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Scale and heterogeneity in habitat selection by elk in Yellowstone National Park[1]

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Abstract: Resource selection functions (RSF) can be used to explore the role of scale in determining patterns of habitat use. We estimated RSFs for 93 radiocollared adult female elk (*Cervus canadensis)* with resource availability defined at four spatial scales and two seasons in Yellowstone National Park. Habitat selection differed markedly among scales and seasonal ranges. During winter elk moved to ranges at lower elevations where snow water equivalents were low and selected landscapes with a mix of forest and open vegetation at all spatial scales. Areas of high vegetation diversity were selected at large spatial scales during summer, whereas elk selected less diverse areas on winter range. During summer elk selected forests that burned 12-14 y earlier, but they used these burns less than expected by chance during winter. Habitat selection by elk occurred at multiple spatial scales; thus, we cannot prescribe a single scale as being best for modelling habitat use by elk. Instead, selection of an appropriate scale will vary depending on the research question or management issue at hand.
Keywords: availability, *Cervus canadensis*, ecological models, elk, extent, functional response, habitat ecology, heterogeneity, logistic regression, resource selection functions, scale, Yellowstone National Park.

Résumé : Les fonctions de sélection des ressources (FSR) peuvent servir à approfondir le rôle de l'échelle dans la détermination des patrons d'utilisation de l'habitat. Nous avons estimé les FSR de 93 wapitis (*Cervus canadensis*) femelles adultes porteuses d'un collier émetteur dans le parc national de Yellowstone. La disponibilité de la nourriture a été définie selon quatre échelles spatiales et pendant deux saisons. La sélection de l'habitat diffère grandement selon les échelles et les saisons. Pendant l'hiver, les wapitis se déplacent vers des sites de basse altitude avec peu de neige. À toutes les échelles spatiales, ils choisissent des paysages où il y a un mélange de forêts et de communautés végétales ouvertes. En été, à de grandes échelles spatiales, les wapitis privilégient les secteurs avec une très grande diversité de végétation, alors qu'en hiver les secteurs fréquentés sont moins diversifiés. Pendant l'été, les wapitis choisissent des forêts ayant brûlé 12 à 14 ans plus tôt, mais ces brûlis sont beaucoup moins fréquentés pendant la période hivernale. La sélection de l'habitat par les wapitis se faisant à diverses échelles spatiales, nous ne pouvons indiquer quelle échelle choisir pour la modélisation de l'utilisation de l'habitat par ce cervidé. Le choix de l'échelle devra plutôt s'appuyer sur le but de la recherche ou de l'aménagement envisagé.
Mots-clés : *Cervus canadensis*, disponibilité, échelle, écologie de l'habitat, étendue, fonction de sélection des ressources, hétérogénéité, modèles écologiques, parc national de Yellowstone, régression logistique, réponse fonctionnelle, wapiti.

Nomenclature: Hitchcock & Cronquist, 1973; Wilson & Reeder, 1993; Randi *et al.,* 2001.

Introduction

Patterns of distribution and abundance can be framed at a variety of scales (Johnson, 1980), and animals have been shown to select different resources at different scales (Kotliar & Wiens, 1990; Danell, Edenius & Lundberg, 1991; Bergin, 1992; Schmidt, 1993; Ward & Saltz, 1994). Understanding how animals respond to temporal and spatial variability at different scales is important for designing ecological research and monitoring programs (Addicott *et al.,* 1987; Wiens, 1989; Kie *et al.,* 2002). Also, consideration of scale is necessary for deciding how habitat data should be applied in resource management. It has been argued that abiotic factors of the environment are primary determinants of broad-scale distribution patterns for large herbivores (Bailey *et al.,* 1996; Fortin *et al.,* 2003). Clearly, forage, cover, and predators also can influence habitat selection by elk and other large herbivores (Laundré, Hernández & Altendorf, 2001; Cook, 2002; Skovlin, Zagar & Johnson, 2002).

The influence of scale and heterogeneity on habitat selection can be studied using resource selection functions (RSF). An RSF is defined to be any function that is proportional to the probability of use for a resource unit (Manly *et al.,* 2002). RSFs can be estimated by comparing environmental covariates at resource units used by animals to those available, *e.g.,* a set of random land-

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scape locations. A stated assumption in the application of RSFs is that availability of resources does not vary (Manly *et al.,* 2002). This assumption has been viewed as a limitation of RSFs, because resource availability is almost certain to vary within and among landscapes, often with the domain identified arbitrarily by the investigator (Garshelis, 2000; Van Horne, 2002). Indeed, if RSFs could be used only for the set of available resource units where the models were estimated, this would severely limit our ability to apply these models across spatial and temporal scales. In this study we explore the consequences of varying the scale (extent) of area over which available resource units are sampled.

We based our analysis on elk habitat use in Yellowstone National Park, where we radiotracked 93 adult cow elk during 2000-2002 and sampled environmental covariates at four spatial scales. Previous studies of elk foraging in Yellowstone National Park concluded that habitat selection in winter occurs at broad spatial scales, whereas habitat selection at fine scales did not differ from random use (Pearson *et al.,* 1995; Turner & O'Neill, 1995; Wallace *et al.,* 1995; Turner *et al.,* 1997a). In our investigation we characterized habitat selection during both winter and summer, drawing random landscape locations for availability from larger scales than were considered in the previous investigations, and we made comparisons using RSFs across four scales. The focus of this paper is on the effect of scale and heterogeneity on use of habitats by elk; subsequent papers will address the effects of wolf recovery (J. S. Mao, M. S. Boyce, E. H. Merrill, D. Smith, F. J. Singer & J. Vores, unpubl. data). Using RSF models we demonstrate how habitat selection changes when based on availabilities at each of the four spatial scales that we studied during winter and summer.

Methods

STUDY AREA

Elk and elk habitats were studied within the boundaries of Yellowstone National Park (8,991 km^2) with a focus on those elk that winter on the Northern Range (1,500 km^2). Elevation varied from 1,500 m to 3,000 m. Vegetation in the park has been described by Despain (1990) and the vegetation consequences of the extensive large-scale fires of 1988 have been documented (Turner *et al.,* 1997b). The ecology and behaviour of elk in Yellowstone have been studied extensively (Houston, 1982; Merrill & Boyce, 1991; Turner *et al.,* 1993; 1994; Pearson *et al.,* 1995; Coughenour & Singer, 1996; Turner *et al.,* 1997a). During our study approximately 14,000 elk wintered on the Northern Range of the park with minor variation among years. In addition to the northern Yellowstone elk herd, several thousand elk in eight other herds use portions of the park, especially in summer; a majority of these elk migrate outside the park during winter. Resource management issues in Yellowstone National Park provide context for our investigations (Keiter & Boyce, 1991; Boyce, 1998; National Research Council, 2002).

