SCALE-DEPENDENT SUMMER RESOURCE SELECTION BY REINTRODUCED ELK IN WISCONSIN, USA

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Abstract: Identifying how habitat use is influenced by environmental heterogeneity at different scales is central to understanding ungulate population dynamics on complex landscapes. We used resource selection functions (RSF) to study summer habitat use in a reintroduced and expanding elk (*Cervus elaphus nelsoni*) population in the Chequamegon National Forest, Wisconsin, USA. Factors were examined that influenced where elk established home ranges and that influenced habitat use within established home ranges. We also determined grain sizes over which elk responded to environmental heterogeneity and the number of categories of habitat selection from low to high that the elk distinguished. At a large spatial extent, elk home-range establishment was largely explained by the spatial distribution of wolf (*Canis lupus*) territories. Forage abundance was also influential but was relatively more important at a small spatial extent when elk moved within established home ranges. Areas near roads were avoided when establishing a home-range, but areas near roads were selected for use within the established home range. Elk distinguished among 4 different categories of habitat selection when establishing and moving within home ranges. Spatial and temporal cross validation demonstrated that to improve the predictive strength of habitat models in areas of low inter-annual variability in the environment, it is better to follow more individuals across diverse environmental conditions than to follow the same individuals over a longer time period. Last, our results show that the effects of environmental variables on habitat use were scale-dependent and reemphasize the necessity of analyzing habitat use at multiple scales that are fit to address specific research questions.

Habitat use by ungulates is influenced by the need to maximize net energy intake, minimize predation risk and thermal stress, and maintain social contacts (Wiens 1976, Krebs and Kacelnik 1991, Aycrigg and Porter 1997, Fryxell and Lundberg 1997, Kie 1999, Porter et al. 2002). Ungulates make hierarchical decisions, and habitat use can occur at multiple scales (Senft et al. 1987, Schmidt 1993, Turner et al. 1997, Kie et al. 2002, Boyce et al. 2003). Thus, selection of where to establish a home range and where to move within an established home range may be influenced by different environmental factors and scales, so animal–landscape relationships should be examined across a range of scales (Johnson 1980, Addicott et al. 1987, Mysterud et al. 1999, Apps et al. 2001, Johnson et al. 2001). Abiotic factors have been suggested as the primary determinants of broad-scale distribution of large herbivores (Bailey et al. 1996, Fortin et al. 2003), but biotic factors also clearly influence habitat use (Wilmshurst et al. 1995, Laundré et al.

2001, Cook 2002, Skovlin et al. 2002). Identifying how environmental heterogeneity and the scale at which it influences habitat use are central to understanding ungulate population dynamics on complex landscapes.

Elk ranged widely across diverse habitats in North America prior to European settlement but were extirpated from much of the eastern portion of the continent by the beginning of the 20th century (O'Gara and Dundas 2002). During the past decade, elk have been reintroduced to several eastern locations (e.g., Wisconsin in 1995; Bancroft in Ontario, 1998–2001; Kentucky in 2000–2001; O'Gara and Dundas 2002; Larkin et al. 2003). Although elk–habitat relationships have been well studied throughout much of the animal's contemporary western range (Boyce 1989, Merrill and Boyce 1991, Turner et al. 1994, Pearson et al. 1995, Wallace et al. 1995, Boyce et al. 2003, McCorquodale 2003), little is known about habitat use by reintroduced elk in eastern North America. Habitat-use decisions may vary under different conditions of resource availability (Mysterud and Ims 1998); therefore, resource selec-

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tion studies in the East are important to make informed predictions on future population expansion and on the probability of successful reintroductions.

We used RSF, defined as the relative probability of use of a resource unit (Manly et al. 2002), to study summer habitat use in a reintroduced and expanding elk population in northern Wisconsin, USA. Three questions were addressed: (1) Over a large spatial extent, what factors influenced where elk established home ranges and at what scales did elk respond to environmental heterogeneity? (2) At a fine spatial extent, what factors influenced habitat use within established home ranges and at what scales did elk respond to environmental heterogeneity? (3) Among how many different categories of habitat selection did elk distinguish? The quantity and spatial heterogeneity of forage biomass, the distance to centers of wolf (*Canis lupus*) territories, the amount of forest cover, and distance to roads were considered potentially important factors in these analyses. We used the results of the RSF models and perceived categories of habitat selection to map the relative probability of occurrence of elk across the landscape.

We expected elk to select areas of high forage biomass to maximize net energy intake. However, we recognized that fiber content varies inversely with biomass (Wilmshurst et al. 1995), and foraging decisions by herbivores may also be sensitive to forage quality (Langvatn and Hanley 1993, Wilmshurst and Fryxell 1995). We expected the use of areas of high biomass to be reduced in areas of relatively high predation risk (Lima and Dill 1990, Brown et al. 1999, Kie 1999, Altendorf et al. 2001). Ungulates may increase their use of forested areas in the presence of predators (Wiens 1976, Tufto et al. 1996, McCorquodale 2003, Wolff and Van Horn 2003), where they are able to be less vigilant (Altendorf et al. 2001). Forest cover also can mediate summer thermal stress (Cook et al. 1998, Porter et al. 2002). Therefore, elk were expected to select locations with a high percentage of forest cover. Finally, we

Fig. 1. The study area for this research was located in the Chequamegon National Forest, Wisconsin, USA.

expected elk to select locations that were farther away from roads and hence less vulnerable to human disturbances (Irwin and Peek 1976, Lyons 1983, Rowland et al. 2000). Several studies of ungulates have suggested that elk may respond to broad-scale environmental variation when choosing general areas in which to range (Pearson et al. 1995, Wallace et al. 1995, Turner et al. 1997) and then cue on fine-scale environmental variation when positioning foraging efforts (Fortin 2003, Fortin et al. 2003). We varied the grain size used to sample the environment to examine the following hypotheses: (1) models of home-range establishment should have greatest explanatory power using coarse-grained environmental variation, and (2) habitat use within a home range should be best predicted by fine-grained environmental variation.

