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Research article

Landscape-level movements of North American elk (*Cervus elaphus*): effects of habitat patch structure and topography*

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Abstract

We examined movements of North American elk (*Cervus elaphus*) in northeastern Oregon, USA. Movement vectors at 449 locations over a 7762 ha area were calculated based on 16,724 sequential observations of 94 female elk-year combinations during spring (15 April–14 May) 1993, 1995, 1996. We calculated movement vectors at the start of morning and evening feeding bouts (0500, 1900 h) and during periods of least activity (0100, 1500 h). Here, we measured characteristics of habitat patches (habitat type, mean patch size, coefficient of variation in patch size, edge density, mean shape index, and mean nearest neighbor) at two levels of habitat grain (eight habitat types, two habitat types) and at three spatial scales (250, 500, and 1000 m) around each movement vector. We also measured topographic features around each vector including distance to nearest stream, direction of drainage, elevation, slope, and convexity (a measure of ridge top vs. valley bottom land form). We used mixed models adjusted for positive spatial correlation among vectors to examine the relationship between vector length, or speed of movement, and habitat patch characteristics, and between vector direction and topographic features. Speed of movements by elk were not related to characteristics of habitat patches that we measured. The direction of movement, however, was dependent on topography. Elk were more likely to move parallel to major drainages than perpendicular to them. Furthermore, elk were less likely to move perpendicular to drainages when close to the nearest stream, in valley bottoms vs. ridge tops, and on steep slopes. The dendritic nature of movements by elk with respect to topography may help elucidate ecosystem processes such as nutrient flows, nutrient cycling, and successional trajectories of plant communities.

Introduction

Landscape structure has important effects on many natural history characteristics among animals including disease processes (Lloyd and May 1996), host–parasite relationships (Ives 1995), predator–prey relationships (Bowman and Harris 1980), population genetics (Good et al. 1997), interspecific competition (Pacala and Roughgarden 1982), population and metapopulation dynamics (Stenseth 1980; Dempster and Pollard 1986; Dunning et al. 1992), community structure, and biotic diversity (Roth 1976; Holt 1984). How patches of different habitats are arranged at the landscape level also can influence distribution of large mammals (Clutton-Brock and Harvey 1978; Beier and McCullough 1990; Moe and Wegge 1994; Kie et al. 2002). Distributional patterns of animals are, in turn, a result of movements of individuals. There-

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fore, determining how individuals move across heterogeneous landscapes is necessary to fully understand the relationship between landscape structure and animal distributions.

Models of animal movements have been proposed to examine a range of ecological questions such as dispersal, distribution, and foraging strategies of terrestrial vertebrates (Turner et al. 1993; Gross et al. 1995; Focardi et al. 1996; Lima and Zollner 1996; White et al. 1996; Grünbaum 1998; Turchin 1998; Carter and Finn 1999; Moorcroft et al. 1999; Zollner and Lima 1999; Bergman et al. 2000; Wu et al. 2000). Models of movement allow a better understanding of complex interactions between animal behavior, habitat heterogeneity, and animal distributions in space and time. In the case of large mammals such as North American elk (*Cervus elaphus*), movement models are useful to test hypotheses concerning foraging behavior and its long-term effects on vegetation succession and ecosystem function (Pastor and Naiman 1992; Molvar et al. 1993; Hobbs 1996; Augustine and McNaughton 1998; Kie and Lehmkuhl 2001; Kie et al. 2003).

Patterns of movement by North American elk have been described in the past, and related to daily cycles as well as differences among seasons (Green and Bear 1990; McCorquodale 1993; Ager et al. 2003), reproductive status in females (Vore and Schmidt 2001), rutting behavior in males (Bowyer 1981), vehicular traffic (Cole et al. 1997), and other factors. Fewer studies have examined elk movements in relation to the juxtaposition of habitat components (Strohmeyer and Peek 1996) or topographic relief (Skovlin 1982; Ager et al. 2003).

We recently have been developing models of animal movement containing spatially and temporally explicit drift and diffusion terms, using estimation methods based on stochastic differential equations (Preisler et al. 1999, 2001, 2004; Brillinger et al. 2001, 2002, 2004). These models use empirically measured movement segments of individual elk to parameterize bivariate differential equations with drift (directional) and diffusion (stochastic) terms. The drift terms are individually estimated for one or more habitat covariates as smooth functions that are dependent on location and time of day. The resulting model encapsulates movement behavior as a time and location dependent attraction to specific habitat features Preisler et al. 2001, 2004; Brillinger et al. 2002, 2004).

