

Research article

Factors influencing female home range sizes in elk (*Cervus elaphus*) in North American landscapes

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Abstract

Home range size is a result of individual movements and the spatial distribution of a population. While body size, sex, and age are known to influence the area over which an animal ranges, it remains uncertain how landscape heterogeneity influences home range size. We examined elk (*Cervus elaphus*) seasonal home range sizes in relation to the quantity and spatial heterogeneity of forage biomass, forest cover, topography, snow–water equivalents, and landscape structure in three study landscapes: Yellowstone National Park, Wyoming, USA; eastern slopes of the Canadian Rockies, Alberta; and northern Wisconsin, USA. We used a 95% fixed kernel estimator to measure the home range size and location of all elk. To identify the scales at which important factors influenced home range sizes, we quantified environmental variables within the estimated home range polygon and within concentric circles with radii of 1000, 2000, 3000, 4000, and 5000 m from the home range center. Results indicate that there was an inverse relationship between forage biomass and summer and winter home range sizes in Alberta and Wisconsin, however the relationship was positive in Yellowstone. The size of summer and winter home ranges was positively related to percent forest cover; however this relationship was significant only when forest cover was quantified within the home range polygon or radii that were greater than or equal to 3000 m. Winter home ranges also had a positive relationship with snow–water equivalents. The predictive strength of summer home range models was greatest when landscape variables were quantified within the concentric circles with a radius of 3000 m or more, whereas the predictive strength of the winter models was greatest within the estimated home range polygon. Results suggest that elk ranging patterns reflected complex trade-offs that affect foraging, group dynamics, movement energetics, predation avoidance and thermal regulation. The multi-scale analysis indicates that elk based home ranging decisions on an area equal to their home range, but areas outside of the estimated home range were also important.

Introduction

Home range size and location are a direct result of individual movements and the spatial distribution of a population. Body size, sex and age have been shown to influence home range sizes in

animals (McNab 1963; Sweeney and Sweeney 1984; Relyea et al. 2000; Mysterud et al. 2001). Independent of these factors, high intra-specific variation in cervid home range sizes has been observed within and among different populations (Nicholson et al. 1997; Kie et al. 2002). The high

variability could be a result of animals making movement decisions under different ecological settings to balance the needs to minimize the predation risk while meeting forage uptake demands (Fryxell and Lundberg 1997; Bowyer et al. 1998; Kie 1999), minimize thermal stress (Porter et al. 2000; Porter et al. 2002), and maintain social contacts (Aycrigg and Porter 1997). Animals make hierarchical decisions from broad to fine scales (Senft et al. 1987), and the scale at which animals survey the environment for one factor may be nested within a scale at which a different factor is surveyed. Identifying environmental factors and the scales at which they influence home range size is central to understanding animal responses to complex landscapes.

The abundance and spatial arrangement of forage should influence an animal's ability to forage efficiently (Kareiva 1983; Cain 1985). Forage availability within a given home range size must meet energy and nutritional requirements, otherwise home range size must be increased to encompass additional resources. Evidence suggests that animals do range over large areas when food is scarce or patchily distributed (Ford 1983; O'Neill et al. 1988; Turner et al. 1993; Tufto et al. 1996; Relyea et al. 2000). If forage availability does influence home range size, then elk should have to range over larger areas in the winter than in the summer because of reduced forage availability due to plant decomposition, snow (Wickstrom et al. 1984), and reduced forage quality (Albon and Langvatn 1992).

The amount of forest cover in an area may influence how ungulates respond to predation risk and thermal extremes, and consequently could influence home range size. Forest patches are used preferentially in areas of high predation pressure (Wolff and Van Horn 2003; Fortin et al. in press), which permits ungulates to reduce vigilance (Altendorf et al. 2001). Forest cover also can mediate thermal stress (Grace and Easterbee 1979; Parker and Gillingham 1990; Demarchi and Bunnell 1993; Porter et al. 2002); however, see Hobbs (1989), Merrill (1991) and Cook (1998). Forests also may be attractive to elk in winter because snow depth tends to be lower under coniferous forest canopy than in open areas (Huot 1974; Crawford 1984), and elk avoid areas of deep snow (Sweeney and Sweeney 1984; Pauley et al. 1993).

Heterogeneity and landscape structure can be important determinants of the distribution of animals on landscapes (Turner et al. 1994; Kareiva and Wennergren 1995; With and Crist 1995; Kie et al. 2002). Deer have been shown to have smaller home ranges on landscapes with smaller patch sizes (or more contagion) and more edge (Moe and Wegge 1994; Kie et al. 2002). Presumably this is due to ungulates needing multiple habitat types for foraging and escape cover. Similarly, topography should influence ranging as upslope movement is substantially more energetically costly than horizontal movement (Parker, 1984; however, see Taylor et al. 1972). Elk do prefer to move horizontally (Skovlin et al. 2002; Kie et al. 2005), which could elongate and increase the size of home ranges in hilly areas.

To test these hypotheses we examined factors that may influence seasonal home range sizes of elk (*Cervus elaphus*) in three North American landscapes: Yellowstone National Park in Wyoming; Canadian Rockies in Alberta; and Chequamegon National Forest in Wisconsin, U.S.A. We addressed three questions. First, what factors influenced the summer and winter home range sizes of elk? We considered quantity and spatial heterogeneity of forage biomass, percent cover of forested areas, quantity and spatial heterogeneity snow-water equivalents, spatial structure of landscape and topography. Second, at what scale did important factors influence home range sizes of elk? Lastly, were home ranges larger in winter than in summer? Our *a priori* general prediction was that when critical resources are readily available locally, home ranges will be relatively small (Oehler et al. 2003).

Methods

Study areas

Wisconsin

In 1995, elk were introduced into the 1852 km² Great Divide District of the Chequamegon National Forest, Wisconsin, U.S.A. (Figure 1). The site has little topographic relief, and is characterized by deciduous and coniferous forest interspersed with wetlands. Mean annual air temperature was 5 °C, and mean annual precipitation ranged from 76 to 86 cm, with snowfall



Figure 1. Location of study areas in Alberta, Wisconsin and Yellowstone.

accounting for less than 25% of the total (USDA 1986). We used 2601 VHF radiotelemetry locations from 57 adult female elk collected diurnally in 1999, 2000, 2001, and 2002. Elk locations were determined for each animal at 10–14 day intervals by triangulation (White and Garrott 1990) and visually confirmed when possible (Anderson et al. in press). Elk locations and 95% confidence intervals were estimated using the Lenth Maximum Likelihood Estimator (Nams 2000). Mean location error was 95 m (8.5 S.E.).

Alberta

Data were collected within a 15,800 km² study site in the central Rocky Mountains and foothills of Alberta, Canada (52°27' N, 115°45' W; Figure 1). Mean annual temperature was 2.3 °C, and the mean annual precipitation was 54 cm (Environment Canada 2004). The area is characterized by rolling to rugged terrain between 500 and 1500 m in elevation and is dominated by conifer forest (69.5% forested; Frair et al. 2005). Approximately 2000 non-migratory elk inhabited the area between 2000 and 2003 (J. Allen, Alberta Sustainable Resource Development, personal communication). Ten adult female elk were fitted with VHF collars and relocated approximately every 20 days during aerial surveys. Mean location error was 169.3 m (28.5 S.E.).