METHODS

Study Area

We collected data in the 1,852-km^2 Great Divide District of the Chequamegon National Forest, Wisconsin, USA (Fig. 1), where elk were introduced in 1995. Mean annual air temperature was 5°C, and mean annual precipitation ranged from 76 to 86 cm, with snowfall accounting for less than 25% of the total (U.S. Forest Service 1986). There was little topographic relief; soils were derived from sandy loam glacial till, and silt covered glacial tills and sandy outwash (U.S. Forest Service 1986). Vegetation cover was primarily forest: 40% deciduous (dominated by *Acer saccha-*
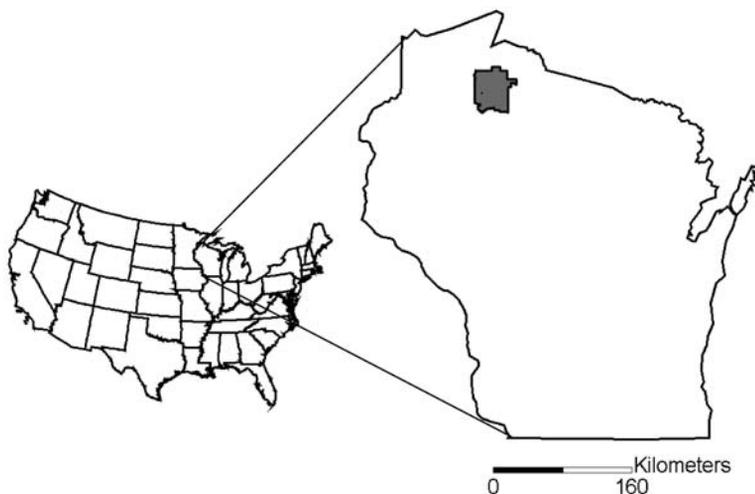
rum, Betula papyrifera, Populus tremuloides), 9% coniferous, (dominated by *Pinus resinosa, Pinus strobus*, and *Abies balsamea*); 8% mixed-coniferous-deciduous, and 7% aspen (*Populus tremuloides*) regenerating from timber harvest. The following 2 wetlands communities covered 26% of the area: emergent wetland (dominated by *Ledum groenlandicum, Chamaedaphne calyculata*) and sparse wetland forest (dominated by *Larix laricina*, and *Picea mariana*). Northern-white cedar wetlands (*Thuja occidentalis*) occupied 5%, and open upland areas occupied 1% of the landscape (Wisconsin Department of Natural Resources 1998). White-tailed deer (*Odocoileus virginiana*) were abundant throughout the region, and predator populations included wolves, coyotes (*Canis latrans*), black bears (*Ursus americana*), and bobcat (*Lynx rufus)*. Wolves began recolonizing the Great Divide District of the Chequamegon National Forest in 1989 (Wydeven et al. 1995).

Twenty-five elk from Michigan were reintroduced in 1995, and 18 were fitted with very high frequency (VHF) radiotelemetry collars (Wisconsin Department of Natural Resources 2000). In subsequent winter months, the animals were corral trapped to replace and deploy new collars. The population increased to approximately 110 elk by 2002 (Stowell, Wisconsin Department of Natural Resources, personal communication). A total of 1,350 VHF radiotelemetry locations from 57 elk were collected diurnally between May 25 and September 5 in 1999, 2000, 2001, and 2002. Elk locations were determined for each animal at 10-14 day intervals by ground-based triangulation (White and Garrott 1990) using vehicle-mounted directional antennas. Visual confirmation of locations was made when possible. Elk locations and 95% confidence intervals were estimated using the Lenth Maximum Likelihood Estimator (Nams 2000). Observations with large positional error were removed so that the mean positional error was less than one-third of the finest grain size of analysis considered in this study (1.13 ha). The reduced sample consisted of 867 telemetry fixes with a mean error of 0.32 ha and a median error of 0.28 ha. We conducted least-squares-means tests (proc glm; SAS Institute 1999) to determine if there was a bias in the removal of location data in relation to distance from roads or wolf-territory centers. There were no significant differences between the removed and retained data for the mean distances to roads ($T_{1,1349}$ = 0.47, P = 0.63) and wolf-territory centers ($T_{1,1349}$ = 1.09, P = 0.29). Furthermore, a chi-square test

demonstrated that the removal of data was not biased by the vegetation-cover type in which the location data were located (df = 7, χ^2 = 7.43, P > 0.25).

Forage Biomass

In 2001, vegetation was sampled along 30-m transects stratified by vegetation-cover type. In 2002, vegetation sampling was conducted along extended 240-m transects that included 8 contiguous 30-m transects (Fig. 2). Vegetation was sampled along 4 of these 30-m transects following a cyclic pattern designed to test for spatial autocorrelation (Clayton and Hudelson 1995). Transect length was reduced by increments of 30 m if it crossed into a different vegetation-cover type.

