Movements and Habitat Use of Rocky Mountain Elk and Mule Deer

Alan A. Ager

U. S. Department of Agriculture, Forest Service, Pacific Northwest Research Station La Grande, Oregon

Haiganoush K. Preisler

U. S. Department of Agriculture, Forest Service, Pacific Southwest Research Station Albany, California

Bruce K. Johnson

Oregon Department of Fish and Wildlife La Grande

John G. Kie

U. S. Department of Agriculture, Forest Service, Pacific Northwest Research Station La Grande, Oregon

Introduction

Understanding how ungulates use large landscapes to meet their daily needs for food, security and other resources is critical to wildlife management and conservation practices (Johnson et al. 2002). For ungulates like Rocky Mountain elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*), landscapes are a mosaic of different resources that are exploited in well-defined seasonal and daily cycles (e. g., Green and Bear 1990). Complex movement patterns emerge when the cyclical behaviors are realized on landscapes that are heterogeneous in space and time (Gross et al. 1995, Etzenhouser et al. 1998). Both the juxtaposition and the grain of habitat patches within a home range are strong determinants of movement patterns, and the overall habitat suitability as well (Etzenhouser et al. 1998). The influence of patch arrangement on habitat quality was recognized in early elk habitat models (Leckenby 1984); although, the linkage between movement patterns and habitat arrangements had yet to be studied.

In this paper, we describe a progression of studies on the Starkey Experimental Forest and Range (Starkey) that concerned Rocky Mountain elk and mule deer movements and habitat use. The work focused on interpatch movements associated with crepuscular habitat transitions and did not consider finer-scale movements associated with foraging activities (Gross et al. 1995, Johnson et al. 2002). We first used the Starkey data to describe the linkage between movements and habitat use at Starkey (Johnson et al. 2000, Rowland et al. 2000) and elsewhere (Mackie 1970, Craighead et al. 1973, Collins and Urness 1983, McCorquodale et al. 1986, Beier and McCullough 1990, Green and Bear 1990, Unsworth et al. 1998). This work motivated a subsequent investigation about spatial patterns of movements. We then explored ways to build a behavioral model of movement that encapsulated both habitat use and spatial organization of movements. The paper concludes with a discussion of the importance of understanding movement patterns in the management of elk and mule deer.

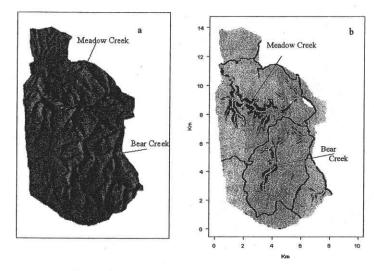
Study Area and Data Collection

Starkey covers 63 square miles (101 km²) on the Wallowa-Whitman National Forest, about 25 miles (40 km) southwest of La Grande, Oregon. Starkey is a mosaic of coniferous forest (ponderosa pine [Pinus ponderosa], Douglas fir [Pseudotsuga menziesii], grand fir [Abies grandis]) and bunchgrass meadows (Pseudorogneria spp.) dissected by numerous small drainages (Figure 1), creating a complex array of topography and vegetation. The project area was enclosed within 8-foot- (2.4-m-) tall woven-wire fence and has been used for studies on Rocky Mountain elk, mule deer and cattle since 1989 (Wisdom et al. 2004). A loran-C telemetry system is used to monitor locations of about 50 elk, 50 mule deer and 50 cows from April to December, obtaining locations every 1 to 2 hours on each animal. The work described here used 400,000 elk and mule deer locations collected over 6 years (1991–1996) within the 48 square mile (77.6 km²) Main Study Area. We used locations from a total of 144 elk and from 58 mule deer. Habitat variables studies were selected based on their importance in previous work at Starkey (Johnson et al. 2000).

