

WHEN TO SLOW DOWN: ELK RESIDENCY RATES ON A HETEROGENEOUS LANDSCAPE

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It remains unclear if patterns of habitat use are driven by animals moving to and increasing residency time in selected areas, or by animals simply returning frequently to selected areas. We studied a population of North American elk (*Cervus elaphus*) in the Chequamegon National Forest, Wisconsin, to examine how spatial and temporal factors influence residency time in localized areas. We used global positioning system telemetry data from 7 elk and addressed 2 questions. First, does residency time vary as a function of spatial and temporal factors and if so does that relationship vary with measurement scale? Second, can residency time in the summer be predicted by a resource-selection map previously constructed for this population? Cross validation demonstrated that the statistical models had very poor predictive strength of independent data, which indicates that the explanatory variables have very little influence on elk residency time. Resources are patchily distributed on this landscape, and results demonstrate that elk preferentially use areas with high resource-selection function values. Unexpectedly, residency time was unrelated to values of resource-selection functions, which indicates that elk do not slow down in preferred areas. We conclude that patterns of elk habitat use are not driven by residency time but by elk returning frequently to favorable areas on the landscape. Random residency times may be a behavioral mechanism to lower predictability on the landscape and reduce predation risk.

Key words: *Canis lupus*, *Cervus elaphus*, cross validation, heterogeneity, life-history strategies, predation, resource selection

Patterns of habitat use by animals are determined by where individuals choose to go on landscapes and how long they stay in particular areas. Resource-selection studies identify frequently used areas on landscapes (Anderson et al. 2005b; Johnson 1980; Johnson et al. 2002b), but whether patterns of habitat use are driven by animals moving to and increasing residency time in preferred areas or by animals returning frequently to these areas while moving at random rates with respect to the environment remains unclear. Theory predicts that an animal should remain in an area as long as the marginal rate of forage intake is greater than the average value of the landscape (Charnov 1976) and that foraging and movement strategies influence energy budgets and fitness (Moen et al. 1997). However, efficient use of resources must be balanced

with relative risks of predation (Brown and Kotler 2004; Fortin et al. 2005; Johnson et al. 2002a; Kie 1999), landscape structure (Crist et al. 1992; With et al. 1999), endogenous factors (Bascompte and Vila 1997; Bergman et al. 2000; Firle et al. 1998; Morales and Ellner 2002; Root and Kareiva 1984), and behavioral state (e.g., resting, foraging, and relocating—Frair et al. 2005; Johnson et al. 2002b; Morales et al. 2004). Although theoretical models necessarily make assumptions about animal movement (Morales et al. 2005; Turchin 1998; Turner et al. 1993), empirical data to support these assumptions are still lacking. Our knowledge of animal movement and our ability to extend fine-scale movements to broadscale predictions of animal distributions are dependent on a clear understanding of factors that influence not only where animals choose to go but also how long they stay.

Analyses of movements and resource selection provide important insights into how animals respond to environmental pressures that affect energy budgets and predation pressure, which has implications for life-history traits (Abrams 1991; Bowyer and Kie 2006) such as survival and reproduction. We

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studied a population of North American elk (*Cervus elaphus*) in the Chequamegon National Forest, Wisconsin, to examine whether residency time was influenced by spatial and temporal factors. We addressed 2 research questions. First, does residency time vary in response to the factors related to spatial and temporal heterogeneity and if so does that relationship vary with measurement scale? We hypothesized that elk would increase residency time in areas with favorable conditions: areas of high forage biomass (Zollner and Lima 1999), low predation risk (Mitchell and Lima 2002), and in areas with forest cover during cold periods (Porter et al. 2002). Because both theoretical (Senft et al. 1987; Turner et al. 1997) and empirical (Bowyer and Kie 2006; Boyce et al. 2003; Johnson et al. 2001; Kie et al. 2002; Nams 2005) studies have suggested scale dependence in animal-habitat relationships, we expected variation in the strength of models estimated at different spatial and temporal scales. Second, can residency time in localized areas in the summer be predicted by a resource-selection map (Manly et al. 2002) previously constructed for this population from very-high-frequency radiotelemetry data (Anderson et al. 2005b)? The resource-selection study demonstrated that elk movement is clearly sensitive to heterogeneity in this landscape. We hypothesized that elk would increase residency time in areas with high resource-selection values, which are generally characterized by high forage biomass, and far from gray wolves (*Canis lupus*) and roads (Anderson et al. 2005b).

MATERIALS AND METHODS

Study site.—We collected data in the 1,852-km² Great Divide District of the Chequamegon National Forest, Wisconsin (latitude: 46.10, longitude: -90.94), where elk were introduced in 1995 (Anderson et al. 2005b). The elk population currently ranges over approximately 500 km². Mean annual air temperature is 5°C, and mean annual precipitation ranges from 76 to 86 cm, with snowfall accounting for less than 25% of the total (United States Department of Agriculture 1986). There is little topographic relief, and vegetation cover is 62% forest, 26% wetland, 7% regenerating aspen stands following timber harvest, 4% open water, and 1% open upland (United States Department of Agriculture 2001; Wisconsin Department of Natural Resources 1998). White-tailed deer (*Odocoileus virginianus*) are abundant throughout the region, and 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 into the Chequamegon National Forest and the population increased to approximately 100 elk by 2004 (L. Stowell, Wisconsin Department of Natural Resources, pers. comm.). Elk were corral trapped in February and March 2002, and global positioning system collars (Lotek Wireless, Newmarket, Ontario, Canada) were deployed on 6 adult females and 1 adult male. Animal capture and handling protocols adhere to the guidelines recommended by the American Society of Mammalogists (Gannon et al. 2007). All research procedures used in this study comply with current laws of the United States.