We sampled a total of 452 30-m transects from June through August in 2001 and 2002. Transects were located within 8 vegetation-cover types identified from a Landsat-derived land-cover map (Wisconsin Department of Natural Resources 1998) that was updated with forest harvesting records (U.S. Forest Service 2001, Table 1). Percent cover of herbaceous vegetation was estimated in 6 0.25-m^2 quadrats located at 5-m intervals along each transect and placed 2 m perpendicular to the transect line on alternating sides (Fig. 2). Using a point-intercept frame with double-layer 49-point grid, cover below each intercept point was scored as forb, grass, sedge, woody plant, fern, or bare substrate (soil, rock, log, etc). To estimate biomass of forbs and graminoids from percent cover, herbaceous vegetation was harvested from the last quadrat of each 30-m transect during 2001 (n = 92). Aboveground biomass of forbs, grasses, and sedges was separated, dried to constant mass, and the mass recorded. Linear regression analysis was used to develop an allometric relationship to convert percent cover to biomass. Percent cover variables were transformed by $2/\pi \times * \arcsin(X_i^{1/2})$ (McCune and Grace 2002) to remove heteroscedasticity. The dependent variables (forb and graminoid biomass) were log transformed to remove heteroscedasticity. Because regression equations for grasses and sedges were not statistically different, as determined by a nonsignificant term for vegetation functional group, the same equation was applied separately to grass and sedge cover to estimate their respective biomass.

Woody vegetation was sampled in 5 × 1-m plots (n = 449) during 2001 and 2002 located either along transects (2002; Fig. 2; n = 217) or at random among the vegetation-cover types (2001; n = 232). In each plot, we measured the height and
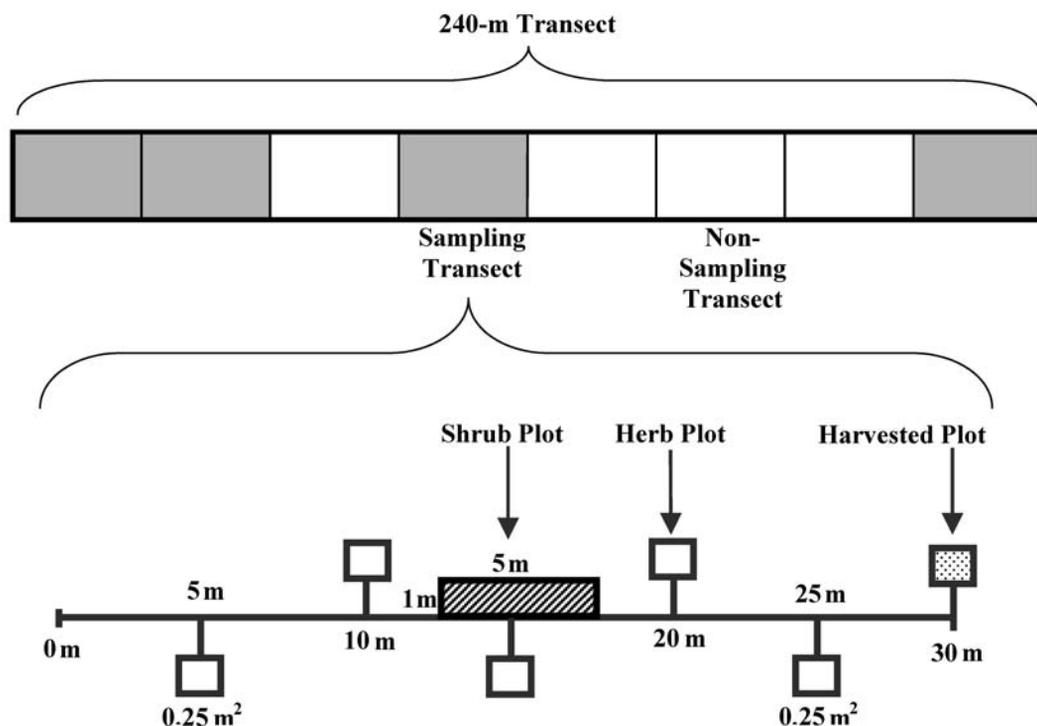
Fig. 2. Transect design for vegetation surveys. Each 240-m transect was subdivided into 4 30-m sampling transects and 4 30-m non-sampling transects. The sampling- and non-sampling transects are represented by gray and white rectangles respectively. The percent cover of forbs and graminoids was measured in 6 0.25 m^2 plots along the 30-m transect. The height and crown width of woody vegetation within the 0–2.5 m browse stratum were measured. No data were collected in the nonsampling transects. Allometrics were developed to convert the percent cover within the survey plots to biomass in g/m^2.

width of each woody plant within the browse stratum (0–2.5 m). Plants were also inspected for evidence of browsing, and we only considered browsed species to represent potential forage and included in subsequent analyses. Height and width were measured, and current year's growth was harvested from woody plants of all sizes ($n = 149$ plants) encountered inside or adjacent to the plot ($n = 35$ species). Vegetation samples were dried to constant mass, and regression analysis was used to relate plant height and width to forage biomass. Plant biomass, height, and width were natural logarithm transformed to remove heteroscedasticity. Because regression models were statistically similar among species, a single allometric equation was applied to all forage species.