Large mammals such as elk have been shown to be keystone species that affect ecosystem processes such as nutrient flows, nutrient cycling, and successional trajectories of plant communities (Kie et al. 2003). In this study, our objective was to better understand landscape-level factors that influence the movements of elk, and hence, their potential impacts on ecosystem function. Specifically, we examined the relationship between drift terms in our stochastic differential equations and landscape structure as measured by characteristics of habitat patches and topography. We specifically tested two hypotheses: (1) speed of movements by elk were related to habitat patch characteristics such as habitat patch type, mean patch size, variation in patch size, amount of habitat edge, shape of habitat patches, and mean distance to nearest habitat patch of the same type; and (2) direction of elk movements were related to topographic variables such as distance to the nearest stream, direction of the drainage, elevation, slope, and convexity with respect to ridge tops and valley bottoms.

Methods

Study site

This study was conducted at Starkey Experimental Forest and Range (Starkey) of the US Forest Service, located 35 km southwest of La Grande (45°13′N, 118°31′W) in the Blue Mountains of northeastern Oregon, USA (Figure 1). Starkey consists of 10,125 ha enclosed by a 2.4-m high fence that prevents immigration or emigration of resident elk and other large herbivores (Rowland et al. 1997). Starkey is divided into multiple subunits, the largest a 7762 ha main study area where data for our research were obtained (Figure 2). Starkey is situated between 1122 and 1500 m in elevation and supports a mosaic of coniferous forests and grasslands that typify summer range for elk in the Blue Mountains (Rowland et al. 1997). A network of drainages creates a complex and varied topography (Figure 2). Streams on Starkey are generally shallow with low to moderate flows, and rarely pose an absolute barrier to movements by elk. Details of the study area and facilities are available elsewhere (Rowland et al. 1997; Johnson et al. 2000).

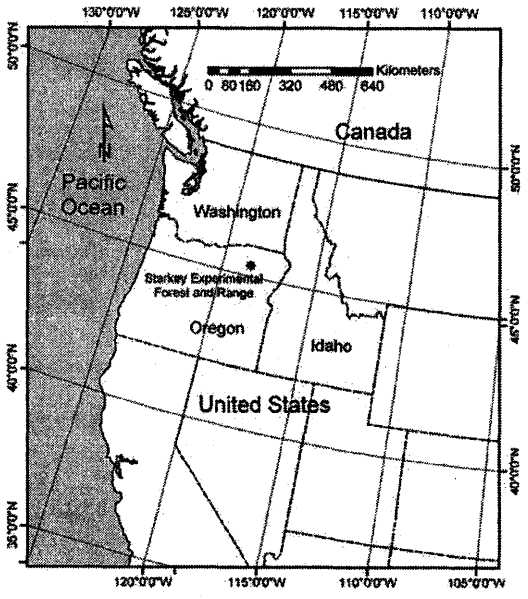

Figure 1. Location of study site at Starkey Experimental Forest and Range, northeastern Oregon, USA.

To define habitat patches, we used two sets of categorical habitat definitions of differing grain size (*sensu* Forman 1995, p. 10; Bowyer et al. 2002). At the coarsest grain, two habitat types were defined; forest and grassland. At the finer grain, eight habitat types were delineated (Figure 2). Grasslands were further subdivided into dry grassland and wet meadow–riparian habitat. Forest habitat was first classified by dominant tree species: grand fir (*Abies grandis*), Douglas fir (*Pseudostuga menziezii*), or other mesic-forest conifers; Ponderosa pine (*Pinus ponderosa*) on more xeric sites; and lodgepole pine (*Pinus contorta*). Each forested type was further classified as small trees (canopy cover ≥40% in trees ≤10.2 cm diameter at breast height = 1.37 m) or large trees (canopy cover in small trees < 40%).

Drainages of major streams (defined as drainages where difference in elevation between stream bottoms and adjacent ridge tops >60 m) were obtained from a digital elevation model. Distances to major streams and slope also were determined from the same elevational model. Topographic convexity was used to describe terrain in terms of morphology of ridge tops and valley bottoms. Convexity was calculated as the difference in elevation between each 30 m × 30 m pixel from the mean of the 3 × 3 pixel neighborhood (Kvamme 1988; Ager et al. 2003). Values > 0 indicated convex (ridge top) and < 0 concave (valley bottom) landforms.