Cycles of Movement and Habitat Use

We studied the daily cycles of elk and mule deer movements and seasonal changes in these cycles by fitting periodic functions to the 1991 to 1996

Figure 1. Map of Starkey, showing topography and major drainages (a), and roads open to vehicular traffic (b). Shaded areas in b are areas where slopes area greater than 40 percent.



location data and by testing for differences among seasons at specific hourly intervals. The key findings of this work are summarized as follows and are reported in detail by Ager et al. (2003). Elk showed pronounced 24-hour cycles with crepuscular transitions for many habitat variables, including canopy cover, distance to hiding cover, cosine of aspect (Figures 2a-c), herbage, and distance to open roads (Figures 3a-b). Habitat transitions appeared to be closely linked to rapid changes in elk movements (Figures 4a-b) for most habitat variables but not all (Figure 5a). Morning movements were uphill (Figure 4b), towards more convex topography (Figure 5b) and at increasing distance to streams (Figure 5c). Afternoon movements were directed towards easterly aspects (Figure 5a), steeper slopes (Figure 4c) in valley landforms (Figure 5b) and towards streams (Figure 5c). At dusk, movements were strongly upslope (Figure 4b), out of drainages and towards foraging areas (lower canopy cover, greater distance to hiding cover, increased herbage production, closer to roads and more southerly and westerly aspects) (Figures 2a-c, 3a-b, 5a). For mule deer, these cycles were largely absent from the data (cf. Figures 2a, 2d), and considerable variation was observed among the individual deer in terms of their habitat use patterns.

The daily patterns of habitat use and movements changed among monthly intervals for elk and, to a lesser extent, mule deer. Canopy, distance to hiding cover (Figures 2a-b) and distance to open roads (Figure 3b) changed across monthly intervals in terms of daily amplitudes and average value. Seasonal differences were most evident between late spring (15 April to 14 June) and early summer (15 June to 14 August). The changes were best explained in terms of

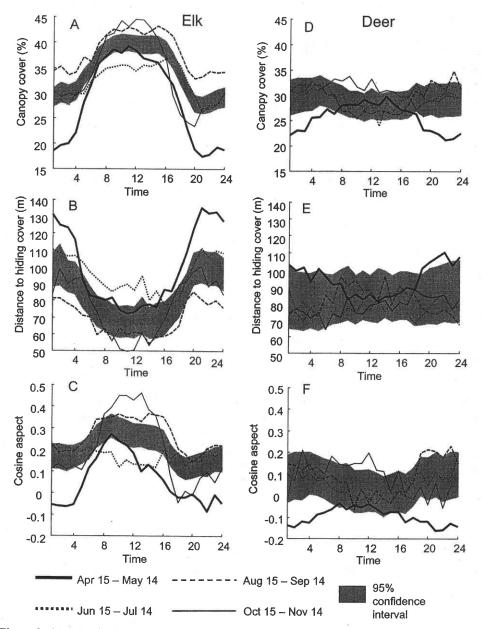


Figure 2. Means of habitat variables canopy cover, distance to cover and cosine aspect by hour and monthly interval for elk (left column) and mule deer (right column). Values plotted are means across animals. For clarity, only 4 of the 71-month time intervals are shown (intervals 1, 3, 5 and 7). Shaded area is the grand mean bounded above and below by 2 pooled, within-interval standard deviation (SD). Pooled within-interval SDs represent the average SD within all 7 monthly intervals studied. Figure is from Ager et al. (2003).

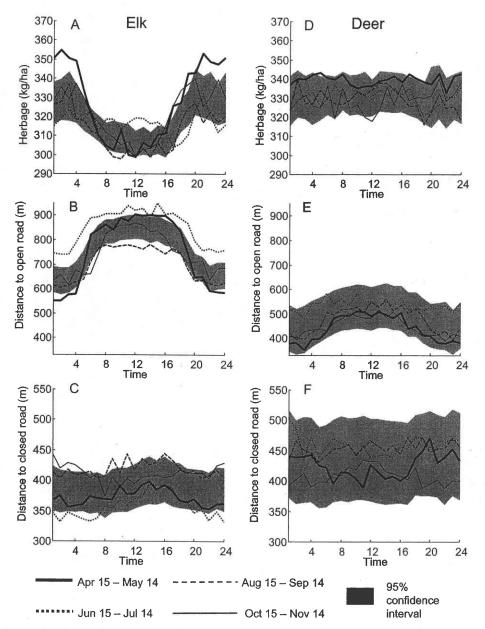


Figure 3. Means of habitat variables herbage production, distance to open road and distance to closed road by hour and montly interval for elk (left column) and mule deer (right column). See Figure 2 for additional explanation. Figure is from Ager et al. (2003).