FIELD PROCEDURES

Elk were captured on the Northern Range by helicopter net gunning during February 2000, 2001, and 2002. We fitted radiocollars on 93 adult female elk, using 50 VHF collars and 15 GPS collars. We obtained locations using 59 rounds of aerial surveys, resulting in each radiocollared elk being located approximately every 10-14 d by UTM coordinates using a global positioning system (GPS). Each round of telemetry flights typically required flights on 2 or 3 d to locate all of the elk. GPS collars also were located during VHF telemetry flights and the locations of GPS-collared elk were included at the same frequency as the sample of VHF-collared elk. We located the elk during daylight hours, usually 0900-1400. Behaviour of elk at the time of radiotracking often could not be ascertained.

SCALE AND HABITAT DATA

Scale is defined by resolution (or grain) and extent (Turner, Gardner & O'Neill, 2001). Resolution is the smallest unit measured, whereas extent is the size of the area over which observations are measured. In all of our analyses the finest resolution was 30 m × 30 m, determined by remote-sensing imagery and the resolution of our digital elevation map (DEM). Extent for available resource units was defined at four levels: ordered from broadest to finest, (1) the entire *ca* 900,000-ha park, approximately 92 km across; (2) fixed-size *ca* 11,200-ha circular plots with buffer radius of 6 km (12 km diameter) centred around each telemetry location (Arthur *et al.,* 1996) with the radius capturing 80% of the movement distances between successive telemetry locations (longer movement distances included migration between winter and summer ranges, not considered in this study); (3) variable circular plots with a buffer radius equal to the movement distance (mean diameter ~8 km) to the next radiotelemetry location, reflecting the resources available given the distance that an individual moved (for justification: Johnson *et al.,* 2002); and (4) minimum convex polygons encompassing all radiotelemetry observations within the elk's seasonal home range, with mean diameter of 5.9 km (Johnson's [1980] level 3). Available resource units were sampled as random landscape locations within these four extents, at a density of $1 \cdot km^{-2}$.

The two buffered scales (levels 2 & 3, see above) include areas beyond the home range. Johnson *et al.* (2002) suggested that what is available to an individual should be reflected by how much the animal moves, and availability might be bounded by the distance moved since its last radiotelemetry location. In practice, this buffers all points within an elk's home range, including those on the outside edge of the home range, effectively creating a buffer surrounding the home range by about 4 km. Consequently, the total diameter of the area over which random landscape locations were accumulated was the average diameter of the home range (5.9 km) plus twice the average movement buffer, or ~14 km. We were concerned that the variable movement buffer might result in reduced habitat selection in areas most strongly preferred, because if small movements indicate good habitats, corresponding small buffers might afford less heterogeneity across which to measure resource selection by elk. Therefore, we added another scale with a fixed buffer equal to the distance that encompassed most of the move-

ments, truncating the top 20% as migratory, reasoning that the animal certainly had the ability to use landscapes within this buffer and that, therefore, resource units in this area were available. Although the extent of the case-control comparison was a circle with a diameter of 12 km, again, the total accumulated diameter over which points were sampled for each individual included the average home-range diameter plus approximately twice the buffer radius for a total diameter of 18 km. Still, we were surprised how little variation in area existed among the smaller three scales; this resulted from the fact that elk move around substantially, visiting much of the area within their home ranges between radiotelemetry relocations.

Temporal resolution was set by the interval between the 59 radiotelemetry flights, ~10-14 d, during the 2-y extent of our study (2000-2002). Elk in Yellowstone show strong fidelity to seasonal home ranges, migrating between summer and winter ranges prompted by snow accumulation during winter and snowmelt in spring (Boyce, 1989; 1991; Smith & Robbins, 1994). The spatial extent and timing of use of winter and summer ranges were defined by the radiotelemetry locations, *i.e.,* individual elk defined their own seasonal ranges. We did not include telemetry locations during migration between winter and summer ranges.

For each of the four spatial extents, habitat covariates associated with each resource unit (30-m × 30-m pixel) were based on various data layers in a geographical information system (GIS) compiled mostly from databases provided by Yellowstone National Park. These included habitat classifications compiled for cumulative effects modelling of grizzly bears (*Ursus arctos*; Mattson *et al.*, 1998) collapsed to 12 vegetation types, of which we focused on six types known to be important to elk, including upland grasslands and shrublands, aspen (*Populus tremuloides*), Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), and early-seral-stage forests. Using a GIS we measured the extent of open non-forested vegetation (open habitats) within 500-m × 500-m buffers surrounding each resource unit. Within the 500-m × 500-m buffer we recorded the number of vegetation types (potentially 1 to 12) and used this as an index of vegetation richness. The location of fires of varying intensity that burned during 1988 was compiled by Despain *et al.* (1989), and we selected canopy burns, mixed burns, and undifferentiated burns as additional habitat covariates superimposed on the map of vegetation types. Snow water equivalent (SWE) was mapped for the period of each of the 59 rounds of radiotelemetry flights using a snow model developed by Farnes, Heydon, and Hansen (1999) and updated by Coughenour (2002).

We used a 30-m resolution DEM prepared by the U.S. Geological Survey to obtain elevation data. The DEM also allowed computation of slope and aspect, but these variables interact in their influence on elk, *i.e.,* we found significant interaction terms when both slope and aspect were used in RSF models. Because these interaction terms were difficult to interpret, we calculated a site-severity index (SSI) developed by Nielsen and Haney (1998) to integrate topographic variables into an index of site moisture from mesic to xeric conditions by combining both slope (%) and aspect (A in degrees):

$$SSI = \sin(A + 225) \times \left(\frac{slope}{45} \right) \quad [1]$$

This metric ranged from -1.67 on northeast slopes to a maximum value of 1.67 on southwest-facing steep slopes.

