use patterns. This influence is not unexpected, given that the behavioral response to traffic is influenced by topography and forest canopy adjacent to roads (Edge and Marcum 1991, Rowland et al. 2005), or lack thereof. In the absence of forest cover, restrictions on vehicular access or limiting road densities may be necessary to maintain an area as effective elk habitat (Lyon 1983, Cole et al. 1997). Research in other elk populations has suggested that moderate levels of human disturbance during the calving season may result in reduced reproductive success (Phillips and Alldredge 2000, Shively et al. 2005). However, recent population trends in the JMHPA (G. Frost, personal communication) suggest that current levels of disturbance or displacement in the JMHPA have not resulted in reduced

Table 2. Distribution of radiomarked elk locations collected from 55 elk from 1999 to 2002 across the 4 elk use categories of the population-level model predictive maps for summer 2003, summer 2004, and winter 2003–2004 in the Jack Morrow Hills Planning Area of southwestern Wyoming, USA.

	Summer 2003		Summer 2004		Winter 2003–2004	
Quartile	Elk locations	%	Elk locations	%	Elk locations	%
High	201	81	211	85	156	56
Medium-high	32	13	21	8	49	18
Medium-low	9	3	10	4	46	16
Low	7	3	7	3	28	10
Total	249	100	249	100	279	100

population performance. Nonetheless, land-use changes that require higher road densities or increased levels of human disturbance may be more difficult to mitigate in nonforested environments compared with forested regions where security cover is more abundant.

Management of roads and related human disturbance is an important consideration for managing elk populations (Christensen et al. 1993, Gratson and Whitman 2000, Rowland et al. 2000); and in some cases, road closures have been shown to decrease elk movements and increase survival (Cole et al. 1997). Our population-level models and predictive maps should improve the ability of agencies and industry to evaluate how future land-use decisions (BLM 2004*a*) and transportation plans may affect elk in the JMHPA and surrounding area. For example, approximately two-thirds of the JMHPA is considered to have moderate-to-high oil and gas development potential (BLM 2004*a*). If or when development plans are proposed, the models could incorporate the proposed changes (e.g., new roads and vegetation loss) to generate new predictive maps and illustrate how proposed development may influence winter and summer use of elk in the JMHPA. Furthermore, the models could be used to evaluate sets of development alternatives by quantifying potential changes in terms of their predicted effect on high-use elk habitat.

We suggest that the development of habitat selection models with interpretable predictor variables, similar to those developed in forested regions (Wisdom et al. 1986, Thomas et al. 1988, Rowland et al. 2000, Benkobi et al. 2004), may provide a basis for managing elk habitat in nonforested environments. Our approach to identifying predictor variables for modeling seasonal elk use in the JMHPA recognized that forage and cover requirements for elk need to be met, but we assumed that forage in nonforested environments tends to be dispersed more evenly than in forested habitats (McCorquodale et al. 1991), and, in the absence of forest cover, that elk rely on a combination of shrubs, topography, and low human disturbance to meet their thermal and hiding cover requirements. Thus, we considered slope, aspect, elevation, distance to road, distance to cover, and habitat diversity to be appropriate predictor variables of elk habitat use during both winter and summer. Additionally, because the variables were easy to measure, the model lends itself to application in other nonforested regions of southwestern Wyoming.

We used a forward-stepwise model-building procedure (Neter et al. 1996) to estimate population-level coefficients for winter and summer. Fitting the same model to each of the n individuals and then estimating population-level coefficients can provide a valid method for obtaining population-level inference (Marzluff et al. 2004, Millspaugh et al. 2006, Sawyer et al. 2006). Our model validation suggested that both the summer and winter population-level models successfully predicted areas of high and low elk use. We recognized that the number of categories in the predictive maps is a subjective decision and may vary depending on study objectives. Nonetheless, we found that dividing the predictive values into quartiles and creating 4 categories was useful for year-to-year and season-to-season comparisons. Additionally, our model validation suggested that the 4 categories were useful for predicting occurrence of elk that occupied the study area 1–3 years before model development.

MANAGEMENT IMPLICATIONS

Although conventional definitions of forage (open meadows and clear cuts) and cover (timber stands) do not generally apply to nonforested regions, our study suggests that basic habitat variables such as slope, aspect, elevation, distance to road, distance to shrub cover, and habitat diversity can successfully predict seasonal habitat use of elk in open environments. We encourage biologists responsible for managing elk populations in nonforested regions to consider these parameters in management decisions, rather than relying on the traditional forage-to-cover ratios (Thomas et al. 1979, 1988; Wisdom et al. 1986) used to evaluate elk habitat in forested regions.

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