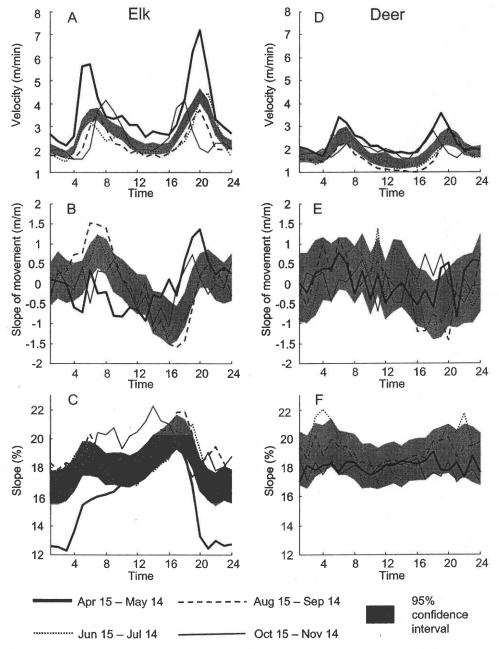


Figure 4. Means of habitat and movement variables velocity, slope of movement and percentage slope by hour and montly interval for lek (left column) and mule deer (right column). See Figure 2 for additional explanation. Figure is from Ager et al. (2003).

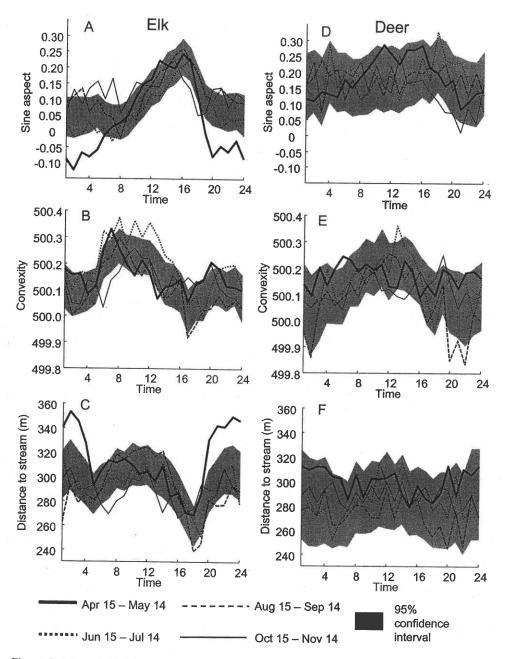


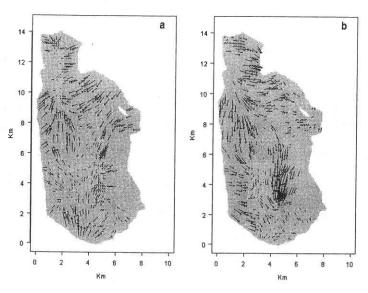
Figure 5. Means of habitat variables sine aspect, convexity and distance to stream by hour and monthly interval for elk (left column) and mule deer (right column). See Figure 2 for additional explanation. Figure is from Ager et al. (2003).

forage phenology at Starkey (Skovlin 1967). High daily amplitudes for velocity and habitat variables in the spring (15 April to 14 May) and autumn (15 October to 14 November) reflected rapid movements to highly preferred meadows at Starkey that produce desired forage in early spring and in autumn after the first substantial rains (Skovlin 1967). The lower velocity and dampened daily cycles during summer reflected a higher use of forested areas throughout the day and night, which are preferred due to their higher midsummer forage production (Edgerton and Smith 1971, Holechek et al. 1982, Unsworth et al. 1998).