Data analysis and statistics

To characterize the spatial pattern of variation for environmental variables we used Geary's C, which can be interpreted as a standardized semivariance reflecting the inverse of spatial autocorrelation (Sokal, 1979). The spatial extent at which Geary's C approaches an asymptote at 1.0 is the extent at which the landscape contains the full scope of variance in the variable of interest and is the extent at which spatial autocorrelation is essentially null.

RSF models were estimated using multiple logistic regression for the park-wide scale and matched case-control logistic regression (equivalent to conditional fixed effects or discrete choice) for the other three spatial scales (Manly *et al.,* 2002). We define our sampling domain to be the period February 2000 through May 2002. Within this sampling domain used points were rare relative to those available; thus, contamination of the control sample was trivial. We used Akaike's Information Criterion (AIC) to select amongst alternative RSF models that were selected *a priori* as ecologically meaningful. Variables considered for inclusion in RSF models were used only when justified by previous research or our field observations. Thus, we followed the evolving paradigm of model selection instead of the usual statistical inference (Johnson, 1999; Burnham & Anderson, 2002).

Prior to estimating models we screened predictor variables for collinearity, ultimately dropping lodgepole pine and early-seral-stage forests from the analysis because of strong correlations with other variables included in our analysis. Aspen was dropped from the analysis because no elk telemetry locations occurred in aspen during summer. For all habitat types not included explicitly in the model, their influence is absorbed into the reference category, *i.e.*, the constant, β_0. We eliminated from the analysis all locations, both telemetry locations and random landscape locations, falling in lakes or mountain talus.

Nonlinearities were detected for the scalar variables elevation, SSI, and open habitats. Adding squared terms to the assumed model accommodated these, creating a Gaussian function of the RSF, $w(\mathbf{x})$, on a predictor variable, x_1, for example:

$$w(\boldsymbol{x}) = \exp(\beta_1 x_1 + \beta_2 x_1^2 + \beta_3 x_2 \ldots) \quad [2]$$

Coefficients, β_i, for this log-linear model were estimated using logistic regression (Manly *et al.,* 2002) for the park-wide extent for both summer and winter models. The β_is are equivalent to selection ratios (Manly *et al.,* 2002), and $\exp(\beta_i)$ can be interpreted directly as the odds ratio. When $\beta_i > 0$, use by elk is occurring more than would be expected if simply in proportion to availability, and less if $\beta_i < 0$.

For spatial scales involving 6-km-radius buffers and variable buffers, we used matched case-control logistic regression where each elk telemetry point was matched to random landscape locations sampled within respective buffers (Compton, Rhymer & McCollough, 2002). Likewise, for home-range extent, matched case-control logistic regression was employed where we treated each elk as a fixed effect, thereby controlling for variation amongst individuals (Breslow, 1996). For comparative purposes we kept the same set of 12 variables in each model even though different sets of variables were identified for individual models using AIC; these 12 variables were those most commonly included according to AIC.

In addition to these eight RSF models (four extents × two seasons), two additional winter models were estimated including SWE as a covariate: one for each of the two buffered case-control extents. Because maps of SWE varied for each sampling occasion, only the buffered matched case-control models could relate SWE at used points to SWE at random points at the same time period. For park-wide and home-range models, used points were pooled over the season, so the design did not allow for time-dependent covariates such as SWE.

Model evaluation was performed using *k*-fold cross validation (Boyce *et al.,* 2002). We randomly divided the radiotelemetry locations into five equal sets based approximately on Huberty's (1994) rule-of-thumb for the model training-to-testing ratio. RSF models were constructed based on 80% of the data (training set), withholding 20% for evaluation (test set). Then the random landscape locations were ranked according to RSF scores calculated from the estimated models, and these were binned into 10 groups with an equal number of random locations in each group. We then tallied the number of elk radiotelemetry locations from the test set where the RSF score fell within each bin. To evaluate the predictive success of the RSF model we calculated a Spearman-rank correlation (r_s) between the frequency of test-set telemetry locations and bin number (Boyce *et al.,* 2002). This process was repeated five times using each 20% as a test set, and correlations were averaged ($\overline{r}_s$).

Results

Among a subset of habitat covariates, Geary's *C* for elevation stands out with a large range of semivariance (Figure 1). Elevation shows strong spatial autocorrelation across distances > 20 km, whereas the spatial autocorrelation of the vegetation variables diminishes rapidly. All vegetation variables achieve asymptotic variances over a short range of spatial extent, with the sill being less than the scale of any of the availabilities that we sampled.

Intermediate elevations were selected by elk during both summer and winter (Figure 2), with local maxima in RSFs at about 3,000 m during summer and about 2,000 m on winter range. The general pattern in elevation use was that the relative strength of model prediction increased with extent. That is, the RSF scores calculated whilst holding all else constant were highest for the park-wide scale, followed by the 6-km-radius (12-km-diameter) fixed buffer and then the variable (*ca* 8-km-diameter) buffer. The weakest influence of elevation was at the home-range scale (< 6-km-diameter).

Park-wide patterns of selection for Douglas-fir forests during winter (Table I) largely reflected the distribution of these forests, most of which occur on the Northern Range. Thus, for the park-wide scale there apparently was strong selection for Douglas-fir during winter (β = 2.24) but random use or weak avoidance of these forest types when availability was restricted to the Northern Range at smaller scales (Figure 3a). At the park-wide scale, 4.5% of the landscape is in Douglas-fir forests, whereas on the Northern Range elk home ranges 20.6% of the landscape is in Douglas-fir. During summer elk showed selection for Douglas-fir forests at all spatial scales, although the selection was not statistically significant at the variable-buffer scale (P = 0.77).