One of the 6 adult females had her collar replaced in winter 2003. We obtained 10–11 months of global positioning system telemetry data for each year the collars were deployed. Location fixes were obtained daily at 4-h intervals, and each Wednesday locations were obtained every 20 min. To determine the positional accuracy of the collars, we collected location data at 15-min intervals for 10 days with collars placed in 3 locations with known coordinates under coniferous forest, deciduous forest, and in an open area. The mean and standard deviation of positional deviation from the true location were determined for each of the 3 collars. The extent of area used by elk was approximately 86 km². Home ranges overlapped, but all elk were determined to move independently.

Residency time.—We calculated residency time in localized areas using the concept of 1st passage time ($t(r)_{ij}$)—Fauchald and Tveraa 2003):

$$t(r)_{ij} = \text{FPTB}_{ij} + \text{FPTF}_{ij},$$

where FPTB_{ij} (1st passage time backward) was the time in minutes it took the animal to move from the edge of a circle with radius r to the center of the circle at location i using the data-relocation interval j , and FPTF_{ij} (1st passage time forward) was the time to move from location i forward to the edge of the circle. A high 1st passage time translates into high residency time. At each location we calculated the residency time for 3 different radii: where the radius was equal to, one-half of, and 2 times the median step length of all animals at 20-min and 4-h intervals.

Time of day.—We created categorical variables for time of day to examine their effects on residency time. For the movement data collected at 20-min intervals, we considered crepuscular hours to be between 0500 and 0700 h, and between 1700 and 1900 h. These crepuscular times separated the day and night time periods. For the movement data collected at 4-h intervals, we grouped the data into day (0800, 1200, and 1600 h) and night (2000, 2400, and 0400 h) periods.

Seasons and calving and rutting periods.—Summer was defined as May–October, and the remaining months as winter. Observations occurring from 15 May to 15 June were considered to be the calving season. We did not have information on the reproductive status of females; therefore, we could not determine if the presence of young influenced residency time. Last, location data collected during September were identified as occurring during rut.

Forest cover.—We used a 30-m-resolution land-cover map derived from Landsat (Wisconsin Department of Natural Resources 1998). This map was updated with forest harvesting records (United States Department of Agriculture 2001) to classify the landscape into forest and nonforest categories. For each analysis, we used ArcGIS (Beyer 2006; ESRI 2005) to calculate the percentage of forest cover within the circle radius r_{ij} centered on each location data point.

Forage biomass.—Vegetation was sampled along four hundred fifty-two 30-m transects stratified by 8 vegetation cover types (United States Department of Agriculture 2001; Wisconsin Department of Natural Resources 1998) from June through August in 2001 and 2002 (see details in Anderson

et al. 2005b). Percentage cover of herbaceous vegetation was estimated in six 0.25-m² quadrats located at 5-m intervals along each transect and placed 2 m perpendicular to the transect line on alternating sides. We used an allometric relationship to convert percentage cover to biomass (Anderson et al. 2005b).

Also during June–August in 2001 and 2002, woody vegetation was sampled in 449 plots (5 × 1 m—Anderson et al. 2005b). In each plot, we measured the height and width of each woody plant within the browse stratum (0–2.5 m). Plants also were inspected for evidence of browsing, and we considered only browsed species to represent potential forage and we included those in subsequent analyses. An allometric relationship was used to relate plant height and width to forage biomass (Anderson et al. 2005b).

Peak forage biomass occurred in July, and differed significantly among 8 vegetation cover types ($P < 0.001$ —Anderson et al. 2005b). Winter biomass was the sum of the peak biomass of graminoids and the current annual growth of woody plants within the browse stratum available in winter (Anderson et al. 2005a). To estimate daily available biomass during spring and autumn, we assumed a linear increase from the beginning of the growing season on 1 May to the period of peak biomass on 1 July, and a linear decrease in biomass from 1 September to 30 October.

Forage biomass is patchily distributed in the study area (Fig. 1). The variogram range of peak forage biomass is approximately 900 m, which is a moderate-sized area relative to the mean home-range size of elk (2,134 ha—Anderson et al. 2005a).

Distances from wolf-territory centers and roads.—The locations of wolf territories from October 2001 through March 2002 were derived from very-high-frequency radiotelemetry data for radiocollared wolves and winter wolf-track surveys conducted by the Wisconsin Department 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. Distance to wolf-territory center was shown to be a very influential variable in highly predictive models of elk resource selection (Anderson et al. 2005b). Data on roads (Wisconsin Department of Natural Resources 1998) were used to create a raster map (30-m resolution) of the distance to the nearest road. Class D roads, designed for minimal use (United States Department of Agriculture 2001), were eliminated from the analysis.