Spatial Patterns of Movements

The results from Ager et al. (2003) motivated a number of questions about how elk and mule deer movements are spatially organized on the Starkey landscape. For instance, are there movement corridors between the different habitats? What is the effect of edge on movements? Are movements organized after topography or after other features in Starkey? Are there areas of high and low speed? Are there habitat features that impede movements? Are the dusk and dawn movements reciprocal? To address these questions we explored movement patterns and found that, by smoothing movement vectors with nonparametric regression (Brillinger et al. 2002, 2004; Preisler et al. 2004) and by plotting these on a rendered terrain of Starkey, we could address a number of questions related to the spatial component of movement. First, we observed that mule deer movement vectors appeared mostly random and, thus, had little or no spatial organization, perhaps due to the spatial resolution of the telemetry data and the sampling frequency (Ager et al. 2003). Elk movement vectors for the midsummer (15 July to 15 August) season also appeared weak, reflecting the lower movement rates during this season (Ager et al. 2003). In contrast, elk movement vectors for spring (15 April to 15 June) showed a strong directional component, especially for crepuscular periods (Figures 6a, b). Vector fields also revealed a dendritic pattern of movement (Forman 1995:270) in areas where there is significant topographic relief (Figure 1a). The consequence of the dendritic movement behavior appeared to split the elk into discrete movement cohorts in the project area. Subsequent analyses of movements relative to drainage directions showed a statistically significant association (Kie et al. in press). The effect of Meadow Creek Canyon (Figure 1b) on movement vectors is readily apparent, where movement vectors do not cross the canyon (Figures

Figure 6. Gradient vector fields for 0500 (a) and 1900 (b) hours estimated from the spring telemetry data. Arrows were plotted where at least one elk was observed. The unit vector corresponds to 0.8 kilometers per hour. The plots illustrate the crepuscular transitions between daytime and nightime habitat. Figure is from Preisler et al. (2004).

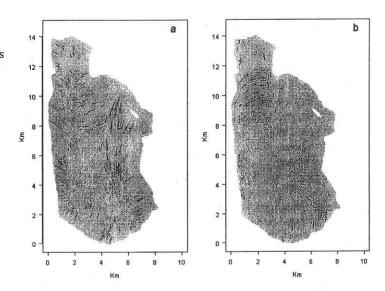


6a, b). Bear Creek had similar effects. Movements also appeared to be reciprocal between dawn and dusk, i. e., the direction of arrows at dawn were opposite of those at dusk at most spatial locations. The dusk movements to grasslands (Figure 6b) appeared stronger and spatially focused as compared to the dawn movements (Figure 6a). The seasonal changes in movement noted in Ager et al. (2003) were also apparent in the estimated vector fields (cf. Figures 6, 7). The plots for summer showed markedly diminished movement vectors; although, there still is some evidence of the elk's avoidance of steep terrain.

Linking Spatial Movement Patterns with Habitat Preferences

Movement vectors were related to habitat variables to explain the spatial cycles of movement on the basis of elk behavior. This work was motivated by the concept of potential fields applied to animal movement (Brillinger et al. 2001) and considers both the stochastic and correlated components of animal movement behavior. A potential field may be visualized by imagining a ball rolling (the animal) around in the interior of a bowl (potential surface), as the bowl is being shaken (random component). In our case, the potential field is a complex surface representing attraction and repulsion to specific habitat features at different times of the day. The potential field is built from a set of additive potential functions for each habitat variable that affects movement. The individual, potential functions

Figure 7. Gradient vector fields for 0500 (a) and 1900 (b) hours estimated from the summer telemetry data. Movement vectors show diminished velocities in summer, as compared to spring, and qualitatively different movement patterns. Figure is from Preisler et al. (2004).



describe movements (attraction versus repulsion) as a function of distance to habitat features at specific times of day. Movements that are seemingly random, like foraging paths in a meadow, or movements that cannot otherwise be explained with environmental covariates are included as stochastic terms in the model. The reader is referred to Brillinger et al. (2004) and Preisler et al. (2004) for details.

For the initial model, we used the data from Ager et al. (2003) for elk in spring (15 April to 15 May), and we focused on the crepuscular movements between foraging and resting areas. We tested a number of habitat covariates and found four that had significant influence on movement vectors, these being distance to security areas, distance to foraging meadows, distance to steep slopes and distance to streams (Preisler et al. 2004). A composite potential field was estimated for the crepuscular periods (Figures 8a, 9a) and, when plotted, showed areas of attraction corresponding to peak foraging and resting areas. When compared to the elk distributions two hours later (Figures 8b, 9b), there is a general agreement between the potential field and the elk densities. The potential functions for each habitat variable also showed specific relationships between the level of attraction versus repulsion and distance (see Preisler et al. 2004). Thus, a model showing habitat selection and habitat transitions was developed from movement vectors and habitat covariates. This work is a first step towards building an empirically based stochastic movement model that accounts for both the spatial and temporal dynamics of movement and habitat preferences. Work

Figure 8. (a) Estimated potential surface for 0500 hours during spring. (b) Kernel density estimate (elk/km2) for observed elk locations between the hours of 1000 and 1300. Most of the areas of low potential (attraction regions) at dawn correspond with regions of high elk density around noon. Figure is from Preisler et al. (2004).