Forests burned during the fires of 1988 were selected by elk at all spatial scales during summer, but avoided during winter (Tables I & II). This pattern was consistent for all four scales in each of the three burn types: canopy burn (Figure 3b), mixed burn, and undifferentiated burn. Avoidance of all burn types during winter was strongest

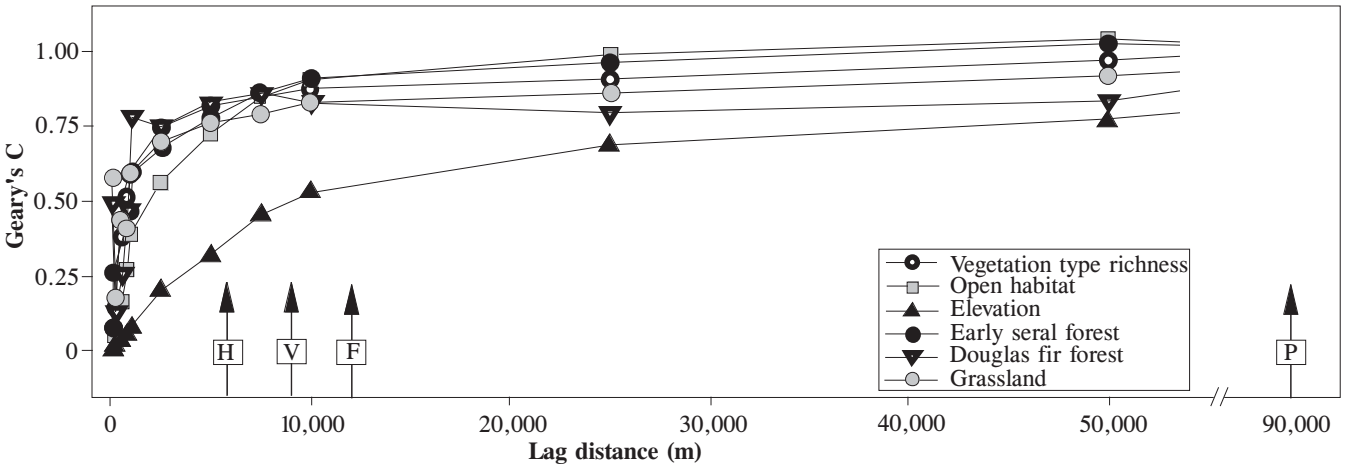

FIGURE 1. Geary's *C* as a function of scale for habitat covariates on the Yellowstone landscape. A total of 5,000 randomly located points were sampled for this analysis. The boxes on the *x*-axis represent the comparable extents for park-wide (P), 6-km-radius fixed buffer (F), variable buffer (V), and home range (H).

in the park-wide model, reflecting the fact that burns were less extensive on the Northern Range. Across the entire park a total of 30.6% of the landscape was in one of the three burn types studied, whereas on elk home ranges of the Northern Range only 9.3% of the forests burned in 1988.

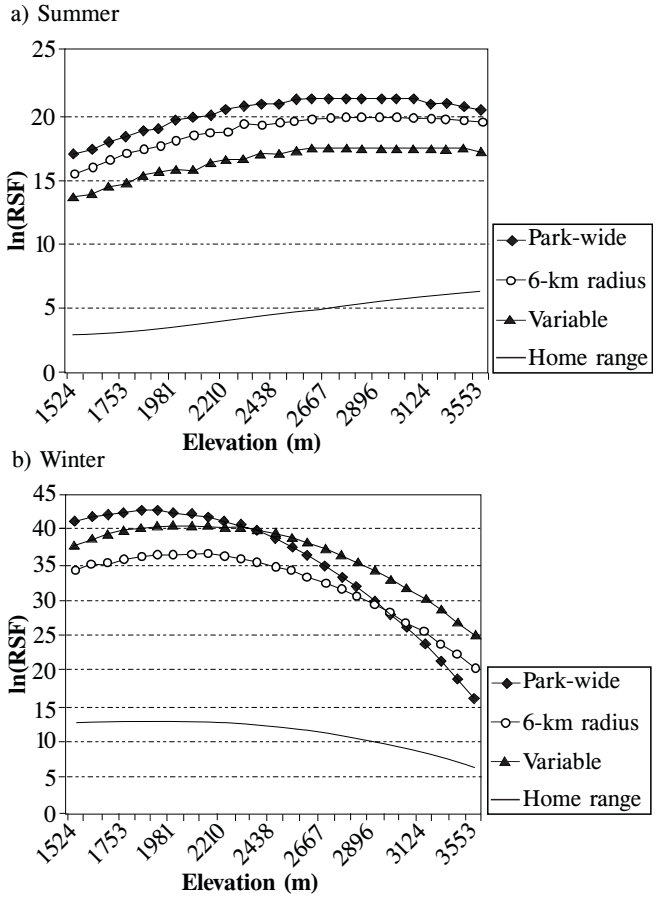

FIGURE 2. The relative probability of occurrence for elk (ln-transformed) as a function of elevation in summer a) and winter b) whilst holding other variables in the model constant (see Tables I and II). Results are presented for each of the four spatial extents that we examined. Note that park-wide scale, 6-km-radius fixed buffers, and variable buffers were all modelled with a squared term included yielding a quadratic relationship in ln transform. The ln (RSF) for the home-range scale in summer does not include the squared term. Each plotted function has 0 intercept, *i.e.,* relative RSFs. See Methods for a full description of spatial extents.

We found low use of areas of high vegetation-type richness at all scales during winter (Figure 3c). We believe that this reflects use of relatively simple winter foraging landscapes comprised of only one or two types, *i.e.,* grasslands with interspersed forests. In contrast, during summer we saw significant ($P = 0.05$) selection for areas of high vegetation richness at the park-wide extent, reflecting low use by elk of the Northern Range grasslands and large homogeneous blocks of lodgepole pine in central and southern portions of the park.

Upland grass and shrublands are more extensive on the Northern Range, where the elk overwinter (62.7% *versus* 12.4% park-wide). Therefore, compared with upland grass and shrublands available to the elk at a park-wide extent, these grassland areas are used by elk during winter at a much higher frequency. But when we restricted availability to random landscape locations sampled from the Northern Range, as is depicted at the three smaller scales, elk use upland grass and shrublands at random relative to availability. So when upland grass and shrublands are abundantly available, the selection for these types is reduced (Figure 4).

Interpretation of the use of open habitats is more complex than suggested by the presence of upland grass and shrubland types at sample points. The open-habitats variable characterizes the amount of grasslands and other non-forested habitats within a 500-m × 500-m window. Based on AIC, inclusion of a squared term for open habitats improved the RSF model at all spatial extents in both seasons (see Tables I & II for coefficients). Again, we see that the strongest influence of open habitats occurred at the broadest spatial extent, with RSF scores diminishing progressively as the extent became smaller (Figure 5).

One of the useful applications of RSFs is to calculate the relative probability of use across the landscape. We illustrate this using park-wide models for summer (Figure 6a) and winter (Figure 6b). Generally, these maps coincide with our observations of elk distribution in the park.