Daily weather conditions and snow-water equivalent values.—We obtained daily measurements of minimum and maximum temperature, precipitation, and snow depth from the Clam Lake weather station (National Climatic Data Center 2005), which was within the study site. Snow-water equivalents (Goodison et al. 1981) is a measure of the amount of water contained within the snowpack and is influenced by snow depth and density. We hypothesized that snow-water equivalents should affect movement and foraging rates. To examine how values of snow-water equivalents varied across the landscape, we made monthly measurements of snow depth and density during winter between December 2001 and April 2003 along transects stratified by vegetation cover type (37

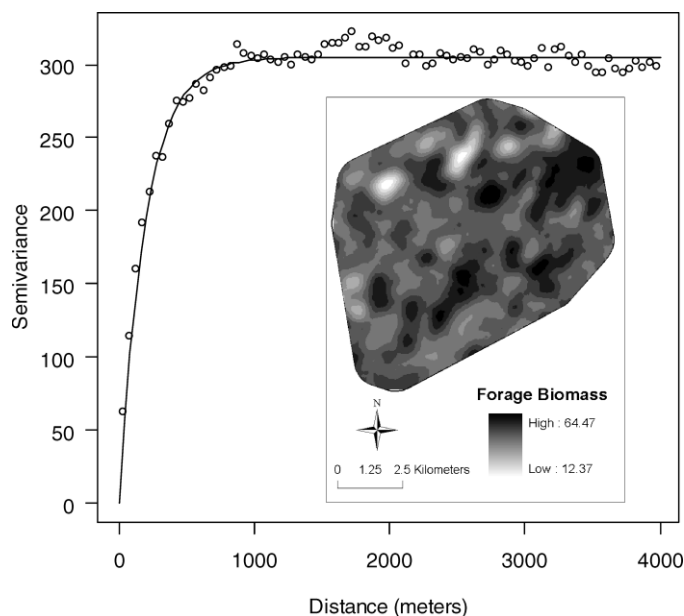


FIG. 1.—Variogram with exponential covariance structure of elk forage biomass across the study area located in the Chequamegon National Forest, Wisconsin. Inset map illustrates the spatial distribution of forage biomass.

transects distributed over 7 cover types—Anderson et al. 2005a). To obtain daily estimates of snow-water equivalents, we developed an empirical relationship between snow measurements collected on transects and daily measurements of snow depth, and minimum and maximum temperature at the weather station. We employed a repeated-measures regression with an autoregressive covariance structure (AR1—SAS Institute Inc. 1999), in which month was the repeated unit.

Resource selection function map.—A raster grid with 30-m resolution was produced in which the cell values took on the values for the resource-selection function (RSF) in summer from a previous analysis we conducted on this elk population using very-high-frequency radiotelemetry (Anderson et al. 2005b). Location data for the analysis of resource selection were collected during summer 1999–2002. Resource selection increased with increasing biomass of forbs and grasses, as well as with increasing distance from wolves and roads; selection decreased with increasing biomass of woody browse and sedges (k-fold cross-validation R^2 ranged from 0.52 to 0.86 across spatial scales). To qualitatively assess whether the elk equipped with global positioning system radiotelemetry collars were preferentially using areas of high RSF values, we used a quantile–quantile plot (R Development Core Team 2005) to compare the distributions of RSF values of actual elk locations with those of 2,000 random locations within the study area.

Analysis.—Six regression analyses were performed: 1 each for the 2 relocation intervals (4 h and 20 min) and the 3 spatial scales. We used linear mixed-effects regression (Pinheiro et al. 2004; R Development Core Team 2005) to control for individual variation among elk while investigating the factors that influence residency time. In addition, 1 of the animals in this study was a male, and we controlled for the effect of this