We used allometric regression equations to convert measurements taken on forbs, grasses, sedges, and woody vegetation to biomass within each 30-m transect. Each 30-m transect was initially treated as an independent sampling plot, and analysis of variance (SAS Institute 1999) was used to determine whether the mean biomass dif-

fered significantly among vegetation-cover types. Because the data were spatial and transects may not have been truly independent, we calculated Moran's I (Kalunzny et al. 1998) on the residuals of the ANOVA to determine whether the errors were spatially independent. Moran's I was nonsignificant for all functional plant groups ($P > 0.05$), and 30-m transects were treated as independent. The mean biomass for each vegetation-

Table 1. Number of transects in which herbaceous and woody vegetation were surveyed.

Vegetation-cover type	Herbaceous vegetation transects	Woody vegetation transects
Coniferous forest	62	91
Deciduous forest	65	106
Mixed forest	50	72
Emergent wetland	8	4
Sparse-forest wetland	32	41
Cedar wetland	24	48
Regenerating aspen	43	51
Open	25	36

cover type was assigned to the 30-m grid cells of the land cover map (Wisconsin Department of Natural Resources 1998) to create a biomass map.

Herbaceous Biomass Phenology

To characterize peak forage biomass across the landscape, an additional 30 vegetation survey transects (30 m) were established in 2002 to monitor changes in herbaceous biomass within and between growing seasons. Seventeen phenology transects were located where the vegetation was sampled in 2001. Five transects were distributed across the landscape in each of the following vegetation-cover types: coniferous forest, deciduous forest, mixed-coniferous-deciduous forest, cedar wetlands, regenerating aspen stands, and open upland areas. Emergent wetlands and sparse-forested wetlands were not included in the phenology analysis because preliminary analysis indicated that elk were avoiding these areas. In 2002, the phenology transects were sampled in early June, mid-July, and late August. Repeated measures ANOVA (SAS Institute 1999) was used to determine whether biomass of forbs, grasses, and sedges differed significantly with phenology sampling period and vegetation-cover type. Similarly, repeated measures ANOVA was used to determine whether biomass differed between 2001 and 2002 at the phenology sampling sites. The phenology of biomass of woody plants was not monitored, as variance of measurement error (height and width of available browse) was greater than variation in both intra- and inter-annual growth (for 2 years).

Distances to Wolf-territory Centers and Roads

The locations of wolf territories from October 2001 through March 2002 were derived from VHF-radiotelemetry data for radiocollared wolves and winter wolf-track surveys conducted by the Wisconsin Departments of Natural Resources (Wydeven et al. 1995, 2002). Center points of wolf home ranges were estimated by calculating the mean longitudinal and latitudinal coordinates of the radiotelemetry and winter-tracking locations. We used a Geographic Information System (McCoy and Johnston 2001) to create a raster map (30-m resolution) of the distance to the nearest wolf-territory center. Road data (Wisconsin Department of Natural Resources 1998) were used similarly to create a raster map (30-m resolution) of the distance to the nearest road. Class D roads designed for minimal use (U.S. Forest Service 2001) were eliminated from the analysis.

Large-extent Analysis: Establishment of Home Ranges

A "used versus available" design was used for the RSFs (Boyce et al. 2002, Manly et al. 2002, Boyce et al. 2003). The area within an ellipse enclosing all of the elk VHF locations was considered available habitat in which the elk could establish home ranges (Fig. 3a). To characterize the available habitat, 2,601 random locations were distributed within the ellipse (3 random locations for each observed elk location; Fig. 3b).

To determine the grain of the environmental data at which explanatory power was greatest, the environmental variables were sampled at radii of 60, 180, 300, 420, 540, 660, 780, 900, and 1,020 m around each elk and random location. The percent area covered by forest and the mean and coefficient of variation of forb, grass, sedge, and woody forage biomass were calculated within each grain size (radius). The distances to the nearest wolf-territory center and road remained the same for all grain sizes.

Resource selection function models were estimated using logistic regression (SAS Institute 1999) for each of the 9 grain sizes. To avoid multicollinearity, a correlation matrix for all of the covariates was examined, and only uncorrelated independent variables were analyzed together in regression analysis. The best model for each grain size was selected from an a priori list of potentially important models using the Akaike's Information Criterion (AIC; Burnham and Anderson 2002). Models with higher order terms of the predictor variables were also examined to determine whether nonlinear relationships existed.