TABLE I. Resource selection functions at four scales for winter telemetry locations for elk in Yellowstone National Park, 2000-2002.

Scale →	Park-wide		6-km buffer		Variable buffer		Home range	
Covariate[1]	β	SE	β	SE	β	SE	β	SE
Elevation	0.0138	0.0014	0.011	0.001	0.0119	0.0013	0.0041	0.0012
Elevation^2	–1.1e-6	1.0e-7	–8.3e-7	7.3e-8	–8.8e-7	9.3e-8	–3.2e-7	8.4e-8
Vegetation type richness	–0.0798	0.0596	–0.124	0.0424	–0.143	0.0485	–0.0967	0.0539
Open	0.0173	0.0023	0.0103	0.0017	0.0091	0.0019	0.0079	0.0022
Open^2	–3.3e-5	6.9e-6	–0.00002	4.8e-6	–2.1e-5	5.5e-6	–1.9e-5	6.3e-6
Grassland	1.54	0.1244	–0.0763	0.0979	–0.101	0.1075	–0.1371	0.1147
Douglas-fir	2.242	0.1517	0.043	0.1129	–0.0375	0.1264	–0.0513	0.1414
Canopy burn	–1.699	0.237	–0.8112	0.2204	–0.7405	0.2306	–0.5379	0.254
Mixed burn	–0.81	0.2094	–0.4191	0.1744	–0.51	0.1933	–0.2479	0.2129
Undifferenciated burn	–0.207	0.2793	–0.1041	0.195	–0.1886	0.214	–0.0496	0.2365
SSI	–0.5	0.0849	–0.2704	0.056	–0.3062	0.0648	–0.2456	0.0693
SSI^2	–0.051	0.1103	–0.4211	0.0721	–0.4241	0.0816	–0.372	0.0876
AIC	3,445		11,976.		7,815.4		4,898.6	
k-fold ($\bar{r}_s$)	0.946		0.950		0.894		0.735	
n	9,728		131,494		50,179		5,056	

[1]For a full description of the covariates, see Methods.

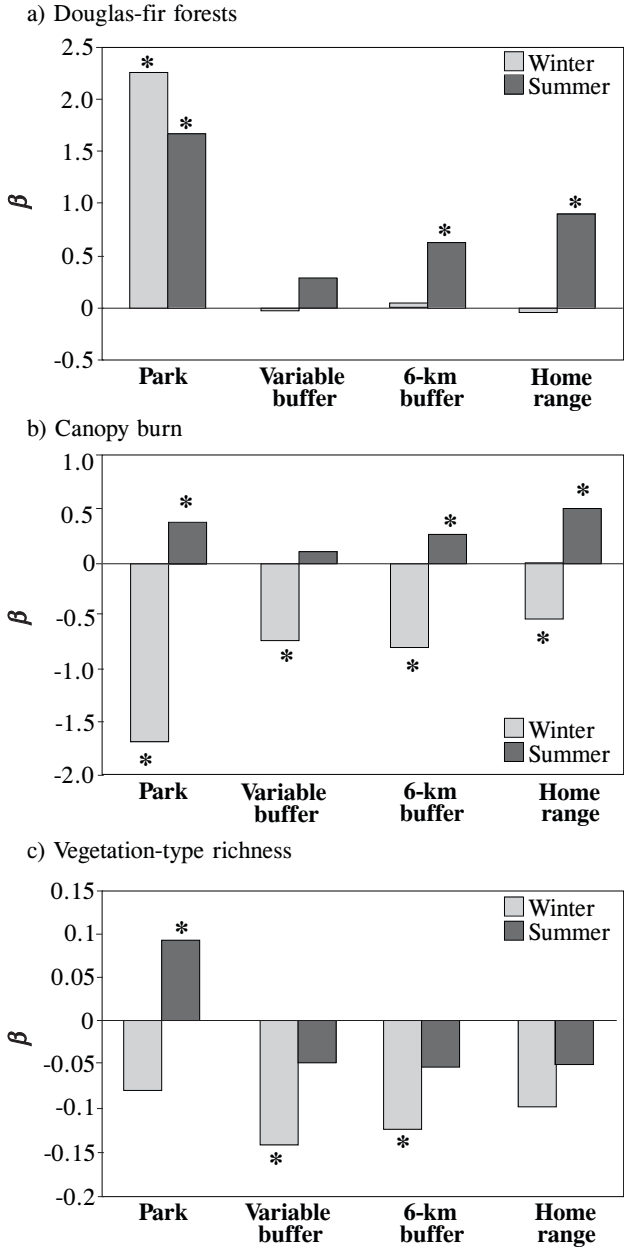

FIGURE 3. RSF selection coefficients (β = ln [odds ratio]) for elk using a) Douglas-fir forests and b) canopy burns, and c) as a function of vegetation-type richness at four spatial extents on both winter and summer ranges for elk in Yellowstone National Park. Vegetation-type richness was measured by counting the number of habitat types within a 500-m × 500-m cell surrounding each telemetry and random landscape location. The * indicates that the β is significantly different from 0 based on a Wald statistic ($P < 0.05$).

One exception is the predicted occurrence of elk during winter in Hayden Valley in the centre of the park (Figure 6b). The plotted model did not include SWE, and inclusion of snow explains the absence of elk from Hayden Valley during winter. For the fixed 6-km-radius buffer and the variable buffer, adding SWE to these case-control models caused reductions in AIC by 81.2 and 25.9, respectively. Including SWE in these two winter models did not change the qualitative patterns of selection, and all covariates retained their statistical significance.

The predictive success of the RSF models generally was high (Tables I and II). Based on our *k*-fold cross validation of predicted *versus* observed in 10 classes (bins) of RSF values (*i.e.,* 10 classes of habitat quality) for summer we found that $\overline{r}_s = 0.968$ for the park-wide extent, $\overline{r}_s = 0.835$ using 6-km-radius fixed buffers surrounding each point, $\overline{r}_s = 0.791$ for the variable-radius buffers, and $\overline{r}_s = 0.882$ at the home-range extent. For winter models the predictive ability was also high, with $\overline{r}_s = 0.946$ at the park-wide extent and $\overline{r}_s = 0.735$ at the home-range extent; fixed and variable buffers predicted well with $\overline{r}_s = 0.950$ and 0.894, respectively. The *k*-fold cross validation method allows evaluation of the assumption that the RSF is proportional to the probability of use. Inspection of plots of the *k*-fold results generally upheld this assumption: frequencies increased linearly with the median RSF in a bin. However, in a few models the RSF scores for the highest bin appeared to be larger than reflected by the frequency of points falling into that bin, probably as a consequence of the assumed exponential form of the RSF model (equation [2]).