Radio-telemetry data

Elk locations were obtained from an automated telemetry system that used retransmitted LORAN-C radio navigation signals (Dana et al. 1989; Findholt et al. 1996; Rowland et al. 1997). Locations had a mean error of 53 m (Findholt et al. 1996). A subset of telemetry data was selected for spring (15 April–14 May) 1993, 1995, and 1996. Elk exhibited large differences in the patterns of habitat use during that time (Johnson et al. 2000; Ager et al. 2003).

We used locations from 91 female elk (a few of which were monitored in more than one year) for a total of 96 elk-year combinations and 16,724 observations. The elapsed time between locations for each animal averaged 59.6 min. We calculated step sizes in the west–east direction (x) and the south–north direction (y) from the distance moved by the animal and time between its successive locations. Observations were deleted if elapsed time was < 5 min or > 150 min between successive observations of an animal. Shorter elapsed times (< 5 min) yield speeds that tend to be positively biased because of random location errors in the telemetry system (Ager et al. 2003). Speeds determined at longer elapsed times tended to be negatively biased as a result of undetected movements between observations. The 7762 ha main study area on Starkey is 3–4 times larger than typical summer home ranges of elk in the Blue Mountains (2000–2900 ha; Leckenby 1984), providing elk with large-scale habitat choices commensurate with free-ranging herds.

Models of elk movement

We previously developed models of elk movements on Starkey using stochastic differential equations, or SDEs (Preisler et al. 1999, 2001, 2004; Brillinger et al. 2001, 2002, 2004). These equations were used to describe the incremental step movement of an animal at time t and location r $(t) = X(t), Y(t)'$. The specific differential equations were:

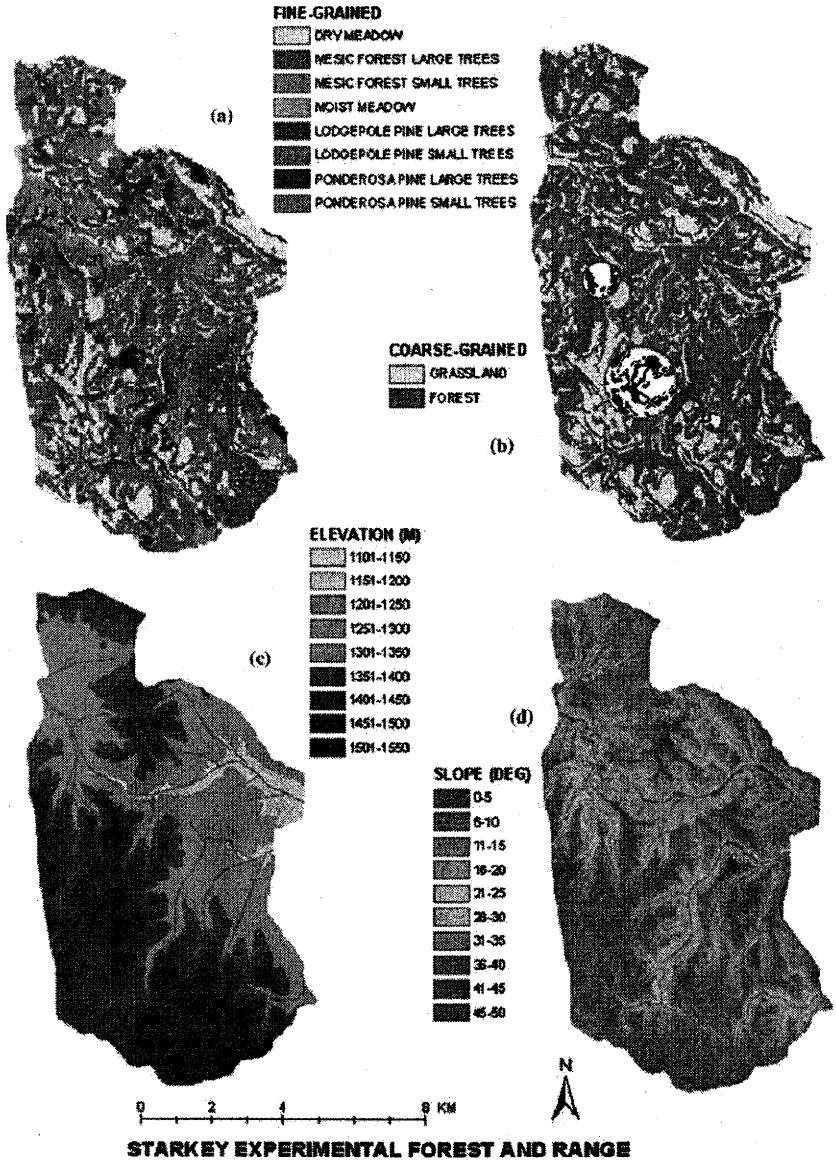

Figure 2. Habitats (fine-grained and coarse-grained), elevation, and slope at Starkey Experimental Forest and Range, northeastern Oregon, USA.