We performed K-fold cross validation to assess the temporal predictive strength of the best model found for the 9 grain sizes. For each grain size, we partitioned VHF-location data by year (1999–2002); 1 year was withheld as a test data set, and the remaining 3 years were used as model training data. Using the best model, RSF values were obtained for all of the random locations to represent the range of habitat selection within the extent of the analysis. The RSF values were sorted from lowest to highest and binned into 8 groups with an equal number of random locations in each group (Boyce et al. 2003). The maximum and minimum RSF values of the bins were recorded to delimit bins from each other. Resource selection function values were obtained for the test data, and these were placed into the bins that were created with the random
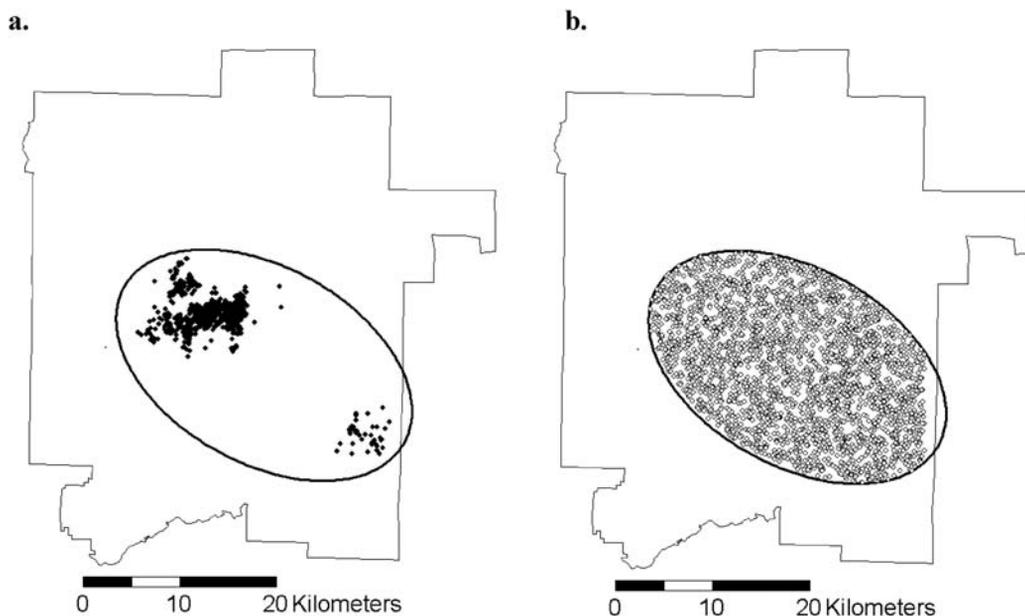
Fig. 3. Location of large-extent analysis within the Chequamegon National Forest, Wisconsin, USA. The elk and random locations are shown in a. and b. respectively.

data. The number of test-RSF values (elk locations from test data) placed in each bin was recorded. The number of test-RSF values in each bin was regressed against the median value of the random-RSF values in each bin, and the R^2 value was recorded. This process was repeated holding each year out in turn as test data sets, and the mean of the R^2 values from the 4 cross validation iterations was used as a measure of predictive strength of the model (R^2_{pred}). A Tukey's pairwise test was conducted to determine whether the R^2_{pred} differed significantly between grain sizes; data were partitioned by year so that each grain size had 4 observations.

To determine categories of habitat selection among which the elk distinguished when establishing a home range, we tested if the percentage of elk locations were significantly different among bins. Data were partitioned by year, as in the temporal cross validation, and for each year of radiotelemetry data the percentage of total elk locations in the test data that were found in each bin was determined. A Tukey's pairwise test was conducted on the 8 bins, for which there were 4 observations for each bin, 1 for each year of data. The test was repeated for each grain size. The proportion data were transformed by $2/\pi \times * \arcsin(X_i^{1/2})$ (McCune and Grace 2002) to remove heteroscedasticity.

Small-extent Analysis: Resource Selection within Home Range

The small extent was defined individually for each elk as a 200-m buffer added around the minimum convex polygon (MCP) of each elk's VHF locations; the MCP and the 200-m buffer were considered as habitat that the elk could easily access. All elk with fewer than 12 total locations were deleted from this analysis. Three random locations were associated with each elk location and distributed within the buffer. The RSFs were estimated using conditional logistic regression (SAS Institute 1999), and the individual elk was considered as a stratified variable to control for variation among individuals. Environmental variables were again sampled using GIS at radii of 60, 180, 300, 420, 540, 660, 780, 900, and 1,020 m around each elk and random location. The same set of potential covariates and model selection techniques were used as in the large-extent analysis. A Tukey's pairwise test was again used to identify the categories of habitat selection to which elk responded within their home ranges.

Cross validation was conducted to examine the predictive strength of the model over time and space. The temporal test of predictive strength was carried out by partitioning the data by year, as in the large-scale analysis. The spatial test of predictive strength was done by partitioning the data by elk. The radiotelemetry-location data for an

individual elk were with-
held as test data, and
the remaining data were
used as training data.
This process was repeat-
ed so data from each elk
were held out as test
data. The predictive suc-
cess of the model was
assessed, as was done in
the temporal test, by cal-
culating the mean of the
R^2 values from all cross-
validation iterations.

Table 2. Factors that influence resource selection at the large extent. The estimated RSF coefficients and the mean R^2_{pred} are shown for each grain size.

Large extent Grain size	RSF coefficients					
	Wolves	Roads	Forbs and grasses	Woody browse	Mean sedges	R^2_{pred}
60	0.0006	0.0002	0.107	–0.011	–0.066	0.86
180	0.0006	0.0002	0.202	–0.036	–0.107	0.85
300	0.0006	0.0003	0.299	–0.069	–0.160	0.84
420	0.0007	0.0004	0.398	–0.123	–0.220	0.85
540	0.0007	0.0005	0.510	–0.184	–0.270	0.82
660	0.0007	0.0005	0.612	–0.234	–0.303	0.83
780	0.0007	0.0006	0.721	–0.282	–0.322	0.82
900	0.0007	0.0006	0.825	–0.317	–0.338	0.78
1,020	0.0008	0.0006	0.920	–0.328	–0.358	0.77

Predicting Elk Habitat

Maps of the relative probability of occurrence of elk were constructed from the large- and small-extent models using coefficients from the 300-m radius. This radius was chosen because of strong predictive strength of the models at this grain size at both extents. Predictions were extrapolated across the entire Great Divide District of the Chequamegon National Forest. The categories of habitat selection displayed were determined by the empirical analyses described above.