Discussion

As we had expected, vegetation type, burn history, topography, and vegetation richness all contributed to models characterizing elk habitats, consistent with other studies of elk ecology (Houston, 1982; Skovlin, Zagar & Johnson, 2002). Likewise, we expected the observed differences in RSF models between seasons (Tables I and II), largely tied to the movement of elk between seasonal ranges driven by snow depth at higher elevations that restricts the ability of elk to travel and to secure forage (Boyce, 1991; Irwin, 2002). What we did not expect, however, were the substantial differences in the magnitude and direction of RSF coefficients among scales.

Fundamental to variation in selection amongst scales is the heterogeneity of resources. In the extreme, selection obviously cannot occur on a homogeneous landscape. What is not so obvious is how heterogeneity of resources can influence selection directly. A study of muskoxen (*Ovibos moschatus*) in the Canadian Arctic concluded that habitat selection was consistent across spatial extents (Shaefer & Messier, 1995). However, environmental heterogeneity in the arctic tundra may be less than in the mountainous landscape of Yellowstone National Park, where, for instance, variance in elevation is substantially different at various scales (Figure 1). Thus, steeper abiotic gradients may lead to greater differentiation among scales in habitat selection.

Consistent with the claim that abiotic factors of the environment are primary determinants of broad-scale distribution patterns for ungulates (Bailey *et al.,* 1996; Fortin *et al.,* 2003), we observed that elevation and SSI had large coefficients and much stronger effects at broader spatial extents (Figure 2; Tables I and II). Also, we observed that Geary's *C* (*i.e.,* semivariance) for elevation increased slowly, such that the full spectrum of elevations was not represented amongst available resource units until a very large area was included within spatial extent. In contrast, semivariance for biological variables increased rapidly with lag distance, such that most of the variation in each

TABLE II. Resource selection functions at four scales for summer telemetry locations for elk in Yellowstone National Park, 2000-2002.

Scale →	Park-wide		6-km buffer		Variable buffer		Home range	
Covariate[1]	β	SE	β	SE	β	SE	β	SE
Elevation	0.0047	0.00082	0.0042	0.001	0.0036	0.0011	0.0006	0.0009
Elevation^2	–2.6e-7	5.0e-8	–2.2e-7	5.6e-8	–1.9e-7	6.89e-8	**	
Vegetation type richness	–0.0911	0.0475	–0.052	0.0456	–0.049	0.0501	–0.0505	0.0566
Open	0.0124	0.0017	0.0079	0.0017	0.0069	0.0018	0.0084	0.002
Open^2	–2.8e-5	5.4e-6	–0.00002	5.14e-6	–1.8e-5	5.6e-6	–2.6e-5	6.5e-6
Grassland	0.5809	0.1188	–0.0687	0.1166	–0.0075	0.129	0.4325	0.1416
Douglas-fir	1.67	0.1617	0.6229	0.1573	0.2802	0.1786	0.8836	0.1981
Canopy burn	0.3845	0.1128	0.2435	0.1098	0.0904	0.1191	0.505	0.1337
Mixed burn	0.318	0.1105	0.1536	0.1064	0.0731	0.114	0.2482	0.1324
Undifferentiated burn	0.4275	0.216	0.1314	0.1975	0.095	0.209	0.6644	0.2537
SSI	–0.343	0.0773	–0.1272	0.0738	0.0013	0.0804	–0.1848	0.092
SSI^2	–0.6714	0.1075	–0.5356	0.1045	–0.5362	0.1135	–0.3831	0.1244
AIC	5,698.2		8,570.3		5,965.5		3,509.9	
k-fold ($\bar{r}_s$)	0.968		0.835		0.791		0.882	
n	9,330		90,617		37,295		3,748	

**linear term only.
[1]For a full description of the covariates, see Methods.

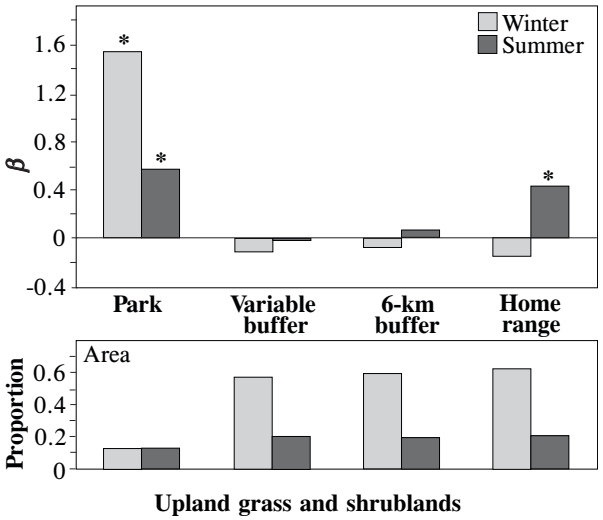

FIGURE 4. RSF selection coefficients (β = ln [odds ratio]) for elk using upland grass and shrubland habitats at four spatial extents on both winter and summer ranges for elk in Yellowstone National Park. The * indicates that the β is significantly different from 0 based on a Wald statistic ($P < 0.05$). The lower panel presents the proportion of the buffer consisting of upland grass and shrublands.