$$\begin{aligned} \mathrm{d}X(t) &= \mu_x\{\mathbf{r}(t), t\}\mathrm{d}t + \sigma_x \mathrm{d}\xi_x(t) \\ \mathrm{d}Y(t) &= \mu_y\{\mathbf{r}(t), t\}\mathrm{d}t + \sigma_y \mathrm{d}\xi_y(t) \end{aligned} \quad (1)$$

Here $\mathrm{d}X(t)$ and $\mathrm{d}Y(t)$ are the incremental step sizes in the x and y directions; vector$\mu = (\mu_x, \mu_y)'$ is the drift vector; $\xi_x(t)$, $\xi_y(t)$ are Gaussian processes with expected values that equal 0. σ_x, σ_y modify the intensity of this random component.

Estimates of the drift terms were calculated by approximating the SDEs in equation (1) by the difference equations:

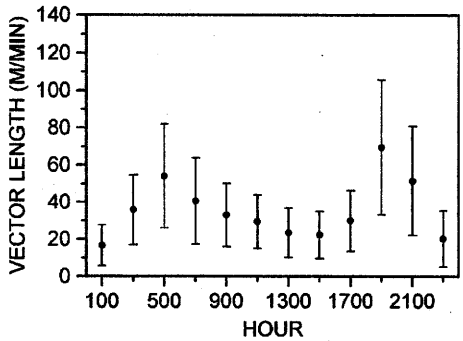

Figure 3. Mean lengths (±1 SD, n = 449) of movement vectors (m/min) estimated for North American elk every 2 h during spring (15 April–14 May) 1993, 1995, and 1996.

$$\begin{aligned}(X_{i+1} - X_i)/(t_{i+1} - t_i) &= \mu_x(X_i, Y_i, t_i) \\ &+ \sigma_x \varepsilon_{1i}/\sqrt{t_{i+1} - t_i} \\ &\times (Y_{i+1} - Y_i)/(t_{i+1} - t_i) \\ &= \mu_y(X_i, Y_i, t_i) + \sigma_y \varepsilon_{2i}/\sqrt{t_{i+1} - t_i}, \qquad (2)\end{aligned}$$

where (X_i, Y_i), $i = 1, 2,\ldots$, is the location of an animal at time t_i, with $t_1 < t_2 < t_3\ldots$;ε_{1i},ε_{2i} are independent standardized errors; and σ_x,σ_y are unknown constants (Preisler et al. 2004). Data on step sizes in the x and y directions (m/min) from all animals were analyzed simultaneously to produce one three-dimensional surface as an estimate of the drift function $\mu_x(X, Y, t)$ in the x-direction, and a second estimate $\mu_y(X, Y, t)$ in the y-direction. Estimates of drift surfaces were calculated by the nonparametric regression routine LOESS (Cleveland et al. 1992), within the generalized additive model GAM (Hastie 1992).

Analysis of habitat patches

We used ARC GIS (ESRI 2001) to analyze habitats at coarse (two habitat types) and fine (eight habitat types) grains as previously defined. We examined structure of habitat patches at three spatial scales: within 250, 500, and 1000 m radii around each of 449 estimated movement vectors. We then used FRAGSTATS to estimate the following landscape metrics within each radius: mean size of each habitat patch (ha); coefficient of variation in patch sizes; edge density (m of edge/100 ha); total core area (size of habitat patch core (ha), defined as that part of each patch >183 m interior to the patch boundary); mean shape index (ranging from 1 for a perfectly square habitat patch (in raster format) to ∞ for increasingly complex, convoluted shapes); and mean distance (m) to the nearest neighbor patch of the same type (McGarigal and Marks 1995).

Some landscape metrics may be dependent on the extent of the area being analyzed. For example, circles at our largest spatial scale could contain larger habitat patches than those at smaller spatial scales. Further, where movement vectors occurred near the edge of the study area, clipped circles often were of less than full size, because those circles were truncated by the boundary of that area. Hence, we also measured the total area (ha) of the clipped circles, and included that variable in our analyses to adjust for analytical artifacts.