RESULTS

Forage Biomass and Phenology

The allometric regression equations for estimating forage biomass from morphological measurements accounted for 72 to 88% of the variation in biomass. The equations for forb and graminoid biomass both included the percent cover of bare substrate as a predictor. Although models of forb biomass were estimated separately by species, the relationships were statistically similar and a single allometric equation was used for all forbs.

Forb biomass = exp(0.64 + (4.5 * %Forbs) – (1.2 * %Bare Substrate))
        ($N = 92$, $R^2 = 0.72$, $P < 0.001$)
Grass or sedge biomass = exp(0.81 + (4.2 * %Graminoid) – (1.3 * %Bare Substrate))
        ($N = 92$, $R^2 = 0.81$, $P < 0.0001$)
Woody-plant forage biomass = exp(–6.98 + (1.06 * ln height) + (0.98 * ln crown))
        ($N = 149$, $R^2 = 0.88$, $P < 0.0001$)

Forb, grass, and sedge biomass at the phenology sites were significantly influenced by phenology sampling period ($F > 16.48$ and $P < 0.0001$ for all

functional groups). A post-hoc pair-wise comparison of biomass between sampling periods demonstrated that biomass was 25% less in June than in July ($T > 5.59$ and $P < 0.001$ for all functional groups) and August ($T > 4.25$ and $P < 0.001$ for all functional groups). There was no significant difference in biomass between July and August. The biomass in 2001 did not differ significantly from 2002 for all functional groups ($P > 0.05$). Therefore, peak biomass was estimated for all vegetation-cover types using data collected in the months of July and August in 2001 and 2002.

The elimination of data collected in June of both years from the regular vegetation survey transects reduced the sample size to 309 transects surveyed for herbaceous vegetation. An ANOVA on the retained data set demonstrated that the mean biomass of the functional groups differed significantly among the 8 vegetation-cover types (forbs $F = 9.36$, $P < 0.0001$; grasses $F = 8.35$, $P < 0.0001$; sedges $F = 8.17$, $P = 0.0001$; and woody plants $F = 22.35$, $P < 0.0001$). Therefore, the mean biomass of the functional groups in each vegetation-cover type was applied to a landcover map (Wisconsin Department of Natural Resources 1998).

Large-extent Analysis: Establishment of Home Ranges

The environmental variables that predicted locations of summer home ranges remained consistent across all grain sizes examined. Elk selected areas that were distant from the centers of wolf territories and farther away from roads (Table 2). Elk also selected areas with high forb and graminoid biomass and avoided areas with high sedge and woody-plant forage biomass. All relationships between the log odds of the relative probability of locating an elk and forage biomass were linear, as all higher order terms were nonsignificant. Percent cover of forests at each grain

size never improved the regression model, as measured by AIC.

The temporal cross validation test showed strong predictive strength across all grain sizes; mean R^2_{pred} values ranged from 0.77 to 0.86 (Table 2). Results of a Tukey's pairwise test showed no significant difference in predictive strength with grain size of the environmental variables.

At all grain sizes in the large-extent analysis, the Tukey's pairwise tests showed that elk differentiated among 4 categories of habitat selection ($P < 0.05$; Table 3). Across all grain sizes, the frequency of observations in the lowest 4 bins did not differ significantly. These bins represent habitat areas of low resource selection and consequently contained very few validation points. The fifth and sixth, or the sixth and seventh bins, (depending on grain size), also did not differ. The percentage of validation points in the eighth bin, which is predicted highly selected habitat, was always higher than the other bins.

Small-extent Analysis: Resource Selection within Home Range

As in the large-extent analysis, the variables that explained habitat use within established home ranges were consistent across all grain sizes (Table 4). Elk selected areas that were distant from wolf-territory centers. Within home ranges, however, elk selected areas near roads, contrary to the large-extent analysis. Elk selected areas of high forb and grass biomass and avoided areas with high woody-browse. Sedge biomass and percent cover of forests were not significant factors in the small-extent analysis.

In both the temporal and spatial cross validation tests of predictive strength, the mean R^2_{pred} values remained consistent across all grain sizes. Tukey's pairwise test showed no significant differ-

Table 3. Large-extent results of the Tukey's test for differences in the percentage of observations found in each bin, indicating that the elk are responding to 4 different categories of habitat selection in the environment at $P < 0.05$.

Large extent	df-error = 24			
Grain size	Habitat selection categories	*F*-value	*P*-value	Minimum significant difference
60	4	115.44	<0.0001	0.0863
180	4	161.03	<0.0001	0.0769
300	4	140.03	<0.0001	0.0858
420	4	131.75	<0.0001	0.0904
540	4	136.10	<0.0001	0.0913
660	4	164.66	<0.0001	0.0842
780	4	140.84	<0.0001	0.0944
900	4	150.87	<0.0001	0.0938
1,020	4	197.72	<0.0001	0.0834

ence in predictive strength with grain size of the environmental variables. The mean R^2_{pred} values were consistently higher in the temporal test than in the spatial test (Table 4). For all 9 grain sizes, the Tukey's pairwise tests indicate that the elk were differentiating between 4 different categories of habitat selection (Table 5).

Predicting Elk Habitat

Based on the RSF models and consistent differences among 4 habitat selection categories, the RSF models were extrapolated across the landscape to display 4 categories of summer habitat selection (Fig. 4) for both home-range selection and use of areas within a home range. The relative probability of habitat use was largely driven by location relative to wolf-territory centers, although this influence was more pronounced in the large-scale model of selecting home-range locations. The large areas predicted to be of low value to elk in the large extent model are centered on wolf-territory centers. At distances far from wolves, the influence of heterogeneity in forage biomass and distance to roads become apparent. Within home ranges, the selection of areas near roads produced a fine-grained mosaic of habitat selection along with the increase influence of forage biomass.