Yellowstone National Park

The landscape in Yellowstone National Park (YNP) is also mountainous, but has more grassland areas than the Alberta site (Figure 1). The climate is generally cool and dry with mean January temperature of -11.4 °C, mean July temperature of 10.8 °C, and mean annual precipitation of 56.2 cm (Dirks and Martner 1982). The capturing, handling and collection of radiotelemetry data were described by Cook et al. (2004). Location data for 32 adult female elk were collected at two to four week intervals between June 2000 and May 2003. Mean location error was 86 m (13 S.E.) (Mao 2003). Many of the elk in Yellowstone are migratory, and in the winter a large herd congregates in the northern area of the park. We included only locations within either the summer or winter ranges in the analysis.

Estimation of seasonal home range size

We subdivided the VHF radiotelemetry location data into summer (June through October) and winter (December through April) seasons. We defined the seasonal home range size as the area in which there was a 95% probability of finding the animal during the specific season over the course of the study (White and Garrott 1990). We used

the Home Range Extension for ArcView (Carr and Rodgers 1998) to estimate seasonal home range size for each elk using a 95% fixed kernel estimator with the least squares cross validation smoothing parameter.

We employed the Animal Movement Analysis Arcview Extension (Hooge et al. 2002) to perform a bootstrapping test to determine if the number of telemetry-location fixes was sufficient for each elk, because small sample sizes tend to over-estimate kernel home range sizes (Seaman et al. 1999). We conducted ten iterations of this test for each sample size, from the total number minus one down to 15 telemetry-location fixes. We constructed 95% fixed kernel with the least squares cross validation smoothing parameter for all iterations. The mean and variance of home range size were calculated for each sample size and plotted against the sample size. If an asymptote was not approached by the data, we eliminated the data for that animal from the analysis. The number of telemetry-location fixes per home range varied from 24 to 96 points. Summer and winter home range size estimates were calculated on 8 and 9 elk respectively in Alberta, 22 and 11 respectively in Wisconsin, and 17 and 24 respectively in Yellowstone. Following the bootstrap tests, most of home range kernels retained for analysis formed contiguous polygons.

Estimation and Extrapolation of Forage Biomass

For each site, we produced summer and winter peak biomass maps for four functional plant groups: forbs, grasses, sedges, and woody browse. The percent cover of functional groups was measured similarly at each site along transects that were stratified by habitat type and elevation. In Wisconsin, a 30-m land-cover map was derived from 1991–1993 Landsat Thematic Mapper (TM) imagery (WiDNR 1998), and updated with recent cover changes (USDA 2001). We stratified transects across eight habitat types. Because the landscape is flat in Wisconsin, topography was not considered in the placement of transects. In Alberta, a 28.5-m landcover map was derived from a 2001 TM image (Frair et al. 2005). We stratified transects across 10 habitat types and distributed evenly between high- (≥ 1300 m) and low-elevation (< 1300 m) areas. For the equally mountainous

landscape of Yellowstone, a 50-m landcover map was developed by compositing a Landsat TM-derived image (Dixon 1997) with a cover type classification based on aerial photography (Despain 1990). Transects were stratified by nine habitat types and those in coniferous forest were further stratified by elevation (high ≥ 2286 m or low < 2286 m) and substrate type.

We developed allometric equations separately for each site, which were used to estimate biomass at the plot level. We used regression analysis to determine the landscape variables (cover, elevation, slope, aspect, etc) that influenced biomass, and to extrapolate results across raster maps. Details of methods used to obtain spatial estimates of forage biomass at each site are provided in Appendix A.

Estimation and extrapolation of snow–water equivalents

The relative levels of snow depth and density were indexed by snow–water equivalents (Goodison et al. 1981), or the equivalent depth in water. We developed monthly raster maps of snow–water equivalents from the Snow Model for Yellowstone National Park (Wockner et al. 2002) for the winter months. We developed similar snow–water equivalents maps for Alberta and Wisconsin using standard field measurement techniques for snow depth and density during the 2001–2002 and 2002–2003 winters (Goodison et al. 1981). To obtain a general indicator of the typical severity of snow–water equivalents for each pixel across the landscape, the snow–water equivalents value for each pixel was averaged over months and years. The Yellowstone model was only parameterized up to 1999, so we calculated typical snow–water equivalents values based on averaging estimates from 1993 to 1999. Details of the methods used to obtain the spatial estimates of snow–water equivalents for Wisconsin and Alberta are provided in Appendix B.

Analysis

We used two approaches to examine how environmental conditions influenced home range size

in elk. First, we quantified environmental factors within each home range polygon that was constructed from the 95% kernel estimator, and used regression analysis to relate these factors to home range size. Second, we determined the center point of each home range based on the mean x and y location. Around each of these center points we created five circles with radii of 1000, 2000, 3000, 4000, and 5000 m, within which we quantified the environmental factors. We conducted separate regression analyses for each circle size. This multi-scale approach allowed us to determine how much of the surrounding landscape influences elk home range size. We used ArcGIS to calculate the mean, standard deviation and the coefficient of variation of forage biomass and snow-water equivalents within the home range polygons and the multiple circles (ESRI 2001; Beyer 2004).

We used the data from Alberta and Yellowstone to examine how topography influences home range size. The digital elevation maps (DEM) from the two sites were used to determine the mean, standard deviation and coefficient of variation slope (in degrees) within the home range polygon of each elk, and within the five circles around the home range center.

We used land-cover classification maps to quantify the percent cover of forested areas and landscape structure. To quantify landscape structure, we reclassified the land-cover maps for each of the sites into three biologically relevant groups representing highly, moderately and less-used habitats. In Wisconsin, highly used habitats in summer were open upland areas, young aspen stands and coniferous forests. In winter, northern-white cedar wetlands were added to the highly used habitats of the summer. We considered all remaining upland areas moderately used, and open wetlands were less used. This classification was based on preliminary habitat-selection analysis (Anderson et al. in press). In Alberta, open areas, aspen stands and coniferous forests were considered highly, moderately and less-used habitats respectively (Jones and Hudson 2002; White et al. 2003). In Yellowstone, aspen stands, open areas and coniferous forests were considered highly, moderately and less-used habitats respectively (Fortin et al. in press). We used Fragstats (McGarigal and Marks 1995) to quantify the following landscape metrics for highly, moderately and less-used habitats within each home range

polygon and the sampling circles: mean patch area; percent cover; patch density; edge density; proximity index; and inter-patch distance.