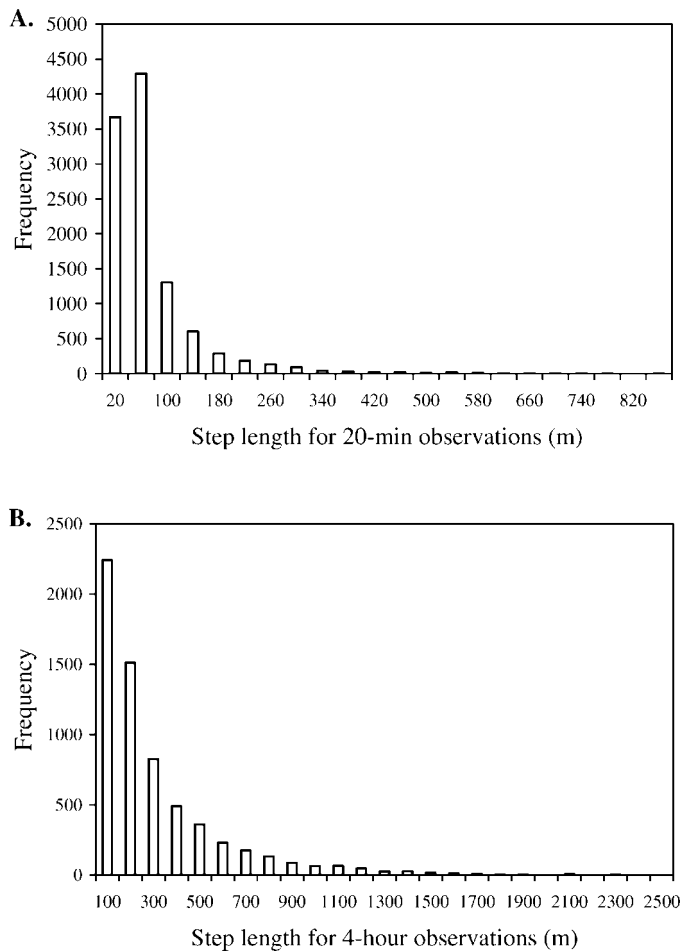


FIG. 2.—Frequency distribution of North American elk (*Cervus elaphus*) step lengths at A) 4-h and B) 20-min relocation intervals. Data were collected between February 2002 and January 2004 in the Chequamegon National Forest, Wisconsin.

individual. At each spatial and temporal scale, we examined a suite of 30 candidate models determined to be biologically meaningful and potentially important based on preliminary exploratory analysis. Correlations among independent variables were examined to identify collinear variables. Collinear variables with correlation coefficients of >0.40 were not included in the same models. The best explanatory models were identified using Akaike's information criterion (AIC) and Akaike weights (ω_i —Burnham and Anderson 2002). The presence of spatial and temporal autocorrelation in model residuals was investigated with variograms (Pinheiro et al. 2004). If autocorrelation was present, a spatial covariance structure was incorporated into the regression errors (Lichstein et al. 2002).

At all spatial and temporal scales, we also regressed the residency time against the resource selection function value on the resource selection function map derived from very-high-frequency radiotelemetry data collected from this population (Anderson et al. 2005b). This analysis was limited to the summer, which corresponded with the map of resource-selection functions.

Cross validation was used to quantify the ability of the models to predict residency time. We employed a leave-one-out procedure in which each data point was held out as a test datum (Fielding and Bell 1997). To predict each test datum, we constructed a new model training data set using randomly selected and spatially independent data from all animals except the animal that contributed the test datum. Data points were considered spatially independent if they were separated by a distance greater than the range of the variogram fit to the residuals of the model without spatial or temporal covariance structure. We then calculated a coefficient of prediction (R_{pred}^2), which measured the relative predictive strength of the model against the mean of the training data to predict residency time:

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

where Y_p is the predicted residency time of the test datum i , Y_i is the observed residency time of test datum i , and $\bar{Y}$ is the mean residency time of the training data set (Turchin 2003).

RESULTS

Positional error.—The mean $\pm$ SD annual number of locations per animal for which residency time calculated was $1,036 \pm 263$ for the 4-h analysis, and $1,730 \pm 415$ for the 20-min interval analysis. The mean positional error for the test collars was 7.3 ± 6.2 m in an open area, 9.0 ± 8.1 m in a deciduous forest, and 10.3 ± 8.7 m in a coniferous forest.

Snow-water equivalent values.—The repeated-measures regression analysis to predict daily snow-water equivalent values across the landscape resulted in a single strongest model. The Akaike weight for this model was 0.91, and a leave-one-out cross validation resulted in a R_{pred}^2 of 0.78, indicating high predictive strength. The following variables (and regression coefficients $\pm$ SE) were included: snow depth (0.81 ± 0.04), forest-cover type as a 2-level class variable including evergreen forest (-2.01 ± 0.06), and open-canopy forests (-1.61 ± 0.07); and mean maximum temperature on the current and preceding day (0.02 ± 0.003).

The best model, as measured by AIC, included forest cover type as a 2-level class variable: evergreen forests (coniferous, mixed coniferous-deciduous, and cedar swamps) and open-canopy forests (the remaining cover types in the winter). This model had an Akaike weight of 0.91, and a leave-one-out cross validation resulted in a R_{pred}^2 of 0.78, indicating high predictive strength.

Step lengths and spatial-scale determination.—The median step lengths at the 4-h and 20-min relocation intervals were 149 m and 28 m, respectively (Figs. 2A and 2B). We calculated the residency time in circles with radii of 75 m, 150 m, and 300 m using the 4-h relocation data, and in circles with radii of 30 m, 60 m, and 90 m using the 20-min relocation data. The finest grain size of our landscape variables was a 30-m grid cell; consequently, we could not examine factors that influence residency time using the 20-min relocation data within circles with a radius of <30 m. As with the distribution of step lengths

TABLE 1.—Residency time for North American elk (*Cervus elaphus*) measured (in minutes) at 2 time intervals (20 min and 4 h). Landscape covariates were measured at 3 radii (spatial scales) for each location-sampling interval. Data were collected between February 2002 and January 2004 in the Chequamegon National Forest, Wisconsin.