DISCUSSION

Results were largely consistent with our hypotheses. The presence of

Table 4. Factors that influence resource selection at the small extent. The estimated RSF coefficients and the mean R^2_{pred} are shown for each grain size.

Small extent Grain size	RSF coefficients					
	Wolves	Roads	Forbs and grasses	Woody browse	Temp. R^2_{pred}	Spatial R^2_{pred}
60	0.0002	−0.0009	0.031	−0.006	0.81	0.58
180	0.0002	−0.0009	0.066	−0.023	0.79	0.57
300	0.0002	−0.0009	0.110	−0.069	0.77	0.57
420	0.0002	−0.0009	0.148	−0.099	0.76	0.57
540	0.0002	−0.0009	0.187	−0.119	0.71	0.55
660	0.0002	−0.0008	0.219	−0.135	0.76	0.53
780	0.0002	−0.0008	0.262	−0.173	0.76	0.53
900	0.0002	−0.0008	0.315	−0.216	0.76	0.53
1,020	0.0002	−0.0008	0.367	−0.241	0.77	0.52

Table 5. Small-extent results of the Tukey's test for differences in the percentage of observations found in each bin, indicating that the elk are responding to 4 different categories of habitat selection in the environment at $P < 0.05$.

Small extent	df-error = 24			
Grain size	Habitat selection categories	*F*-value	*P*-value	Minimum significant difference
60	4	48.72	<0.0001	0.1194
180	4	51.46	<0.0001	0.1166
300	4	53.67	<0.0001	0.1149
420	4	56.59	<0.0001	0.1120
540	4	57.96	<0.0001	0.1114
660	4	61.70	<0.0001	0.1058
780	4	59.20	<0.0001	0.1073
900	4	57.00	<0.0001	0.1092
1,020	4	60.23	<0.0001	0.1076

wolves was expected to cause elk to alter movement and foraging patterns (Fryxell and Lundberg 1997, Ripple et al. 2001, Johnson et al. 2002), and our results showed that the reintroduced elk established home ranges in the periphery of wolf territories where the relative risk of predation should be reduced (Mech 1977). They also preferred areas within their home ranges that were far from wolf-territory centers. Previous research has demonstrated that elk prefer forest-

ed areas when wolf predation pressure is high (Wolff and Van Horn 2003), but in our study, elk did not use forested areas disproportionately to their availability. This may be because forest covers more than 63% of the landscape (Wisconsin Department of Natural Resources 1998), and elk have close access to forest throughout their home range.

Elk are flexible foragers, but not all forage types are of equal preference (Merrill 1994). Elk were attracted to areas with high grass and forb biomass at the large and small extents and avoided areas with high biomass of woody browse and sedges. The relationship between the grass and forb biomass and resource selection was linear, as all higher order terms were nonsignificant. This suggests that elk selected habitats that permitted a maximization of intake rates (Illius et al. 1999, Bergman et al. 2001). It is possible, however, that elk may cue in on high biomass areas at broad scales and make selections of high quality vegetation at a finer grain (<60 m) than was considered here. Forage quality may also influence fine-scale movements by ungulates (Wilmshurst et al. 1995, 1999; Cook 2002; Fortin 2003), but this effect was not quantified in the current study.

High sedge and woody-browse biomass areas may have been avoided because of poor forage
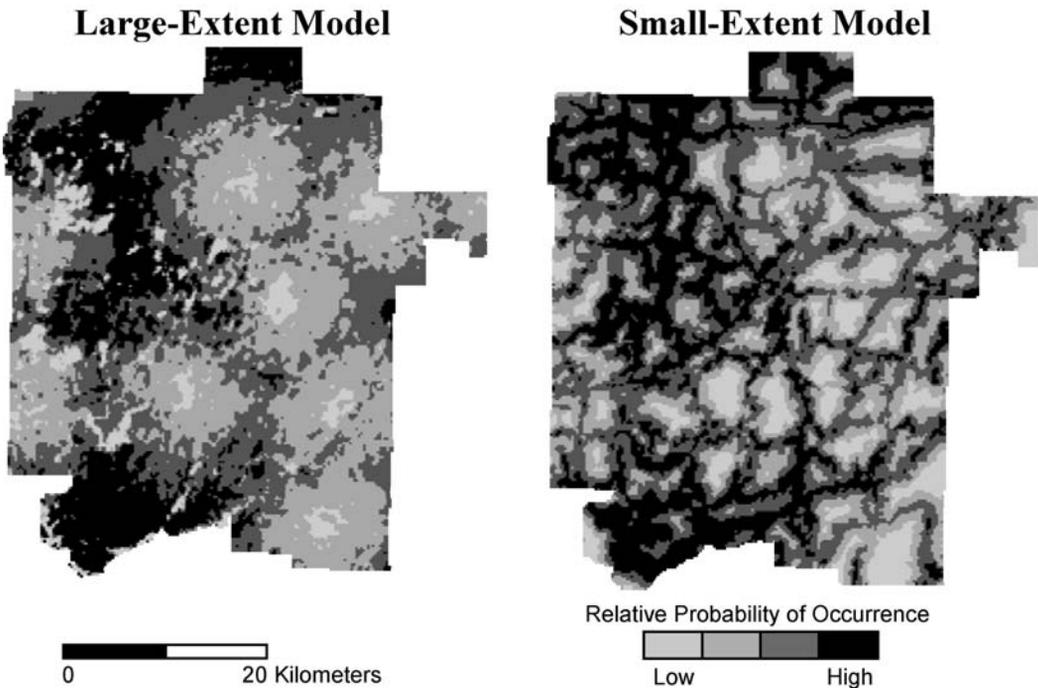