We used multiple regression (SAS Institute Inc. 1999) to explore the relationship between home range size of individual elk and the landscape variables quantified within the home range polygons and the five sampling circles (1000-m to 5000-m radii). We explored polynomial and log transformations to determine if non-linear relationships existed. We examined a correlation matrix for all of the covariates, and only orthogonal variables were entered into candidate regression models. Additional regression analyses were done using data from only Alberta and Yellowstone to examine the effect of topography on home range size. We selected the best models for each analysis from an *a priori* list of potentially important models using the Akaike Information Criterion (AIC; Burnham and Anderson 2002). *Post-hoc* comparisons were conducted among sites to determine differences between home ranges size and independent variables ($\alpha=0.05$).

We performed cross validation to assess the predictive strength of the best model for each analysis. The data were partitioned by elk; one elk was withheld as a test data set, and the remaining data were used for model training. This process was repeated holding each elk out in turn as test data sets. We calculated a coefficient of prediction (R_{pred}^2), which measures the relative predictive strength of the model against simply using the mean of the training data to predict home range sizes of independent elk:

$$R_{\text{pred}}^2 = 1 - \frac{\sum(Y_p - Y_i)^2}{\sum(\bar{Y} - Y_i)^2}$$

where Y_p is the predicted home range size of elk i , Y_i is the observed home range size of elk i , and \bar{Y} is the mean home range size of the training data set (Turchin 2003). Values of R_{pred}^2 approaching one demonstrate excellent predictive strength, while values approaching zero indicate poor predictive strength and that using the mean value of the training data is better than the model. Negative values indicate that the model is fitting noise in the data.

Lastly, we used a paired t -test to compare home range sizes between summer and winter for each animal. The sample size of this analysis was

reduced to 35 elk, because many elk used in the preceding analyses did not have adequate sample sizes for both summer and winter home range analyses.

Results

We calculated Moran's I spatial autocorrelation statistic on the residuals of each regression analysis to determine if the errors were spatially independent (Kalunzny et al. 1998). Moran's I was not significant at any scale ($p > 0.05$), therefore we treated individual elk as independent.

Summer home range size

Mean forage biomass was the only significant factor when summer home range size was regressed against environmental variables quantified within the home range polygon and radii of 1000 and 2000 m (Table 1). Mean forage biomass and

percent forest cover were both significant predictors of home range size when quantified within the 3000-, 4000-, and 5000-m radii. The intercept and regression coefficients for mean forage biomass differed for the three sites, as indicated by the significant interaction term between site and mean forage biomass. In Alberta and Wisconsin the mean forage biomass coefficient was negative, indicating that home range sizes decreased as forage biomass increased. In contrast, the size of home ranges in Yellowstone had a positive relationship with mean forage biomass. Results from the cross validation test demonstrate that the predictive strength (R^2_{pred}) of the models was greatest at 3000-m scale.

Forage biomass, site and an interaction between these two main effects were present in the five best models, as determined by AIC (Table 2). The proximity index, patch density, and the percent cover of highly used patches were found in the second, third and fourth best models respectively. All other factors, including the coefficient of variation of forage biomass, variables of landscape

Table 1. Factors that influence summer home range size across all scales of analysis ($N=47$ elk).

Effects	HR Polygon β 's	1000-m β 's	2000-m β 's	3000-m β 's	4000-m β 's	5000-m β 's
Intercept Alberta	14.32	13.17	15.65	22.77	22.58	22.06
Intercept Wisconsin	17.13	18.28	23.72	28.74	19.42	24.54
Intercept Yellowstone	3.07	3.46	1.87	2.73	2.27	2.37
Ln Forage Alberta	-1.32	-0.89	-1.37	-2.45	-2.45	-2.36
Ln Forage Wisconsin	-2.40	-1.72	-4.99	-5.34	-2.78	-3.84
Ln Forage Yellowstone	1.54	1.43	1.82	2.01	2.11	2.08
Ln % Forest Cover	0	0	0	2.10	1.14	1.07
AIC	92.2	106	101.0	83.4	85.7	86.3
R^2_{pred}	0.33	0.31	0.42	0.65	0.61	0.59

The estimated regression coefficients, sample size, AIC and the R^2_{pred} are shown for each scale.

Table 2. The five best statistical models predicting summer home range size across the three sites, as determined by AIC.

Parameters	Model 1	Model 2	Model 3	Model 4	Model 5	Null Model
Ln Forage	X	X	X	X	X	
Ln % Forest	X	X				
Ln Patch Density			X			
Ln Proximity Index		X		X		
Ln % Cover Highly Used					X	
Site	X	X	X	X	X	
Site*Forage	X	X	X	X	X	
No. of parameters	7	8	7	7	7	1
Δ AIC	0.0	+3.9	+5.0	+5.7	+6.8	+63.8

Model 1 represents the best model, and the Δ AIC values are changes in AIC relative to the best model. An "X" indicates that a particular variable was included in the model.

structure and slope did not improve the predictive strength of the model.

Given the inverse relationship found between mean forage biomass and summer home range size in Alberta and Wisconsin, one might expect the relatively high forage biomass in Alberta to result in the smallest home range sizes (Table 3). However, *post-hoc* pair-wise comparisons using least square means showed that summer home range sizes were not different between Alberta and Wisconsin ($T=0.94$, $p=0.3518$; Table 4). The mean home range size was larger in Yellowstone than in Alberta ($T=2.38$, $p=0.021$) and Wisconsin ($T=4.44$, $p<0.0001$). Examination of data collected at all scales demonstrated that mean forage biomass was greater in Alberta than in Wisconsin and Yellowstone (e.g. at the 3000-m scale $F_{2,44}=133.3$, $p<0.0001$; Table 3). Mean forage biomass was not different between Wisconsin and Yellowstone. Percent forest cover in summer also differed across all three sites (e.g. at the 3000-m scale $F_{2,44}=65.4$, $p<0.0001$; Table 3).

Winter home range size

The mean forage biomass, snow–water equivalents and the percent cover of forests measured within the home range polygons and sampling circles were included in the best model predicting winter home range size (Table 5). There was a significant interaction term between site and mean forage biomass, indicating different regression coefficients for each site. As in the summer analysis, increasing forage biomass resulted in decreased winter home range sizes in Alberta and Wisconsin, but increased size in Yellowstone. Percent forest cover and mean snow–water equivalents had positive relationships with winter home range size at all sites. Snow–water equivalents improved the predictive strength of the models at all scales, but percent cover of forest was important only when quantified within home range polygons and the 3000-, 4000- and 5000-m sampling circles.

Forage biomass, site, and an interaction term between forage biomass and site were present in the five best models, as determined by AIC

Table 3. Means and standard deviations of forage biomass and percent forest cover from the summer analysis within each sampling scale at Alberta, Wisconsin and Yellowstone National Park.