Residency time	20-min interval			4-h interval		
	30 m	60 m	90 m	75 m	150 m	300 m
Median	48.4	133.4	208.2	277.5	522.7	960.1
Minimum	0.9	1.8	2.6	19.3	38.6	77.2
Maximum	3,339.0	6,669.0	9,023.0	2,755.0	4,247.0	7,596.0

(Fig. 2), a highly skewed distribution occurred for the residency times at 20-min and 4-h intervals (Table 1).

Residual autocorrelation.—At the 4-h relocation interval, the best competing models all showed a similar pattern of spatial and temporal autocorrelation in the residuals. The observations that were at least 350 m apart were spatially independent, and observations that were separated by >32 h were temporally independent. The spatial and temporal dependence in the residuals was removed when an exponential spatial covariance structure was incorporated into the regression errors.

Examination of variograms of model residuals at 20-min interval relocations demonstrated that observations that were >200 m apart were spatially independent, and observations that were separated by >240 min were temporally independent. As in the analysis of the 4-h relocation interval data, the addition of an exponential spatial covariance structure to the regression model removed all spatial and temporal dependence in the residuals.

Twenty-minute interval analysis of residency time.—In the 20-minute interval analyses, the Akaike weights indicated strong support for a single best model at the 30-m and 90-m spatial scales, and only moderate support at the 60-m scale (Table 2). However, the cross-validation tests demonstrated that all models had poor ability to predict residency time in spatially independent data for animals not included in model building (R_{pred}^2 range: < 0.01–0.04; Table 2). Despite the low predictive power of the independent variables, the following trends were observed. Variables related to forest cover, forage biomass, snow, temperature, time of day, and calving period were consistently important in the top 3 models across the 3 spatial scales (Table 2). Residency time was lowest during crepuscular hours and the calving period, but increased with increasing snow-water equivalents (Table 3). Residency time had an inverse relationship with forest cover at the 30-m scale, but a U-shaped polynomial relationship at the 60- and 90-m scales, which indicated a minimum residency time when forest cover equaled 66% and 57%, respectively. Forage biomass had a positive linear relationship with residency time at the 30-m scale and a humpbacked polynomial relationship at the 60-m scale that reached a maximum when forage biomass was 45 g/m². At the 90-m scale, there was a significant interaction effect between forage biomass and distance from the center of wolf territories. Residency time decreased with increasing forage biomass and distance from wolves until reaching a local minimum residency

TABLE 2.—Top 3 regression models relating residency time of North American elk (*Cervus elaphus*) in Wisconsin to spatial and temporal variables using 20-min relocation data at 3 spatial scales. The change in Akaike information criterion (AIC) from the model with the lowest AIC value (ΔAIC), the Akaike weights (ω_i), and the coefficient of prediction (R_{pred}^2) are presented for each model.

20-min model parameters ^a	ΔAIC	ω_i	R_{pred}^2
30-m spatial scale			
Forest, Forage, Snow, Road, Temp, Time, Calf	0.00	0.941	0.01
Forest, Forage, Snow, Temp, Time, Calf	6.16	0.043	<0.01
Forest, Forage, Snow, Temp, Time, Calf, Wolf	8.83	0.011	<0.01
60-m spatial scale			
Snow, Time, Calf, Wolf, Forest poly, Forage poly, Temp poly	0.00	0.611	0.02
Snow, Time, Calf, Forest poly, Temp poly, Forage*Wolf	1.45	0.296	0.02
Snow, Temp, Time, Calf, Forest poly, Forage*Wolf	4.21	0.074	<0.01
90-m spatial scale			
Snow, Time, Calf, Forest poly, Forage*Wolf	0.00	0.995	0.04
Snow, Temp, Time, Calf, Forest poly, Forage*Wolf	11.04	0.004	<0.01
Snow, Time, Forest poly, Temp poly, Forage*Wolf	13.28	0.001	<0.01

^a Forest = percentage of forest cover; Forage = log(mean forage biomass); Snow = mean snow-water equivalents value; Road = log(distance to nearest road); Temp = mean daily temperature; Time = time period categorized as day, crepuscular, or night; Calf = in or out of calving season; Wolf = log(distance from nearest wolf-territory center); Forest poly = 1st-order and polynomial terms of percentage of forest cover; Forage poly = 1st-order and polynomial terms of mean forage biomass; temp poly = 1st-order and polynomial terms of mean daily temperature; Forage*Wolf = 1st-order and interaction effects between mean forage biomass and distance from wolf-territory center.

when forage biomass equaled 47 g/m² and distance from wolf-territory center was 7.1 km. At the 30-m scale, mean temperature had an inverse relationship with residency time, and at the 60- and 90-m scales there was a U-shaped polynomial relationship, which results in a local minimum residency time when mean temperature is 10°C at both spatial scales.