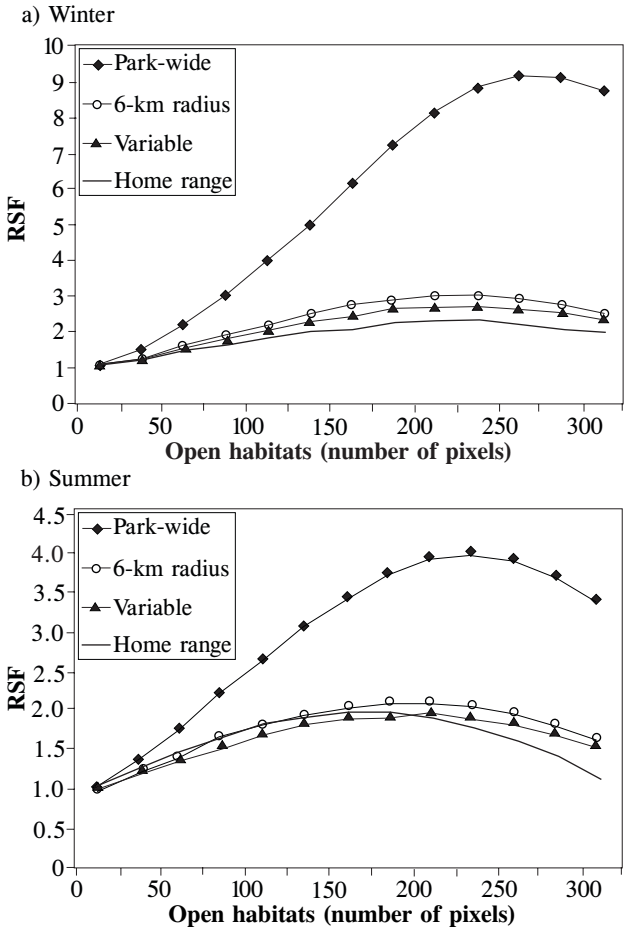

FIGURE 5. The relative probability of use of resource units as a function of the amount of open habitats within a 500-m × 500-m cell surrounding the telemetry location at four spatial extents on elk a) winter and b) summer ranges in Yellowstone National Park. At all extents both linear and squared terms were statistically significant ($P < 0.05$) based on Wald statistics. See Methods for a full description of spatial extents.

of the biological variables was represented within each of the four extents that we evaluated. Therefore, it is unlikely that autocorrelation limited our ability to capture resource selection associated with biological habitat variables.

Models built at finer extents are expected to have smaller β simply because the extent does not present the full range of variance that is available on a larger extent. In our analysis, for example, we observed that < 50% of the semivariance in elevation was represented at the scale of an average home range in comparison to the park-wide scale. Phenology and snowmelt variation are major factors that are constrained by topography and elevation. Migratory behaviour of elk is driven at large temporal and spatial scales in Yellowstone by snow depth, elevation, and phenology (Boyce, 1991; Irwin, 2002), all tied to elevation and topography that are highly autocorrelated in space, requiring large-scale analysis to uncover the patterns of selection. This is not to imply that abiotic features of the landscape do not influence resource use patterns at

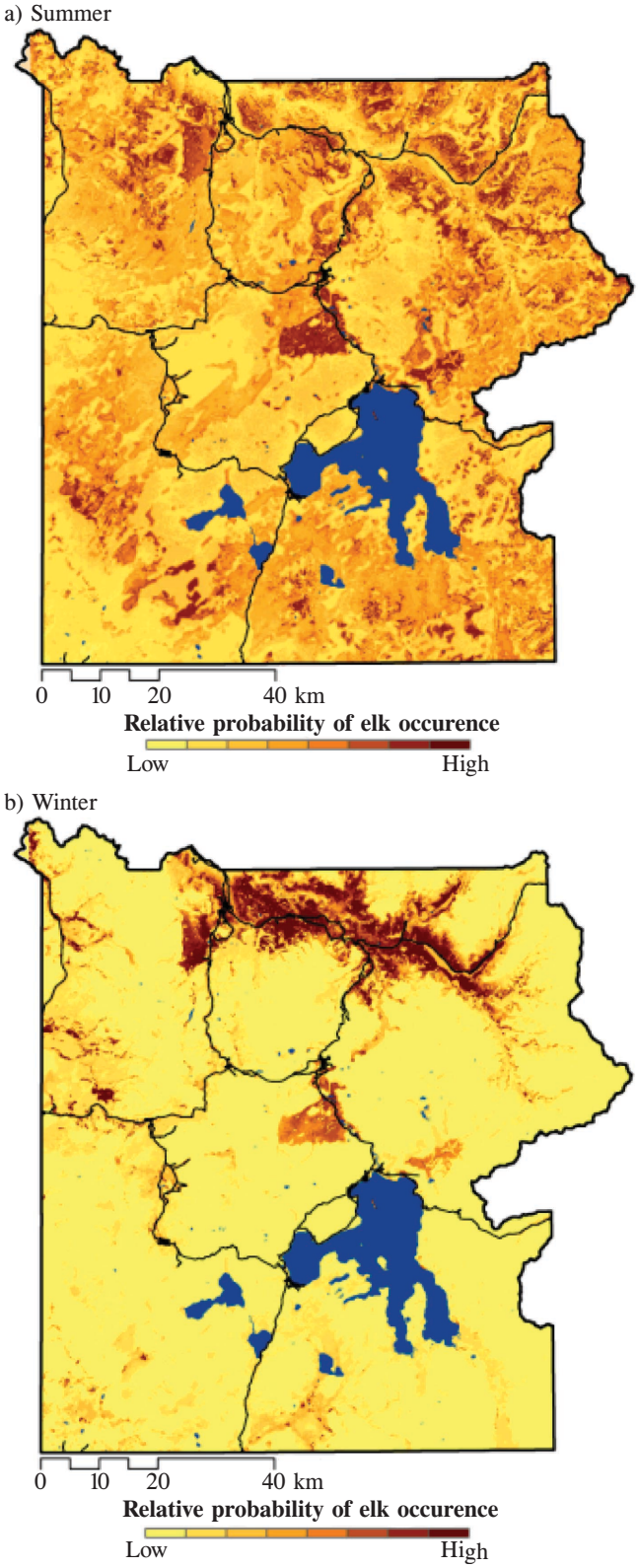

FIGURE 6. Relative probability of occurrence of elk throughout Yellowstone National Park based on park-wide RSF models for a) summer and b) winter distributions.

finer scales of time and space, but the spatial autocorrelation of abiotic features can restrict our ability to measure selection at finer extents.

Not only does spatial heterogeneity influence our ability to detect habitat selection, but elk directly select heterogeneous environments. Elk are known to select edge habitats (Skovlin, Zagar & Johnson, 2002). Consistently, we found that intermediate levels of open habitats are selected, indicating the tendency of elk to forage near forested escape cover. As observed by Kie *et al.* (2002) for deer and by Jones and Hudson (2002) for elk, we found that during summer elk selected heterogeneous landscapes at large spatial scales.