Variable	Scale	Alberta		Wisconsin		Yellowstone	
		Mean	S.D.	Mean	S.D.	Mean	S.D.
Forage biomass	Kernel	218.6	67.2	55.5	5.8	59.2	18.3
Forage biomass	1000	224.5	95.0	53.5	6.2	58.3	17.7
Forage biomass	2000	211.0	70.6	52.7	5.2	58.3	14.4
Forage biomass	3000	202.4	55.3	53.1	5.1	57.0	11.8
Forage biomass	4000	198.7	52.4	52.3	5.0	55.5	10.4
Forage biomass	5000	196.6	50.7	51.7	4.5	55.0	9.6
% Forest	Kernel	0.82	0.18	0.65	0.10	0.89	0.08
% Forest	1000	0.80	0.18	0.63	0.11	0.94	0.08
% Forest	2000	0.81	0.15	0.64	0.04	0.92	0.09
% Forest	3000	0.83	0.11	0.64	0.02	0.90	0.09
% Forest	4000	0.83	0.10	0.62	0.02	0.90	0.09
% Forest	5000	0.84	0.09	0.62	0.02	0.89	0.10

Table 4. Summary statistics for summer home range sizes in hectares across the three sites.

Summer Home Range Size (ha)					
Site	N	Mean	S.E.	Minimum	Maximum
Alberta	8	5296	2879	1052	10684
Wisconsin	22	2134	1736	668	8433
Yellowstone	17	13468	1868	1504	33288

Table 5. Factors that influence winter home range size across all scales of analysis: mean forage biomass, percent forest cover, and snow–water equivalents ($N=44$ elk).

Effects	HR Kernel β 's	1000-m β 's	2000-m β 's	3000-m β 's	4000-m β 's	5000-m β 's
Intercept Alberta	14.82	21.31	15.26	14.16	14.18	15.87
Intercept Wisconsin	57.33	9.96	64.66	36.93	66.43	73.52
Intercept Yellowstone	-19.61	4.20	-0.83	-3.72	-8.35	-12.56
Ln Forage Alberta	-6.18	-2.72	-1.40	-1.61	-1.04	-1.28
Ln Forage Wisconsin	-22.05	-1.09	-17.57	-8.95	-18.09	-20.16
Ln Forage Yellowstone	6.94	1.34	2.84	3.72	5.36	6.74
Ln % Forest cover	1.9	0	0	0.92	1.12	0.30
Ln snow–water equivalent	0.68	0.48	0.37	0.59	0.61	0.54
R_{pred}^2	0.57	0.20	0.31	0.38	0.49	0.32

The estimated regression coefficients, sample size, and the R_{pred}^2 are shown for each scale.

(Table 6). Although not found in the best model, patch density and edge density of highly used patches were included in some of the top five competing models.

Winter mean home range sizes across the three sites averaged 11,421 ha (s.d. = 10,877), but were different only between Wisconsin and Yellowstone ($T=3.57$, $p=0.0009$; Table 7). Examination of data collected at all scales demonstrated that mean forage biomass was greater in Alberta than in Wisconsin and Yellowstone (e.g. at the 4000-m scale $F_{2,41}=182.83$, $p<0.0001$; Table 8). Mean forage biomass did not differ between Wisconsin and Yellowstone. Percent forest cover (e.g. at the 4000-m scale $F_{2,41}=81.98$, $p<0.0001$) and snow–water equivalents (e.g. at the 4000-m scale $F_{2,41}=21.82$, $p<0.0001$) varied across all three sites (Table 8).

Summer–winter home range comparison

The results of the paired t -test, in which summer and winter home range sizes of individual elk were

paired, showed that home ranges were larger in winter than in summer ($N=35$, $T=192.6$, $p<0.0001$). The mean increase in home range area from summer to winter was greatest in Alberta (4664 ha, coefficient of variation = 1.6), second most in Yellowstone (1708 ha, coefficient of variation = 11.8), and least in Wisconsin (847 ha, coefficient of variation = 1.1).

Discussion

Our results support the hypothesis that home ranges are smaller where important resources are abundant. Summer and winter home range sizes were inversely related with mean forage biomass at all scales of analysis in Alberta and Wisconsin, which is consistent with established evidence (Ford 1983; Turner et al. 1993; Tufto et al. 1996; Mysterud 1999; Relyea et al. 2000). Further, when resources are scarce, such as in winter when reduced quality and quantity of forage is covered by snow (Wickstrom et al. 1984; Albon and Langvatn 1992), elk increased home range sizes. The unequal

Table 6. The five best statistical models predicting winter home range size across the three sites, as determined by AIC.

Parameters	Model 1	Model 2	Model 3	Model 4	Model 5	Null model
Ln Forage	X	X	X	X	X	
Ln % Forest	X			X		
Ln snow–water equivalent	X	X	X		X	
Ln patch density					X	
Ln edge density		X		X		
Site	X	X	X	X	X	
Site*Forage	X	X	X	X	X	
No. of Parameters	8	8	7	8	8	0
Δ AIC	0.0	+2.9	+4.2	+4.7	+4.9	+69.5

Model 1 represents the best model, and the Δ AIC values are changes in AIC relative to the best model. An “X” indicates that a particular variable was included in the model.

Table 7. Summary statistics for winter home range sizes in hectares across the three sites.

Winter home range size (ha)					
Site	N	Mean	S.E.	Minimum	Maximum
Alberta	9	10104	3948	2713	22927
Wisconsin	11	2841	3571	1415	7893
Yellowstone	24	17974	2280	2181	43973

intercepts and forage biomass regression slopes between Alberta and Wisconsin may be partially attributable to factors not measured here, such as digestible fiber and protein content of forage (Langvatn and Hanley 1993; Wilmshurst et al. 1995), or availability of water (Bowyer 1981; Stewart et al. 2002), which should influence patch selection and movement decisions. In contrast, home range sizes in Yellowstone were positively related to forage biomass, which may be due to the migratory behavior and the relatively high density of this population.

Summer and winter population densities in Yellowstone (2.1 and 16.5 elk/km² respectively; Boyce, unpublished data) were substantially higher than both Alberta (0.2 elk/km²; Allen, Alberta Sustainable Resource Development, personal communication) and Wisconsin (0.35 elk/km²; Stowell, WiDNR, personal communication). While non-migratory animals living in high density

conditions tend to contract their home range sizes (Larson et al. 1978; Lesage et al. 2000) to reduce competition, the migratory elk may respond to high density by ranging over relatively large areas. In addition, each winter the migratory elk must adapt to the changing distribution of wolves across the landscape. The density of wolves in the northern winter range is nearly seven times higher than elsewhere in the park (Smith et al. 2003). Elk in the Yellowstone Northern Winter Range tend to aggregate in large groups (Mao 2003), which may be a response to increased predation pressure. The positive relationship between forage biomass and home range size in Yellowstone may be related to large groups in high biomass areas needing to range over large areas to access forage for all individuals.

It will be important in future research to investigate interactions between landscape factors (including carrying capacity; see Kie et al. 2002), herding behavior, population density and home range size among ungulates. Evidence suggests that deer home range size is inversely related to population density (Loomis et al. 1991; Loft et al. 1993). While this may hold for elk in forested environments, such as in Wisconsin where being cryptic in small groups and unpredictable on the landscape may be the prevalent anti-predation strategy, our findings demonstrate that large

Table 8. Means and standard deviations of forage biomass, snow–water equivalents (SWE) and percent forest cover from the winter analysis within each sampling scale at Alberta, Wisconsin and Yellowstone National Park.