Fig. 4. Relative probability of elk occurrence in the Chequamegon National Forest, Wisconsin, USA, based on the large- and small-extent RSF model.

quality (Cook 2002) or because intake rates may be lower for these functional groups (Wickstrom et al. 1984). Additionally, elk may have had difficulty moving through very dense shrubby areas or open wetlands, which were associated with high sedge biomass. The lack of a significant influence of sedge biomass in the small-extent analysis may have simply reflected that home ranges were already established away from wetlands. The avoidance of areas with high sedge and woody-browse biomass may have been a seasonal effect as these functional plant groups (woody browse in particular) may be important resources in winter when grass and forb biomass and quality are reduced.

Roads are a ubiquitous feature of most landscapes in eastern North America, and the influence of roads on elk habitat use in summer was different at large and small extents. Habitat-use decisions within a home range (third-order selection) are dependent on where the home range is located (second-order selection; sensu Johnson 1980). Several empirical studies have concluded that elk avoided roads at large extents (Lyons 1979, Cole et al. 1997, Rowland et al. 2000, McCorquodale 2003) because roads present a mortality risk due to cars and hunters. Of the 33 elk deaths investigated in Wisconsin since the reintroduction in 1995, 9 have been attributed vehicle collisions (Stowell, Wisconsin Department of Natural Resources, personal communication). At smaller extents, however, roads are both openings and edges in this predominantly forested landscape, and it has been well documented that ungulates favor areas with high densities of edges (Beier and McCullough 1990, Tufto et al. 1996, Kie et al. 2002). The forest-road edge provides high biomass of forbs and grasses and immediate access to forest cover to potentially reduce predation risks (Tufto et al. 1996, McCorquodale 2003, Wolff and Van Horn 2003) and thermal stress (Porter et al. 2002).

While results were sensitive to changes in the extent of the analysis, the RSF models were insensitive to a change in the grain size of the environmental data at both the large-extent and small-extent analyses. This may reflect the lack of strong environmental gradients, such as topographic relief, that characterize other landscapes in which modeled relationships change substantially with grain size (Pearson et al. 1995, Wallace et al. 1995).

The temporal cross validation demonstrated that we could predict with reasonable precision resource selection of animals in independent years, despite the imperfect overlap of data collection on elk locations (1999–2002), forage biomass (2001–2002), and wolf-territory centers (winter 2001–2002). This corroborates the phenology results that there was little inter-annual variation in forage biomass. Furthermore, strong inter-wolf-pack dynamics (Mech 1977) were expected to prevent large displacements of territories over the time scale of this study. In contrast, the cross validation test of predictive strength was lower when the data were partitioned by individual elk than by year. The differences in the cross validation results may be explained by the relatively small inter-annual variation in summer resources in comparison with spatial variation in resource availability across the landscape.

The maps derived from the large- and small-extent RSF models demonstrated the 4 categories of habitat selection that influenced elk habitat use (Fig. 4). Our quantitative approach avoided creating potentially misleading maps that display either more or fewer habitat selection categories than were perceived by the study animal (Loman and Von Schantz 1991, Andrén 1992, Tufto et al. 1996). The maps clearly illustrate scale dependence. The distance to wolf-territory centers had a relatively greater impact on where elk established home ranges (large-extent model) than on how they used home-range areas (small-extent model). The increased patchiness of the map depicting the results of the small-extent model demonstrated the increased influence of forage availability and presence of roads relative to the influence of wolves on elk habitat use within home ranges.

MANAGEMENT IMPLICATIONS

Our results are informative for management of the growing elk population in northern Wisconsin and for proposed elk introductions across eastern North America. Home-range selection and habitat use were largely affected by heterogeneous patterns of forage availability and wetlands, the spatial distribution of predators and road density. By projecting RSF predictions across more extensive landscapes, managers could identify potential locations of preferred habitat and areas likely to be colonized by an expanding population. Similarly, if plant diversity is of management interest, our results could suggest areas of the landscape that might be susceptible to increased herbivory and areas that might serve as refugia from herbivory.

We predict that the elk population in Wisconsin and at other introduction sites will expand in an irregular spatial pattern influenced by landscape heterogeneity. Consequently, management zones at introduction sites should anticipate the habitat selection patterns of elk and ensure that sufficient area of highly selected habitat is included. While elk appear to favor areas distant from wolf-territory centers, our results do not suggest that the presence of wolves on the landscape will restrict elk population expansion. We predict that elk will slowly spread across entire the Great Divide District, including into wolf territories; however, expansion should be more rapid in the peripheral areas of wolf territories than toward the center. Presence of wolf pack territories may reduce elk spatial use of these portions of the landscape. Assessment of the potential impact of roads at future elk-introduction sites should consider the scale-dependent influence of roads found in our study. Elk favored areas with fewer roads at broad scales, but they used roadsides, which often have abundant herbaceous biomass, within their home ranges. In addition, even though forest cover did not influence summer resource selection in our study, it may be important at other sites that have less forest cover or during other seasons.

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