Four-hour interval analysis of residency time.—As in the preceding analysis, all statistical models at the 4-h interval had poor ability to predict residency time in spatially independent data for animals not included in the model building (R_{pred}^2 range: < 0.01–0.04; Table 4). Nevertheless, residency time was lowest during daytime and the calving season, and increased with increasing snow-water equivalent values (Table 5). At the 75-, 150-, and 300-m spatial scales, there was a U-shaped polynomial relationship with percentage of forest cover, which resulted in a minimum residency time when forest cover was 60%, 55%, and 43%, respectively. Mean forage biomass had an inverse linear relationship with residency time at the 75-m scale, and a significant interaction effect with distance from wolf-territory center at the 150- and 300-m scales. At the 150-m scale, this interaction effect resulted in decreasing residency time with increasing mean forage biomass and distance from wolves until a local minimum residency time was reached when mean forage biomass equaled 78 g/m² and distance from wolf-territory center was 7.7 km. A minimum residency time also was reached at the 300-m scale when mean

TABLE 3.—Regression results relating residency time of North American elk (*Cervus elaphus*) in Wisconsin to spatial and temporal variables using 20-min relocation data. Models with the lowest Akaike information criterion for each spatial scale are presented. Estimated coefficients and standard errors are shown for model covariates. The regression procedure splits the class variables (season and time of day) into reference and nonreference levels. The parameter estimate for the intercept equals the presented intercept value when the animals are in the “Reference” class variables (i.e., during calving season and crepuscular hours). The parameter estimates in the nonreference class variables are the deviations from the intercept (i.e., out of calving season and not crepuscular hours). The coefficient of prediction (R_{pred}^2) value is the result of the cross validation and demonstrates the predictive strength of the model.^a

Explanatory variables of log residency time	Variable type	Estimated coefficients (SE)		
		30-m	60-m	90-m
Intercept	—	7.319 (0.093)	9.636 (0.477)	26.808 (2.926)
% forest cover	Continuous	−0.16 (0.02)	−0.709 (0.097)	−0.926 (0.096)
% forest cover squared	Continuous	—	0.539 (0.091)	0.810 (0.095)
Log forage	Continuous	0.078 (0.016)	—	−4.61 (0.834)
Forage	Continuous	—	0.009 (0.002)	—
Forage squared	Continuous	—	−0.0001 (2×10^{-5})	—
Snow-water equivalent	Continuous	0.032 (0.008)	0.034 (0.008)	0.013 (0.008)
Log distance to nearest road	Continuous	0.035 (0.009)	—	—
Mean temperature	Continuous	−0.012 (0.001)	−0.006 (0.001)	−0.004 (0.001)
Mean temperature squared	Continuous	—	0.0003 (7×10^{-5})	0.0002 (7×10^{-5})
Log distance from wolves	Continuous	—	−0.141 (0.054)	−2.01 (0.333)
Time of day (crepuscular)	Class	Reference	Reference	Reference
Time of day (day)	Class	0.371 (0.021)	0.459 (0.20)	0.435 (0.019)
Time of day (night)	Class	0.417 (0.025)	0.361 (0.124)	0.293 (0.023)
Season (calving)	Class	Reference	Reference	Reference
Season (not calving)	Class	0.132 (0.027)	0.138 (0.028)	0.119 (0.026)
Log distance from wolves $\times$ log forage	Interaction	—	—	0.520 (0.095)
R_{pred}^2		0.02	0.02	0.04

^a A dash (—) indicates that the variable is not included in the corresponding model.

forage biomass equaled 47 g/m² and distance from wolf-territory center was 7.5 km. Mean temperature had a hump-back-shaped polynomial relationship with residency time at all spatial scales that results in a local maximum in residency time between 10°C and 11°C.

Residency time and resource selection.—A quantile–quantile plot comparison of the distributions of RSF values of elk and

random locations clearly demonstrates that elk preferentially use high RSF areas (Fig. 3). The RSF values at the random locations tend to be smaller and more variable than at the elk locations. However, the regression of residency time against the RSF values showed that there was no relationship across all spatial and temporal scales as determined by a log-likelihood ratio test ($P > 0.2$). Elk made long and short movements in

TABLE 4.—Top 3 regression models relating residency time of North American elk (*Cervus elaphus*) in Wisconsin to spatial and temporal variables using 4-h relocation data at 3 spatial scales. The change in Akaike information criterion (AIC) from the model with the lowest AIC value (ΔAIC), the Akaike weights (ω_i), and the coefficient of prediction (R_{pred}^2) are presented for each model.

4-h model parameters ^a	ΔAIC	ω_i	R_{pred}^2
75-m spatial scale			
Forage, Snow, Calf, Wolf, Forest poly, Temp poly, Day-night	0.00	0.640	0.01
Snow, Calf, Forest poly, Temp poly, Forage*Wolf, Day-night	1.15	0.359	0.01
Forest, Snow, Temp, Calf, Wolf, Day-night	16.63	0.001	<0.01
150-m spatial scale			
Snow, Calf, Forest poly, Temp poly, Forage*Wolf, Day-night	0.00	0.790	0.02
Forage, Snow, Calf, Wolf, Forest poly, Temp poly, Day-night	2.65	0.209	0.02
Snow, Calf, Wolf, Forest poly, Forage poly, Temp poly, Day-night	29.06	0.001	<0.01
300-m spatial scale			
Snow, Calf, Forest poly, Temp poly, Forage*Wolf, Day-night	0.00	0.998	0.04
Forage, Snow, Calf, Wolf, Forest poly, Temp poly, Day-night	44.77	0.001	<0.01
Snow, Temp, Calf, Forage*Wolf, Day-night	50.67	0.001	<0.01

^a Forage = log(mean forage biomass); Snow = mean snow-water equivalent value; Calf = in or out of calving season; Wolf = log(distance from nearest wolf-territory center); Forest poly = 1st-order and polynomial terms percentage of forest cover; Temp poly = 1st-order and polynomial terms of mean daily temperature; Day-night = day or night; Forage*Wolf = 1st-order and interaction effects between mean forage biomass and distance from wolf-territory center; Forest = percentage of forest cover; Temp = mean daily temperature; Forage poly = 1st-order and polynomial terms of mean forage biomass.