Variable	Scale	Alberta		Wisconsin		Yellowstone	
		Mean	S.D.	Mean	S.D.	Mean	S.D.
Forage biomass	Kernel	116.1	30.8	26.3	2.9	31.8	5.6
Forage biomass	1000	109.2	16.6	25.0	2.2	31.9	7.5
Forage biomass	2000	112.5	23.7	25.8	2.5	31.6	6.5
Forage biomass	3000	113.2	24.5	25.4	2.5	31.3	5.0
Forage biomass	4000	115.2	27.4	25.2	2.5	31.6	4.1
Forage biomass	5000	112.6	27.6	25.1	2.4	32.0	3.3
SWE	Kernel	2.8	0.36	2.4	0.09	3.9	1.0
SWE	1000	2.6	0.35	2.3	0.09	3.2	1.1
SWE	2000	2.7	0.32	2.3	0.03	3.4	1.1
SWE	3000	2.7	0.32	2.3	0.04	3.6	1.0
SWE	4000	2.7	0.33	2.4	0.02	3.8	0.8
SWE	5000	2.8	0.37	2.4	0.02	4.0	0.7
% Forest	Kernel	0.78	0.19	0.60	0.06	0.39	0.16
% Forest	1000	0.80	0.16	0.61	0.08	0.31	0.24
% Forest	2000	0.82	0.12	0.61	0.04	0.34	0.18
% Forest	3000	0.83	0.09	0.60	0.02	0.36	0.15
% Forest	4000	0.84	0.09	0.60	0.02	0.37	0.12
% Forest	5000	0.76	0.27	0.60	0.02	0.40	0.11

groups congregating in open areas in Yellowstone results in very large home ranges. Typical summer and winter group sizes in Yellowstone (85 and 199 elk respectively; Mao 2003) were much larger than in Wisconsin (7 and 10 elk respectively; Stowell, WiDNR, unpublished data), and in Alberta (5 elk; Frair unpublished data). It remains unknown how landscape factors influence herd behavior, which will dictate how home range sizes will change with growing or decreasing populations of elk.

We predicted that home ranges would be small in areas with a high percent of forest cover, because forest cover is an important resource for reducing predation risk (Wolff and Van Horn 2003; Fortin et al. in press) and thermal stress Cook et al. 1998; Porter et al. 2002). However, the relationship was positive across all sites. The high availability of forest cover in an area may help reduce predation risk and thermal stress, but it may also come at the cost of increased travel to access areas of high forage biomass, as forage biomass tends to be lower in forested than in open areas. This does not suggest that forested areas are not important for elk, but it indicates that low forest cover is sufficient or preferred. Indeed, our analysis of landscape structure concurs with previous research that has demonstrated that ungulate home ranges are smaller in areas of high patch and edge density (Kie et al. 2002), which should allow elk to move easily between cover and open areas.

Our results also demonstrate that analysis of factors influencing home range size is scale dependent. Forage biomass and snow–water equivalents were important at all scales, but percent forest cover was important only at the broadest scales. The increased influence of percent forest cover at broad scales corresponds with the increased predictive strength of models of summer home range size when habitat variables were quantified within the 3000- to 5000-m radii sampling circles. Predictive strength was lowest when habitat variables were quantified within the home range polygons and the fine scale circles. The 5000-m radius approached the mean summer home range size of 7102 ha. This demonstrates that to understand landscape factors that influence ungulate movements one must sample the habitat variables in areas where the animals choose not to go as well as where they choose to go (Kie et al. 2002).

In contrast, the predictive strength of winter home range size was highest when environmental variables were quantified within the home range polygon. This may be due to the increase in home range size in winter in comparison with summer (winter mean = 12916 ha and summer mean = 7103 ha). Many of the home ranges were substantially larger than the 5000-m sampling circle; therefore quantifying habitat variables within the home range polygons captured the environmental conditions on which the elk were basing ranging decisions better than sampling within the circles around home range centers.

Conclusion

We found that the effects of forage biomass, percent cover of forest and snow–water equivalents on home range size were generally consistent across landscapes with different terrain, vegetation patterns, snow conditions, and elk densities. The different intercepts and forage biomass regression slopes across the three sites may have been due to site-specific decision trade-offs related to factors not directly measured in this study; such as spatial distribution of predation pressure, forage quality, water availability and local population density or group sizes. The animals at Yellowstone, for example, may have been more responsive to large group dynamics and predation risk than elk at the other sites where they may have focused more on finding hotspots of forage abundance and quality. Lastly, our results demonstrated the importance of measuring habitat variables at multiple scales to determine the scale(s) of influence of each variable and to determine the scale at which we can best predict animal responses to landscapes.

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Appendix A

Estimation and Extrapolation of Forage Biomass

Vegetation sampling was conducted at each site along extended 240-m transects that included eight contiguous 30-m transects (Anderson et al. in press). Vegetation was sampled along four of these 30-m transects following a cyclic pattern designed to test for spatial autocorrelation (Clayton and Hudelson 1995). Transect length was reduced if it crossed into a different habitat type. Site-specific details on the methods used to estimate forage biomass within each section are provided below.

Wisconsin

Details on procedures employed to obtain estimates of summer herbaceous and browse biomass are available in Anderson et al. (in press). The peak biomass of graminoids in winter was simply the same as the peak summer biomass. Forb biomass in winter was considered zero due to senescence and decomposition.

To determine the winter browse biomass, we measured the crown height and width of woody plants in 1 by 5 m plots distributed across all habitat types ($N=449$; Anderson et al. in press). All woody plants (trees and shrubs) that presented current annual growth in the browse stratum from 0 to 2.5 m were measured. An allometric regression equation was developed to relate the crown height and width of woody plants to the current annual growth available in winter. This was done by measuring and

marking multiple individuals from all species in the summer of 2001 ($N=303$ plants), and then re-locating the individuals following senescence in early November to clip the current annual growth. The clippings were dried to constant mass, and the mass was recorded. Using regression analysis (SAS Institute Inc. 1999), we found that the relationship was statistically similar for all woody species, therefore a single allometric equation was used for all species:

$$\begin{aligned} \text{woody-plant biomass} \\ &= \exp(-6.64 + (1.05 * \ln \text{height}) \\ &\quad + (0.59 * \ln \text{crown})) \\ &(N = 303, R^2 = 0.58, p < 0.0001) \end{aligned}$$

The woody-plant height and width variables were all transformed with the natural logarithm. Using this allometric equation, we obtained woody forage biomass estimates for each habitat type across the landscape.