Relating elk movements to landscape structure

From the drift-response surfaces estimated at various times of day, we calculated a movement vector (speed and direction) at points on a 180 × 180-m grid across the study area on Starkey. Vectors were not calculated where there were insufficient numbers of raw data points to accurately portray drift (Preisler et al. 1999, 2004). The result was estimates of drift at 449 points spread across the 7762 ha study area. Plotting mean vector length as a function of time of day indicated periods of least movement during early morning (0100 h) and late afternoon (1500 h; Figure 3). Drift was greatest prior to early morning (0500 h) and early evening (1900) feeding bouts by elk (Figure 3). We therefore used those four time periods as focal points for our analyses. Vector plots indicated differences not only between resting and feeding, but also between resting periods at 0100 and 1500 h, and between feeding periods at 0500 and 1900 h (Figure 4).

Movement vectors calculated on a 180-m grid did not appear to be independent, but suggested strong spatial correlation. We then constructed preliminary linear models using PROC GLM (SAS Institute 1999) and examined the residuals from those models using Moran's I test statistic in SPLUS Spatial Stats (Insightful Corporation 2001). Moran's I was significant ($P < 0.01$) for all models, indicating that the error terms indeed were not independent. We therefore examined spatial

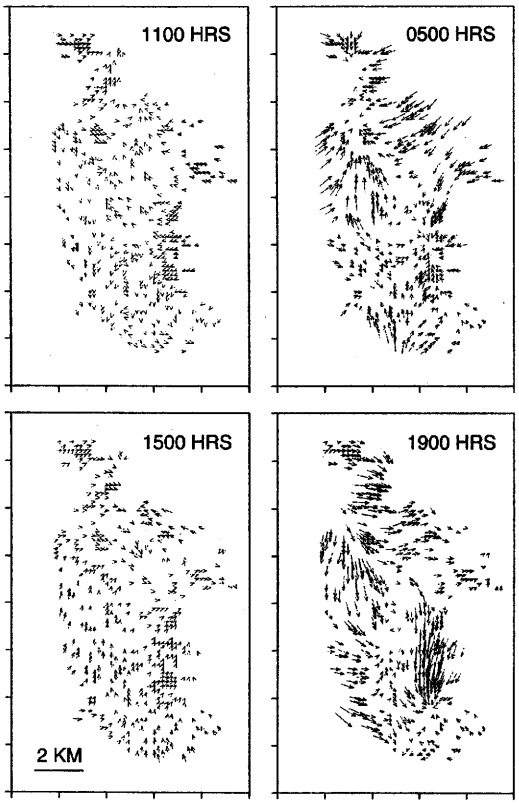

Figure 4. Vector plots on Starkey Experimental Forest and Range at periods of least movement (0100, 1500 h) and at periods of greatest movement prior to feeding bouts (0500, 1900 h).

structure by calculating semivariograms for vector lengths at the four time periods using S-PLUS (Insightful Corporation 2001) and SAS (SAS Institute 1999). We examined fit of different semivariance models, and based on minimized Akaike's Information Criterion scores (Burnham and Anderson 1998), concluded that a spherical model with no nugget effect best fit the vector data at all four time periods (Figure 5).

To examine relationships between vector length and landscape patch characteristics during time periods, we used a mixed-model approach (SAS PROC MIXED) adjusted for positive spatial correlation (Littell et al. 1996). At each spatial scale, and for each habitat graininess, we constructed a model relating vector length (VEC_i) as a function of habitat patch characteristics (*HABTYPE, MPS, PSCV, ED, TCA, MSI, MNN, TA*), where VEC_i was vector length at time *i*, *HABTYPE* was habitat type, *MPS* was mean patch size (ha), *PSCV* was patch size coefficient of variation, *ED* was edge density (m/ha), *TCA* was total core area (ha), and *TA* was total area of the circular landscape analyzed (ha). Correlation matrices among independent variables were examined to insure lack of multicolinearity. TA was included to test for analytical artifacts resulting from effects of the size of the circular landscape (radii of 250, 500, or 1000 m) on other independent variables. We considered all effects as fixed rather than random because points at which we calculated movement vectors were evenly and densely spread across the study area, the points represented all possible levels of independent variables considered, and we limited our scope of inference only to this specific study site (Littell et al. 1996). This approach resulted in a less-conservative model than had we classified effects as random. We adjusted *P* values for coefficients in each model using a sequential Bonferroni process to adjust for overall, experiment-wide error rate (Rice 1989).

We also examined the relationship between vector direction (azimuth) and the dominant direction of each stream drainage. We only were concerned with whether the azimuth of the movement vector was predominantly parallel or perpendicular to the direction of the drainage; not whether the vector was pointed upstream or downstream, as elk might move in either direction depending on time of day. Hence, we derived a variable called perpendicularity (*PERP*), which took a value of 0° when the direction of movement was perfectly parallel to the direction of the drainage, and 90° when the movement was perpendicular to the drainage. This calculation transformed the circular variable (azimuth) into a bounded linear one.