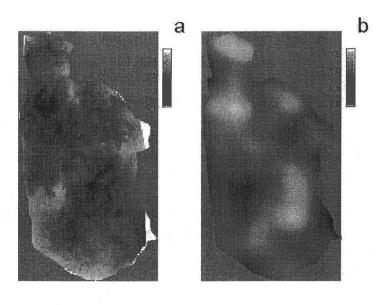
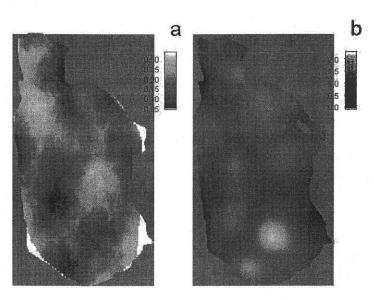


Figure 9. (a) Estimated potential surface for 1900 hours during spring. (b) Kernel density estimate (elk/km²) for observed elk locations between the hours of 2200 and 0100. Areas of low potential (attraction regions) at dusk correspond with regions of high elk density around midnight. Figure is from Preisler et al. (2004).



is ongoing to incorporate finer-scale navigational cues that elk use during the crepuscular transitions that are relative to specific animal positions. This includes modeling the dendritic movement patterns (Forman 1995) that ungulates exhibit on steep terrain. Here, the potential function might change relative to the animal's position. Using potential fields to model fine-scale foraging movements like those among swards and adjacent feeding stations presents further challenges.

Management Implications

Our description of daily and seasonal cycles of habitat use, spatial patterns of movement vectors, and linkage between habitat use and movements adds to the interpretation of previous studies at Starkey (Johnson et al. 2000, Rowland et al. 2000). The daily and seasonal cycles of habitat use exhibited by elk and, to a lesser extent, mule deer show the dynamic nature of habitat-use patterns and underscore the importance of movement studies. The movement analyses were limited to summer range conditions, and the consideration of movement on larger landscape, including seasonal migrations offer additional challenges and insights into ungulate behaviors (Bergman et al. 2000, Johnson et al. 2002). Due to the sampling interval of the Starkey data (1–2 hours), telemetry location error and perhaps the scale of the habitat data, we could not explain finer scale movements outside of the crepuscular periods. Modeling movements during the foraging periods would require additional consideration of variables, like forage intake rate, forage biomass and other foraging behavior factors (Shipley and Spalinger 1995).

Current elk and mule deer habitat models do not consider interpatch landscape movements in their measurement of habitat quality. The influence of topographic pattern on crepuscular movements between preferred resting versus ruminating and foraging habitats was manifested in movement patterns that were aligned with drainages. Thus, the observed elk density in a given foraging habitat was dependent on the ability of elk to connect to suitable security areas using movements that parallel the topographic pattern of drainages. We hypothesize that the fit of Starkey resource selection functions on other landscapes will be influenced by the spatial arrangement of habitats on the landscape and the presence of suitable movement corridors to link daytime and nighttime habitats. For instance, a canyon that lies between highly desirable foraging and security areas will degrade the resource value of these two habitats due to the lack of a suitable connection between them. Further work is needed to better understand how movement patterns might influence elk and mule deer densities in specific habitats and whether these considerations are problematic in the extrapolation of resource selection functions.

The dynamic nature of habitat use and movements by elk and, to a lesser extent mule deer, has important implications for the development and application of habitat suitability models. Diel changes in habitat use needs to be considered when telemetry data are used to estimate resource selection functions.

The need for empirical methods to analyze movements will rapidly grow as the rapid advances in automated telemetry systems materialize and as large telemetry data sets are generated. New GPS telemetry with higher accuracy and sampling frequency will enable significant advances in our ability to build movement models that represent a broad range of ungulate behavior and spatiotemporal scales.

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