Alberta

Details on the procedures employed to obtain estimates of summer herbaceous and browse biomass are available in Frair et al. (2005). Peak biomass was estimated to occur on Julian day 218. To estimate forage components, a double layer mesh grid was used to identify plant species composition by percent hits along each transect ($N=298$). A probit model was produced for each vegetation class to estimate the proportion of total herbaceous biomass that was graminoid as:

$$\begin{aligned} \Pr(y_j \neq 0 \mid x_1, x_2, x_3) \\ &= \Phi(\beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3) \end{aligned} \quad (2)$$

where β_i is the coefficient estimated for variable x_1 (Julian Day), x_2 (Julian Day²), and x_3 (elevation) and Φ represents conversion of probit values using a standard cumulative normal distribution (StataCorp 2001). Percent forb was estimated as 1 – proportion graminoid. As at all sites, the peak biomass of graminoids in winter was simply the same as peak summer biomass. Forb biomass in winter was set to zero due to senescence. Browse biomass in winter was set as the mean twig biomass available during summer in each vegetation type.

Yellowstone National Park

In Yellowstone National Park, forage biomass was quantified in aspen stands and open areas using the disk method described above in the Alberta section, however woody plants were surveyed in a 2×4 m quadrat instead of a 1×8 m quadrat. Biomass of woody plants was quantified for three common species known to be browsed by elk: *Populus tremuloides*, *Rosa acicularis*, and *Symphoricarpos albus*. Between 26 June and 11 July 2002, 75 transects were sampled in aspen stands and open areas (dry and mesic shrubland, mesic and wet grassland). Of these, 10 locations were sampled at both 26 June and 15 July (the beginning of peak biomass). Biomass estimates were adjusted to account for growth during the sampling period. Allometric regression equations were developed to relate biomass of graminoids and forbs to disk height, and woody-plant biomass to stem diameter (Fortin unpublished data).

In coniferous stands, we quantified biomass of graminoids, forbs and woody plants using a percent cover method described by (Turner et al. 2004). Sampling occurred at peak biomass, between 15 July and 15 August. Thirty-three cyclic transects were randomly stratified based on elevation, substrate type (andesite or rhyolite) and stand age. Only lodgepole pine (post disturbance, early successional, and climax) and douglas fir (climax) stands were sampled because these cover types account for most of the park area frequented by the collared elk. Within each 30-m transect, we recorded percent cover of each species in ten 0.25-m^2 quadrats located at 5-m intervals and 2-m perpendicular to the transect line on both sides. These data were converted to dry biomass using the growth-form allometrics developed by Turner et al. (2004).

Spatial linear regression models (Kalunzny et al. 1998) were developed to relate biomass of graminoids, forbs, and woody plants to cover type, soil type, elevation, precipitation, slope and aspect (Forester unpublished data). The final models were chosen using backwards selection based on AIC values. Variables that were significant predictors of biomass of each of the functional plant groups in are shown in Table A1. Regression equations were used to extrapolate biomass across Yellowstone National Park. Winter biomass was assumed to be peak biomass of grass and stem biomass of shrubs.

Table A1. Significant predictors of biomass of graminoids, forbs, and woody plants ($p < 0.05$) in aspen stands, and open and forested areas.

Open/Aspen	Cover type	Elevation	Soil type	Precipitation
Graminoid	X			
Forb	X			
Shrub	X	X		
Forest				
Graminoid		X		
Forb	X		X	
Shrub	X			X

Appendix B

Estimation and extrapolation of snow-water equivalents

In Alberta and Wisconsin, snow courses were established to measure “baseline” snow depth and density in relatively flat and open areas. Snow courses were intended to be few in number and sampled relatively frequently. There were six samples per snow course separated by 30 m. Additional habitat snow sampling sites were numerous and placed across the landscape to capture variations in snow depth and density due to canopy cover, slope, aspect, and elevation. Three samples at 5-m intervals were taken at each habitat snow sampling site. An allometric regression equation was developed to predict snow-water equivalents at the habitat snow-sampling sites using measures of snow-water equivalents from the snow courses. Snow-water equivalents extrapolated across the landscape using the allometric equations.

Wisconsin

Seven snow courses and 30 snow sampling sites were sampled on a monthly interval in Wisconsin during the winter months between December 2001 and April 2003. The snow sampling sites were distributed among six habitat types: coniferous forest, deciduous forest, mixed-coniferous-deciduous forest, cedar wetland, open wetland, and young aspen stands. Snow conditions in open-upland areas were characterized by the measurements taken on the snow courses. Repeated measures ANOVA with an autoregressive covariance structure (AR(1); SAS Institute Inc. 1999) was used to determine if snow-water equivalents differed among habitat types. Due to the flat

topography, the only difference in snow–water equivalents across the landscape was among habitats with closed canopy forests (coniferous, mixed-coniferous-deciduous, or northern-white cedar wetlands) and open canopy forest (all others). Snow–water equivalents were greater under open canopies than under closed canopies ($F_{1,9} = 6.83$, $p = 0.0474$). For each winter month of the study, the mean snow–water equivalents value for closed and open canopy habitats were extrapolated across the landscape.

Alberta

Eight snow courses were sampled every two weeks from 26 January to 19 April 2001, and nine courses were sampled monthly from 14 November 2001 to 19 April 2002. In addition, a total of 142 broadly dispersed snow sampling sites were measured early, mid-, and late-winter in 2002–2003 to account for changes in snow–water equivalents due to habitat type, elevation, slope, and aspect. A linear regression model was developed to predict snow–water equivalents across the landscape based on habitat, the distance weighted estimate of snow–water equivalents from the snow courses, the distance weighted difference in elevation between a point on the landscape and the snow courses, slope and aspect ($R^2 = 0.56$, $F_{10,424} = 53.07$, $p < 0.0001$). Slope and aspect were quantified using the following categories: flat ($< 3^\circ$), low ($3\text{--}15^\circ$), medium ($15\text{--}30^\circ$) and high ($> 30^\circ$) for slopes; and north ($316\text{--}45^\circ$), south ($136\text{--}225^\circ$), east ($46\text{--}135^\circ$) and west ($226\text{--}315^\circ$) for aspects. For each snow sampling period, snow–water equivalents were extrapolated across the landscape.