TABLE 5.—Regression results for residency time from 4-h relocation data analysis of North American elk (*Cervus elaphus*) in Wisconsin. Only the models with the lowest Akaike information criterion for each spatial scale are presented. Estimated coefficients and standard errors are shown for model covariates. The regression procedure splits the class variables (season and time of day) into reference and nonreference levels. The parameter estimate for the intercept equals the presented intercept value when the animals are in the “Reference” class variables (i.e., during calving season and daytime hours). The parameter estimates in the nonreference class variables are the deviations from the intercept (i.e., out of calving season and nighttime hours). The coefficient of prediction (R_{pred}^2) value is the result of the cross validation and demonstrates the predictive strength of the model.

Explanatory variables of log residency time	Variable type	Estimated coefficients (SE)		
		75-m	150-m	300-m
Intercept	—	11.220 (0.367)	19.350 (2.588)	45.214 (2.925)
% forest cover	Continuous	−0.404 (0.085)	−0.686 (0.094)	−0.586 (0.131)
% forest cover squared	Continuous	0.339 (0.081)	0.623 (0.087)	0.679 (0.120)
Log forage	Continuous	−0.024 (0.017)	−2.114 (0.744)	−8.980 (0.857)
Snow-water equivalent	Continuous	0.027 (0.003)	0.019 (0.003)	0.016 (0.003)
Mean temperature	Continuous	0.006 (0.001)	0.006 (0.001)	0.009 (0.001)
Mean temperature squared	Continuous	−0.0003 (6×10^{-5})	−0.0003 (6×10^{-5})	−0.0004 (6×10^{-5})
Log distance from wolves	Continuous	−0.196 (0.041)	−1.029 (0.295)	−3.866 (0.335)
Season (calving)	Class	Reference	Reference	Reference
Season (not calving)	Class	0.182 (0.026)	0.168 (0.025)	0.259 (0.025)
Time of day (day)	Class	Reference	Reference	Reference
Time of day (night)	Class	0.246 (0.016)	0.177 (0.015)	0.089 (0.015)
Log distance from wolves $\times$ log forage	Interaction	—	0.236 (0.085)	1.006 (0.098)
R_{pred}^2		0.01	0.02	0.04

^a A dash (—) indicates that the variable is not included in corresponding model.

both favorable and less favorable habitats. We did not do cross-validation tests because there was no relationship between these variables.

DISCUSSION

Theoretical and empirical studies suggest that variables related to resource acquisition (Charnov 1976; Zollner and Lima 1999), predator avoidance (Fortin et al. 2005; Mitchell and Lima 2002), and thermoregulation (Porter et al. 2002) should influence residency time and movement rates. However, the statistical models in our analyses did not validate our a priori hypotheses. Ecologically plausible variables and scales had very poor predictive strength of residency time, as tested with cross validation (Tables 2 and 4). This outcome indicates that spatial and temporal factors have very little influence on elk movement rates in Wisconsin, which corroborates similar findings in other locations (Forester et al. 2007; Kie et al. 2005). This conclusion is further supported by the finding that the integrated measure of habitat use represented in the resource-selection function had no explanatory power for residence time. Consequently, patterns of resource selection are formed from elk selecting for particular habitat conditions and revisiting those sites rather than slowing their movement rates within favorable areas.

A previous RSF study on this population demonstrated that elk spend a disproportionate amount of time in areas with high forage biomass and reduce time spent in areas relatively close to wolf-territory centers (Anderson et al. 2005b). Although the predicted RSF maps were generated from diurnal locations collected at 10-day intervals, our results show that elk locations obtained at 4-h intervals with global positioning system telemetry tend to occur in areas with high RSF values (Fig. 3).

Despite the clear preferential use of certain areas of the landscape, elk do not have higher residence in these areas.