To examine effects of topography on perpendicularity of elk movements, we again used a mixed-model approach adjusted for positive spatial correlation based on a spherical semivariogram model with no nugget effect (Littell et al. 1996). At each spatial scale, we constructed a model with perpendicularity ($PERP_i$) as the dependent variable and topography characteristics (*STR_DIST, CONVEX, ELEV, SLOPE*) as independent variables, where $PERP_i$ was vector perpendicularity to drainage direction at time *i*, *STR_DIST* was distance to the nearest stream (m),

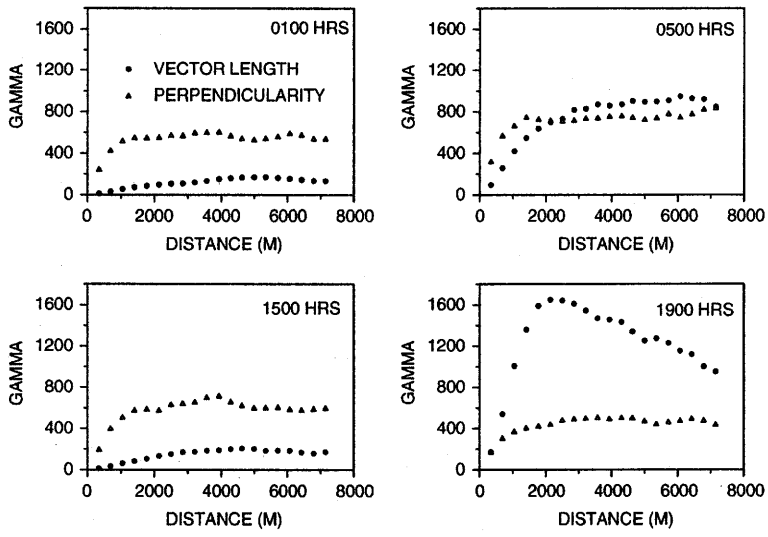

Figure 5. Semivariograms of vector length (●) and perpendicularity of movements by elk (△) at Starkey Experimental Forest and Range. Ranges for vector length at 0100, 0500, 1500, and 1900 h were 2955, 2761, 5495, and 2363 m, respectively. Ranges for perpendicularity were 1168, 1460, 1250, and 1049 m, respectively.

CONVEX was the measure of topographic convexity as described above, *ELEV* was elevation (m), and *SLOPE* was slope (deg). We adjusted *P* values for coefficients in each model using a sequential Bonferroni process to adjust for overall, experiment-wide error rate (Rice 1989).

Results

The length of movement vectors (speed) as well as their orientation differed among time periods (Figure 4). Vector lengths were spatially correlated at large scales among all time periods. Ranges on semivariograms of vector length varied from 2363 m at 1900 h to 5495 m at 1500 h (Figure 5).

In our models of vector length as a function of landscape patch characteristics, Akaike's Information Criterion (AIC) values indicated the best models at all four periods occurred with eight habitat types at the 1000-m scale. No independent variables, however, were significant at any spatial scale or habitat graininess with a single exception. Total area (TA) was significant ($P < 0.01$) for both habitat grains and all spatial scales at 0100 h, for eight habitat types (500 m, 1000 m) and two habitat types (1000 m) at 0500 h, and for eight habitat types (1000 m) and two habitat types (1000 m) at 1500 h. TA was not significant ($P > 0.10$) in models at 1900 h. Where significant, the coefficient of TA was negative, indicating higher movement rates where landscape circles analyzed were smaller. Circles were smallest near the boundaries of the study area, indicating higher movement rates near the boundary fence. No other characteristics of habitat patches were significant in any of the models once adjusted for experiment-wide error rates using a sequential Bonferroni process.

Unlike correlations between movement-vector length and habitat-patch characteristics, there were strong relationships with respect to direction of elk movements and direction of major stream drainages. There was a preponderance of movements parallel rather than perpendicular to stream drainages (Figure 6), with the value of perpendicularity differing significantly ($P < 0.01$) from an expected uniform distribution at all time periods using Kolmogorov–Smirnov goodness-of-fit tests.