References

- Albon T.F. and Langvatn R. 1992. Plant phenology and the benefits of migration in a temperate ungulate. *Oikos* 65: 502–513.
- Altendorf K.B., Landré J.W., López Gonzáles C.A.L. and Brown J.S. 2001. Assessing effects of predation risk on foraging behavior of mule deer. *J. Mammal.* 82: 430–439.
- Anderson D.P., Turner M.G., Forester J.D., Zhu J., Boyce M.S., Beyer H. and Stowell L. in press. Scale-dependent summer resource selection by reintroduced elk in Wisconsin USA. *J. Wildlife Manag.*
- Aycrigg J.L. and Porter W.F. 1997. Sociospatial dynamics of white-tailed deer in the Central Adirondack Mountains, New York. *J. Mammal.* 78: 468–482.
- Beyer H.L. 2004. Hawth's Analysis Tools for ArcGIS. Version 2. <http://www.spatialecology.com>.
- Bowyer R.T. 1981. Activity, movement, and distribution of Roosevelt elk during rut. *J. Mammal.* 62: 574–582.
- Bowyer R.T., Kie J.G. and Van Ballenberghe V. 1998. Habitat selection by neonatal black-tailed deer: climate, forage, or risk of predation? *J. Mammal.* 79: 415–425.
- Burnham K.P. and Anderson D.R. 2002. *Model Selection and Inference*. Springer-Verlag, New York.
- Cain M.L. 1985. Random search by herbivorous insects: a simulation model. *Ecology* 66: 876–888.
- Carr A.P. and Rodgers A.R. 1998. HRE: The Home Range Extension for ArcView. Ontario Ministry of Natural Resources, Thunder Bay.
- Clayton M.K. and Hudelson B.D. 1995. Confidence intervals for autocorrelations based on cyclic samples. *J. Am. Stat. Assoc.* 90: 753–757.
- Cook J.G., Irwin L.L., Bryant L.D., Riggs R.A. and Thomas J.W. 1998. Relations of forest cover and condition of elk: a test of the thermal cover hypothesis in summer and winter. *Wildlife Monographs* 141: 1–61.
- Cook R.C., Cook J.G. and Mech L.D. 2004. Nutritional condition of northern Yellowstone elk. *J. Mammal.* 85: 714–722.
- Crawford H.S. 1984. Habitat Management. In: Halls L.K. (ed.), *White-Tailed Deer Ecology and Management*. Stackpole Books, Harrisburg, pp. 629–646.
- Demarchi M.W. and Bunnell F.L. 1993. Estimating forest canopy effects on summer thermal cover for Cervidae (deer family). *Can. J. Forestry Res.* 23: 2419–2426.
- Despain D.G. 1990. *Yellowstone Vegetation: Consequences of Environment and History in a Natural Setting*. Robert Rinehart Publishers, Bolder, CO.
- Dirks R.A. and Martner B.E. 1982. *The Climate of Yellowstone and Grand Teton National Parks*. U.S. Department of Interior/National Park Service. Occasional Paper, Number 6.
- Dixon G.D. 1997. *Cumulative Effects Modeling for Grizzly Bears in the Greater Yellowstone Ecosystem*. Montana State University, Bozeman.
- Environment Canada, 2004. *Canadian Climate Normals or Averages 1971–2000*. http://climate.weatheroffice.ec.gc.ca/climate_normals. Environment Canada.
- ESRI, 2001. *ArcGIS Version 8.1*. Environmental Systems Research Institute, Redlands.
- Ford R.G. 1983. Home range in a patchy environment: optimal foraging predictions. *Am. Zool.* 23: 315–326.
- Fortin D., Beyer H., Boyce M.S., Smith D.W., Duchesne T. and Mao J.S. in press. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology*.
- Frair J.L., Merrill E.H., Beyer H.L., Morales J.M., Visscher D.R. and Fortin D. 2005. Scales of movement by elk (*Cervus elaphus*) in response to heterogeneity in forage resources and predation risk. *Landscape Ecology*.
- Fryxell J.M. and Lundberg P. 1997. *Individual Behavior and Community Dynamics*. Chapman & Hall, New York.
- Goodison B.E., Ferguson H.L. and McKay G.A. 1981. Measurement and data analysis. In: Gray D.M. and Male D.H. (eds), *Handbook of Snow: Principles, Processes, Management and Use*. Pergamon, New York, pp. 191–274.
- Grace J. and Easterbee N. 1979. The natural shelter for red deer (*Cervus elaphus*) in a Scottish glen. *J. Appl. Ecol.* 16: 37–48.