The correlation structure of habitat components results in apparent selection that is largely an artifact of selection for other resources in the area. Correlations between habitats vary among extents. To illustrate, the presence of Douglas-fir forests was inversely correlated with elevation at a park-wide scale (r = -0.228, $P < 0.0001$), whereas the correlation was weak but positive on winter home ranges (r = 0.059, P = 0.05). Elk move to lower elevations during winter because snow is a limiting factor at higher elevations (Skovlin, Zagar & Johnson, 2002), and because most Douglas-fir occurs at lower elevations on the Northern Range, elk appear to be selecting Douglas-fir. When the scale was restricted to the Northern Range, this apparent selection disappeared (Table I; Figure 3a).

Which scale is best? If the objective is to construct maps showing the broad distribution of elk across large areas (*e.g.,* Figure 6), models must be constructed at the scales over which selection is occurring (Van Deelen *et al.,* 1997; Didier & Porter, 1999). However, if the objective were to design management to improve winter-range habitats, then clearly we must understand selection as it occurs on the winter range with a restricted domain of availability.

Deciding on the domain of availability in RSF studies has been considered by previous studies. If habitats are aggregated, the size of the study area can influence the results of habitat selection analysis (Porter & Church, 1987). The matter is complicated by the fact that a hierarchy of spatial and temporal scales is involved in the actual selection of habitats by a species (Senft *et al.,* 1987; Orians & Wittenberger, 1991). Attributes broadly associated with the winter range on Yellowstone National Park, *e.g.,* Douglas-fir forests, appear to be strongly selected at large spatial scales. But when availabilities are restricted to the Northern Range at home-range or movement-radius scales, elk were seen to be neutral or appeared to avoid Douglas-fir forests. This illustrates why we do not recommend using only large study areas for the domain of availability as proposed by McClean *et al.* (1998). Our understanding of habitat selection and our ability to predict patterns of habitat use require that we appreciate selection at multiple spatial scales.

Several methods exist for evaluating the role of scale in habitat selection, and we have addressed only the consequence of varying extent for sampling available resources. The grain or resolution of our analysis limits our ability to discern selection at fine scales and over short time intervals. The resolution in our study is 30 m × 30 m and the average time between observations is ~10-14 d. Many foraging responses are occurring at a finer spatial resolution and over shorter time periods

(Senft *et al.,* 1987; Jones & Hudson, 2002; Lesage *et al.,* 2002; Fortin *et al.,* 2003). In particular, the data that we present here cannot be expected to unveil much information about diet selection and foraging. We have begun to accumulate observations on GPS-collared elk that will allow us to examine finer scales of temporal and spatial resolution in future analyses.

One of the advantages of RSFs is that they can be constructed using variables over a variety of scales, and availabilities can be evaluated at multiple spatial scales. For example, food resources might be measured at a fine scale whereas within the same model cover variables might appropriately be measured at a coarser scale. Another approach that also is evaluated ideally using RSF is to measure habitat attributes within buffers of varying size surrounding used locations and random landscape locations (Meyer, Irwin & Boyce, 1998). We examined such buffers for two of our habitat covariates: open area and vegetation-type richness, each of which was measured within a 500-m × 500-m buffer surrounding each point. We note that the amount of open area in the buffer was an important variable in our models at all spatial scales during both winter and summer, in addition to the habitat attributes at the sample point. Indeed, elk show selection for intermediate levels of open area, requiring a mix of open foraging habitats and forested types for cover (Thomas, 1979; Marcum & Loftsgaarden, 1980; Manly *et al.,* 2002). More research could be focused on the optimization of buffer size to discern the scale at which various resources or limiting factors are important to the animal.

Although there is potential for mixing spatial scales for various resources by measuring covariates within buffers of varying sizes (Pearson, 1993; Meyer, Irwin & Boyce, 1998), we do not yet see an easy solution to variation occurring at different temporal scales. At a coarse temporal scale we separated seasons because resource use patterns were so markedly different during winter and summer (Apps *et al.,* 2001). For example, selection of canopy burns was positive at all spatial scales during summer but negative at all scales during winter. Forbs present in these 12- to 14-y old burns are attractive to foraging elk in summer (Boyce & Merrill, 1991), but leaves of forbs have largely senesced and even decomposed by winter (Cook, 2002). Furthermore, old burns can have heavier snow accumulation, making foraging and travel more difficult. We cannot imagine being able to accommodate these large seasonal differences in a single RSF model, so we built different models for different seasons; equivalently, we could have modeled seasonally varying β coefficients.

Aerial radiotelemetry limited our temporal scale to daytime observations. Roe deer (*Capreolus capreolus*) and brown bears showed different patterns of habitat selection during the day than at night (Mysterud, Lian & Hjermann, 1999; Schwartz & Arthur, 1999). We often see crepuscular foraging by elk, which might alter RSFs by time of day.

Temporal and spatial scales often are linked (Delcourt, Delcourt & Webb,1983; O'Neill *et al.,* 1986; Urban, O'Neill & Shugart, 1987). Our results illustrate how the influence of scale varies among seasons because the distribution of elk use changes markedly, becoming more aggregated across the landscape during winter.

To summarize, we note at least four mechanisms which may influence elk habitat selection at different extents of availability. First, constraints or limiting factors (*e.g.,* snow) influencing habitat use can occur at different scales (Huston, 2002; O'Connor, 2002), and there can be interactions among scales (Mysterud *et al.,* 1999). Second, spatial autocorrelation of a habitat covariate can limit spatial heterogeneity, thereby reducing apparent selection for that variable at spatial extents smaller than the range of autocorrelation (Bailey *et al.,* 1996; Meisel & Turner, 1998). In other words, potential explanatory variables must display a range of values in order for them to influence a response variable at a given scale. Third, a functional response to resource availability can exist such that certain resources are selected either more or less depending on their abundance (Mysterud & Ims, 1998). Fourth, the correlation structure of habitat covariates can vary among scales and can create apparent selection where the animal actually is responding to other features of the landscape.

In addition, habitat selection can vary as a consequence of population density (Hobbs & Hanley, 1990) or vegetation succession (Boyce & Merrill, 1991). This does not imply, however, that models created at various scales are spurious (Porter & Church, 1987; Garshelis, 2000; Van Horne, 2002). Instead, we are reminded that habitat selection is a dynamic process that varies in space and time. We submit that RSF models are a powerful way to characterize habitat selection and permit prediction of animal distribution and abundance (Boyce & McDonald, 1999).

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