There also were positive spatial correlations among the direction of the movement vectors in relation to topography (perpendicularity) with ranges on semivariograms between 1049 m at 1900 h and 1460 m at 0500 h (Figure 5). Mixed models, adjusted for such correlation, indicated significant positive relationships between

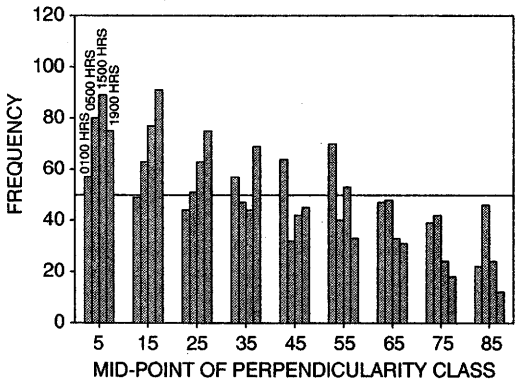

Figure 6. Frequency distribution of the variable perpendicularity (*PERP*). *PERP* ranged from 0° when elk movement was perfectly parallel to the direction of the nearest stream drainage, and 90° when the movement was perpendicular to the drainage. Blocks of histograms in each class represent *PERP* for movement vectors at 0100, 0500, 1500, and 1900 h respectively. Reference line at 49.89 represents the expected value of each bin (n = 449 movement vectors/time period/nine classes) under a uniform distribution.

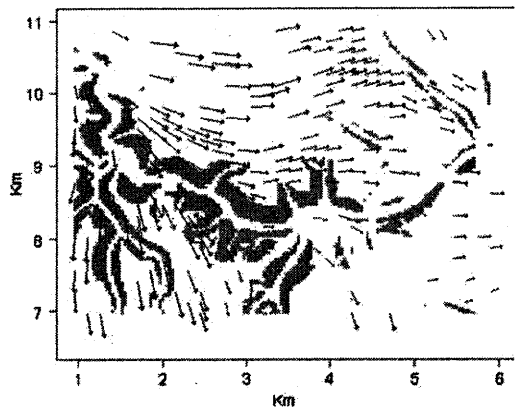

Figure 7. Estimated vector field for a major stream drainage on Starkey Experimental Forest and Range indicating how elk movements at 1900 h are influenced by topography (from (Preisler et al. 2004). Gray areas indicate slopes that exceed 21.8° (40%).

perpendicularity of movement and distance to nearest stream at 0500, 1500, and 1900 h (Table 1), with movements close to streams being less likely to be perpendicular to the drainage. Movements also were more likely to be perpendicular to drainages on ridge tops where topographic convexity was positive than in valley bottoms (at 1500 and 1990 h), and where slopes were gentle (at 0100, 1500, and 1900 h, Table 1). This pattern is clearly demonstrated in a detailed view of a portion of the study area (Figure 7).

Discussion

We observed few significant relationships between speed of elk movements, as represented by the length of movement vectors, and characteristics of habitat patches across the landscape. Reasons for this lack of correlation may be several fold. First, we only examined a limited subset of possible habitat patch characteristics previously demonstrated to be of importance in determining the distribution of another cervid upon the landscape (Kie et al. 2002). This subset, however, did span a range of characteristics including mean patch size and variability, patch shape, and arrangement of patches. Hence, it seems unlikely that the lengths of movement vectors would be correlated with other, unexamined patch variables. Secondly, the covariate total area (over which patch characteristics were measured) was significant in most models, indicating that the position of the movement vector in relation to the boundary fence was a factor in model results. Vectors calculated near the boundary of the study area were associated with smaller total areas over which landscape

Table 1. Significant (P < 0.10) coefficients and P-values for spatially-correlated, mixed models of perpendicularity of elk movements (range 0° = movement parallel to drainage, 90° = movement perpendicular to drainage) as a function of distance to stream (m), convexity (<0 = drainage bottoms, >0 = ridge tops), elevation (m), and slope (%).

Time	AIC	Distance to stream (m)/ Coefficient (P)	Convexity/ Coefficient (P)	Elevation (m)/ Coefficient (P)	Slope (deg)/ Coefficient (P)
0100 h	3846				−0.2822 (0.05)
0500 h	3870	0.01478 (0.02)			
1500 h	3813	0.01007 (0.06)	1.7387 (0.01)		−0.2295 (0.10)
1900 h	3752	0.01016 (0.03)	1.2496 (0.05)		−0.2179 (0.09)

metrics could be calculated because of the boundary fence surrounding the study area, as we did not include habitat patches outside the boundary fence. These results suggests the possibility of a boundary or fence-effect on the speed of elk movements, although distance to fence did not significantly affect selection of habitats by elk in a previous analysis (Stewart et al. 2002).