- Hobbs N.T. 1989. Linking energy balance to survival in mule deer: development and test of a simulation model. *Wildlife Monographs* 101: 1–39.
- Hooge P.N., Eichenlaub B., Hooge E.R. and Soloman E.K. 2002. The Animal Movement Program. Alaska Biological Science Center, U.S. Geological Survey, Anchorage.
- Huot J. 1974. Winter habitat of white-tailed deer at the Thirty-one Mile Lake, Québec. *Can. Field Nat.* 88: 293–301.
- Jones P.F. and Hudson R.J. 2002. Winter habitat selection at three spatial scales by American Elk, *Cervus elaphus*, in west-central Alberta. *Can. Field Nat.* 116: 183–191.
- Kalunzny S.P., Vega S.C., Cardoso T.P. and Shelly A.A. 1998. S+ Spatial Stats: User's Manual for Windows and Unix. Springer-Verlag, New York, 327pp.
- Kareiva P. 1983. Influence of vegetation texture on herbivore populations: resource concentrations and herbivore movements. In: Denno R.F. and McClure M. (eds), *Variable Plants and Herbivores Natural and Managed Systems*. Academic Press, New York.
- Kareiva P. and Wennergren U. 1995. Connecting landscape patterns to ecosystem and population processes. *Nature* 373: 299–302.
- Kie J.G. 1999. Optimal foraging and risk of predation: effects on behavior and social structure in ungulates. *J. Mammal.* 80: 1114–1129.
- Kie J.G., Ager A.A. and Bowyer R.T. 2005. Landscape-level movements of North American elk (*Cervus elaphus*): effects of habitat patch structure and topography. *Landscape Ecology*.
- Kie J.G., Bowyer R.T., Nicholson M.C., Boroski B.B. and Loft E.R. 2002. Landscape heterogeneity at different scales: effects on spatial distribution of mule deer. *Ecology* 83: 530–544.
- Langvatn R. and Hanley T.A. 1993. Feeding patch choice by red deer in relation to foraging efficiency. *Oecologia* 95: 164–170.
- Larson T.J., Rongstad O.J. and Terbilcox F.W. 1978. Movement and habitat use of white-tailed deer in southcentral Wisconsin. *J. Wildlife Manag.* 42: 113–117.
- Lesage L., Crête M., Huot J., Dumont A. and Ouellet J.-P. 2000. Seasonal home range size and philopatry in two northern white-tailed deer populations. *Can. J. Zool.* 78: 1930–1940.
- Loft E.R., Kie J.G. and Menke J.W. 1993. Grazing in the Sierra Nevada: home range and space use patterns of mule deer as influenced by cattle. *Calif. Fish Game* 79: 145–166.
- Loomis J.B., Loft E.R., Updike D.R. and Kie J.G. 1991. Cattle-deer interactions in the Sierra Nevada: a bioeconomic approach. *J. Range Manag.* 44: 395–399.
- Mao J.S. 2003. Habitat Selection by Elk Before and After Wolf Reintroduction in Yellowstone National Park, Wyoming. M.S. Thesis, University of Alberta, Edmonton.
- McGarigal K. and Marks B.J. 1995. *Fragstats: Spatial Analysis Program for Quantifying Landscape Structure*. USDA Forest Service General Technical Report PNW-GRT-351. USDA Forest Service, Pacific Northwest Research Station, Portland.
- McNab B.K. 1963. Bioenergetics and the determination of home range size. *Am. Nat.* 97: 133–140.
- Merrill E.H. and Boyce M.S. 1991. Summer range and elk population dynamics in Yellowstone National Park. In: Keiter R.B. and Boyce M.S. (eds), *The Greater Yellowstone Ecosystem*. Yale University, New Haven, pp. 263–273.
- Moe S.R. and Wegge P. 1994. Spacing behaviour and habitat use of axis deer (*Axis axis*) in lowland Nepal. *Can. J. Zool.* 72: 1735–1744.
- Mysterud A. 1999. Seasonal migration pattern and home range of roe deer (*Capreolus capreolus*) in an altitudinal gradient in southern Norway. *J. Zool. (London)* 247: 479–486.
- Mysterud A., Pérez-Barbería F.J. and Gordon I.J. 2001. The effect of season, sex and feeding style on home range area versus body mass scaling in temperate ruminants. *Oecologia* 127: 30–39.
- Nams V.O. 2000. *Locate II User's Guide*. Pacer, Truro.
- Nicholson M.C., Bowyer R.T. and Kie J.G. 1997. Habitat selection and survival of mule deer: tradeoffs associated with migration. *J. Mammal.* 78: 483–504.
- Oehler M.W.Sr., Bowyer R.T. and Bleich V.C. 2003. Home ranges of female mountain sheep, *Ovis canadensis nelsoni*: effects of precipitation in a desert ecosystem. *Mammalia* 67: 385–401.
- O'Neill R.V., Milne B.T., Turner M.G. and Gardner R.H. 1988. Resource utilization scales and landscape pattern. *Landscape Ecol.* 2: 63–69.
- Parker K.L., Robbins C.T. and Hanley T.A. 1984. Energy expenditures for locomotion by mule deer and elk. *J. Wildlife Manag.* 42: 113–117.
- Parker K.L. and Gillingham M.P. 1990. Estimates of critical thermal environments for mule deer. *J. Range Manag.* 43: 73–81.
- Pauley G.R., Peek J.M. and Zager P. 1993. Predicting white-tailed deer habitat use in Northern Idaho. *J. Wildlife Manag.* 57: 904–913.
- Porter W.P., Budaraju S., Stewart W.E. and Ramankutty N. 2000. Calculating climate effects on birds and mammals: impacts on biodiversity, conservation, population parameters, and global community structure. *Am. Zool.* 40: 597–630.
- Porter W.P., Sabo J.L., Tracy T.R., Reichman O.J. and Ramankutty N. 2002. Physiology on a landscape scale: plant-animal interactions. *Integr. Comp. Biol.* 42: 431–453.
- Relyea R.A., Lawrence R.K. and Demarais S. 2000. Home range of desert mule deer: testing the body-size and habitat productivity hypothesis. *J. Wildlife Manag.* 64.
- SAS Institute Inc. 1999. *SAS OnlineDoc, Version 8*. SAS Institute, Cary, 846pp.
- Seaman D.E., Millsbaugh J.J., Kernohan B.J., Brundige G.C., Raedeke K.J. and Gitzen R.A. 1999. Effects of sample size on kernel home range estimates. *J. Wildlife Manag.* 63: 739–747.
- Senft R.L., Coughenour M.B., Bailey D.W., Rittenhouse L.R., Sala O.E. and Swift D.M. 1987. Large herbivore foraging and ecological hierarchies. *Bioscience* 37: 789–799.
- Skovlin J.M., Zager P. and Johnson B.K. 2002. Elk habitat selection and evaluation. In: Towell D.E. and Thomas J.W. (eds), *North American Elk: Ecology and Management*. Smithsonian Institution, Washington, D.C., pp. 531–557.
- Smith D.W., Peterson R.O. and Houston D.B. 2003. Yellowstone after wolves. *Bioscience* 53: 330–340.
- Statacorp. 2001. *Stata Reference Manual, Release 7*. Stata Press, College Station, Texas, USA.
- Stewart K.M., Bowyer R.T., Kie J.G., Cimon N.J. and Johnson B.K. 2002. Temporospatial distributions of elk, mule deer, and cattle: resource partitioning and competitive displacement. *J. Mammal.* 83: 229–244.

- Sweeney J.M. and Sweeney J.R. 1984. Snow depths influencing winter movements of elk. *J. Mammal.* 65: 524–526.
- Taylor C.R., Rowntree V.J. and Caldwell S.L. 1972. Running up and down hills – some consequences of size. *Science* 178: 1096–1097.
- Tufto J., Andersen R. and Linnell J. 1996. Habitat use and ecological correlates of home range size in a small cervid: the roe deer. *J. Anim. Ecol.* 65: 715–724.
- Turchin P. 2003. *Complex Population Dynamics: A Theoretical/Empirical Synthesis*. Princeton University Press, Princeton.
- Turner M.G., Tinker D.B., Romme W.H., Kashian D.M. and Litton C.M. 2004. Landscape patterns of sapling density, leaf area, and aboveground net primary production in postfire lodgepole pine forests, Yellowstone National Park (USA). *Ecosystems*. 7: 751–775.
- Turner M.G., Wu Y., Romme W.H. and Wallace L.L. 1993. A landscape simulation model of winter foraging by large ungulates. *Ecol. Model.* 69: 163–184.
- Turner M.G., Wu Y., Wallace L.L., Romme W.H. and Brenkert A. 1994. Simulating winter interactions among ungulates, vegetation, and fire in Northern Yellowstone Park. *Ecol. Appl.* 4.
- USDA, 1986. Final Environmental Impact Statement: Chequamegon National Forest Land and Resource Management Plan. USDA Forest Service, Region 9, Eastern Region.
- USDA, 2001. CDS Data Dictionary. USDA Forest Service, Region 9.
- White C.A., Feller M.C. and Bayley S. 2003. Predation risk and the functional response of elk-aspen herbivory. *Forest Ecol. Manag.* 181: 77–97.
- White G.C. and Garrott R.A. 1990. *Analysis of Wildlife Radio-Tracking Data*. Academic, San Diego.
- Wickstrom M.L., Robbins C.T., Hanley T.A., Spalinger D.E. and Parish S.M. 1984. Food intake and foraging energetics of elk and mule deer. *J. Wildlife Manag.* 48: 1285–1301.
- WiDNR 1998. WISCLAND Land Cover (WLCGW930). Wisconsin Department of Natural Resources, Madison.
- Wilmschurst J.F., Fryxell J.M. and Hudson R.J. 1995. Forage quality and patch choice by wapiti (*Cervus elaphus*). *Behav. Ecol.* 6: 209–217.
- With K.A. and Crist T.O. 1995. Critical thresholds in species responses to landscape structure. *Ecology* 76: 2446–2459.
- Wockner G., Singer F.J., Coughenhour M.B. and Farnes P. 2002. Snow Model for Yellowstone National Park. Nat. Resour. Ecol. Lab., Fort Collins.
- Wolff J.O. and Van Horn T. 2003. Vigilance and foraging patterns of American elk during the rut in habitats with and without predators. *Can. J. Zool.* 81: 266–271.