From an energetics perspective, animals that preferentially use certain areas of the landscape should minimize energy expenditure by slowing down in favored areas as opposed to moving frequently between them. However, movement rates

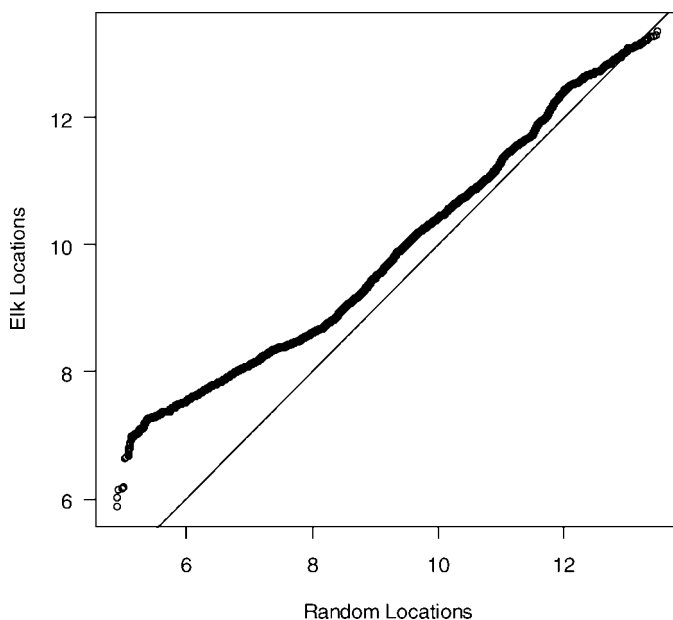


FIG. 3.—Quantile–quantile plot comparison of the distributions of values for resource-selection functions of location data for North American elk (*Cervus elaphus*) and for resource-selection functions at 2,000 random locations. Data were collected between February 2002 and January 2004 in the Chequamegon National Forest, Wisconsin.

across a landscape may be indicative of trade-offs balancing the relative risk of predation associated with increased residence time with the energetic costs of moving across resource-poor areas. This is consistent with evidence that foraging behavior is highly variable in natural settings (Focardi et al. 1996) and is influenced by predation risk (Clarke 1983; Kie 1999; Lima and Dill 1990; Newman and Caraco 1987).

Is there a biological advantage to having random residence rates with respect to landscape factors? Random residency rates may make prey species less predictable on the landscape to predators (Bowyer et al. 1999). Reducing predictability on the landscape should lower encounter rates with predators and consequently reduce predation risk. In environments where resources are not spatially limited and energy costs of locomotion between preferred areas are not excessive, residency rates should not necessarily differ across habitat types. Although forage biomass in the study area is patchily distributed relative to elk home-range sizes (Fig. 1), elk behavior reflected in the data suggests that energetic needs are met while moving and foraging with random residency rates.

In contrast, populations that depend on resources that are spatially limited would not be expected to move with random residency rates with respect to landscape factors. For example, mice (*Peromyscus maniculatus*—Kotler and Brown 1988; Stapp and Van Horn 1997) that depend on shrub cover, or bighorn sheep (*Ovis canadensis*—Krausman et al. 1999) that depend on rugged precipitous terrain reduce predation risk by spending a disproportionate amount of time in these areas. Although predators are at a disadvantage when prey are in specialized areas, whether there are features in the Wisconsin landscape, such as forest cover, that offer physical protection for the elk against predation requires further study. Although ungulates may increase the use of forested areas in the presence of predators (Altendorf et al. 2001; Fortin et al. 2005; McCorquodale 2003; Tufto et al. 1996; Wolff and Van Horn 2003), elk also might use movement to decrease predictability and reduce encounters with predators. Further research is needed to determine how elk movement rates will vary in response to spatially limited resources such as forage, water, or forest cover in more heterogeneous landscapes (Bowyer 1981; Boyce et al. 2003; Truett 1996).

Despite the poor predictive ability of the statistical models, some of the observed trends in these data merit discussion. Across spatial and temporal scales, models of residency time identified a consistent effect of time of day (Tables 3 and 5). Residency time was lowest during crepuscular hours and highest during night, which concurred with results from other studies on elk (Forester 2005; Frair et al. 2005; Wolff and Van Horn 2003). Our analysis also produced the counterintuitive result that residency time was lower during the calving period than during the remainder of the year. We expected elk to be more sedentary during the time of limited calf mobility; however, animals may alter behavior and increase movement in the face of predation risk (Kie 1999; Lima and Dill 1990). Because we did not have complete information on which specific females had neonates, we were unable to explore this relationship in more detail. Residency time

consistently increased with increasing snow-water equivalent values, which may be a response to the relatively high energetic costs of locomotion in snow (Parker et al. 1984). In 5 of 6 analyses, residency time was lowest when percentage of forest cover was 43–66%. There were no significant interactions between percentage of forest cover and temperature or distance to wolves. This does not imply that elk do not use forested areas for concealment or thermal cover, but rather it indicates that they do not slow down or speed up relative to these factors while in forests. The effects of variables related to temperature and distance from wolf territories and roads exhibited inversions of coefficient signs across scales, which may be related to the weak relationships with residency time (Tables 3 and 5).

The inclusion of the spatial covariance structure in the models removed both the spatial and temporal autocorrelation, which indicates a close linkage between these 2 models. The autocorrelation is likely because of endogenous temporal autocorrelation of elk movement (Forester et al. 2007; Morales et al. 2004). Residual spatial autocorrelation is less likely to be important here because it should have been absorbed by the spatial variables explored in our analyses, which have been shown to be important in resource selection (Anderson et al. 2005b; Boyce et al. 2003; Forester 2005). Further, evidence indicates that spatial environmental variables have little influence on autocorrelated movement by elk (Forester et al. 2007; Kie et al. 2005).

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