The most likely explanation for the lack of relationship between speed of elk movements and habitat patch characteristics is the rate at which elk locations were observed. The difference equations that formed the basis for our analyses were calculated from elk locations that on average were determined once every 59.6 min. A more frequent observation rate (less time between estimates of elk location) may have revealed patterns not seen with our data set. The difference equations we did derive were smoothed over two-dimensional space and time to arrive at estimates of movement vectors (Figure 4). The length of these vectors, in turn, showed positive spatial correlations as far out as 2363 to 5495 m, depending on time period (Figure 5). The largest spatial scale at which we measured habitat patch characteristics was within 1000 m, however, and we believe that the smoothing process may have obscured possible relationships between speed of movement by elk and landscape patch metrics; a topic that requires further investigation.

Conversely, we did find significant models relating the direction of elk movements as a function of landscape topography (Figure 6), (Table 1). Spatial correlation among vector perpendicularity measurements was less (ranges for semivariograms between 1049 and 1460 m; Figure 5) than among vector lengths, which may have aided the detection of a relationship between vector directions and topography. With increasing topographic relief, vertical flows of material and movements of animals tend to increase in a dendritic manner, at the expense of horizontal movements (Forman 1995). Consistent with conventional wisdom among biologists working with North American elk (Skovlin 1982), elk in this study often traveled parallel to ridge lines. To our knowledge, however, this is the first attempt to quantify relationships between directions of elk movements and directions of stream drainages, an outcome important in understanding the distribution of elk across the landscape.

The reluctance of elk to move perpendicular across steeper slopes has obvious energetic advantages to an individual. The cost of locomotion of an 180-kg elk on a horizontal plane has been estimated at 91 kcal/km, but 327 kcal/km for upslope movement (Parker et al. 1984), an over three-fold increase. Some reduction in energetic costs accrue when walking downhill compared with walking on a horizontal plane, but the increased net cost of moving across rugged terrain is still positive (Parker et al. 1984). Female elk in our study showed clear preferences for walking parallel to ridge lines whenever possible rather than moving perpendicularly across stream drainages.

High rates of movement observed at 0500 and 1900 h by female elk in this study were driven by phenology of primary forage species (Skovlin 1967; Ager et al. 2003). Rapid movements prior to the early morning and evening feeding bouts reflected attraction to specific meadows at Starkey that produce abundant, desirable forage in early spring (Skovlin 1967). Lengths of movement vectors were much shorter, as expected, during periods of rest and rumination (0100 and 1500 h). Differences in vector perpendicularity, and to some extent vector length, however, were evident between periods of maximum movement (0500 and 1900 h) and between periods of least movement (0100 and 1500 h). These differences within a dominant activity (feeding vs. resting) resulted from complex daily cycles in movement and behavior (Ager et al. 2003).

Models of elk movements presented here do not in themselves reflect preferences for specific habitats. We expect, however, that if elk movements were consistently high in a particular habitat, that the models would result in few individuals accumulating in that habitat type, and an apparent avoidance of that type. We observed no clear relationship between the length of elk movement vectors and habitat types defined at either fine (eight habitat types) or a coarse grains (two habitat types). Yet, potential functions estimated from the differential functions upon which these models are based do show significant attraction to specific sites, and these also are sites at which elk concentrate (Preisler et al. 2001, 2004; Brillinger et al. 2002, 2004). Again, we suspect that the lack of relationship between vector lengths in this study and characteristics of habitat patches, including patch type, are functions of the manner and scale

over which raw data were smoothed, reflecting analytical artifacts to a greater extent than actual than elk behavior.

Directional persistence Turchin 1998) may have affected movement patterns for short periods of time, but it is unlikely that such persistence caused elk to follow drainages for several kilometers during landscape moves that were sum totals of many individual movement decisions. If directional persistence had been significant, then one might have expected elk to cross the drainages when those drainages changed direction. In such instances, however, elk tended to turn as well and follow topography.

The immediate value of the models examined here will be to add to our understanding of how and why female elk move across the landscape. In previous reports, we provided methods to estimate potential functions based on the differential equations (Preisler et al. 1999, 2001; Brillinger et al. 2001, 2002, 2004). These potential functions show how elk movements are related to specific habitat features such as roads with high rates of vehicular traffic (Preisler et al. 2004). Data derived from the current analysis will allow us to also incorporate information about landscape topography in the formulation of those potential functions. Ultimately, models of movements by North American elk such as those presented here can be used in assessing the effects of this keystone species on ecosystem processes such as nutrient flows, nutrient cycling and successional trajectories of plant communities (Kie et al. 2003).

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